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Correcting widespread misidentifications of the highly abundant and commercially important sardine species *Sardinella lemuru*, Bleeker, 1853 in the Philippines

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Summary

Morphology, meristics, and molecular genetics tools were used to determine the species level identification of the most commonly landed sardine species in the Philippines. Results from this study indicated that the historical and widely applied nomenclature of the Indian oil sardine, *Sardinella longiceps*, is incorrect and that this species is instead the Bali sardinella *Sardinella lemuru*. Developing an effective strategy for managing one of the Philippines most important commodity sardine species first requires accurate identification of this species. Results of this study provide needed information that is now being applied to emerging management policies.

Introduction

Sardines are, and have been, the dominant landed fishes in the Philippines for the past two decades (Barut et al., 2003). They contribute billions of pesos in domestic economic revenue (Bureau of Agricultural Statistics, 2011) and serve as one of the most accessible sources of animal protein to millions of Filipinos (FAO, 2011). Sardines are a fast-growing, wide-spread species with high fecundity; species with these life-history characteristics will likely fair well as the seas warm in response to climate change (Gaughan and Mitchell, 2000; Clarke and Gorley, 2006). Thus, as food security moves to the forefront of national priorities, precedence should be given to establishing and managing a sustainably-harvested sardine fishery. Intuitively, developing an effective strategy requires first knowing which species are to be managed, yet considerable confusion surrounds which species are present in the Philippines. For the most common genus of sardines in the Philippines, *Sardinella*, Herre (1953) originally identified 11 species of sardines. This number was reduced to seven species by Conlu (1986), and, most recently, Quilang et al. (2011) revised this to nine species, while Willette et al. (2011a) recognized only six species. Consistently included in the first three reports is the presence of the Indian oil sardine, *Sardinella longiceps*, the most abundant and commonly landed sardine species in the Philippines according to government databases (Willette et al., 2011b; Bureau of Agricultural Statistics, 2011). It is uncertain why *S. longiceps* has been included in lists of Philippine *Sardinella* species, except perhaps that it has historically been a frequently studied sardine species (Hornell, 1910; Hornell and Nayudu, 1924). The earliest report citing the presence of *S. longiceps* in the Philippines, specifically Manila Bay, is a short narrative 1908 article in the Philippine Journal of Science (Seale, 1908). Seale reported about 13 species of herrings occurring in Philippine waters, but specified only three species of sardines *S. longiceps*, *S. moluccensis*, and *S. gibbosa* [all listed in genus *Harengula*]; no measurements for diagnostic morphological features were provided.

Sardinella longiceps is commonly cited as a member of the Philippine sardine fishery (Ingles and Pauly, 1984; Dalzell et al., 1990; Ganaden and Lavapie-Gonzales, 1999; Samonte et al., 2000, 2009; Quilang et al., 2011), yet discrepancies exist when considering the known geographic range of the Indian oil sardine. *Sardinella longiceps* is endemic to the Indian Ocean and has a range extending from eastern Africa north to the Gulf of Oman and Gulf of Aden, along the Indian coastline to Sri Lanka and possibly as far east as the Andaman Sea (Whitehead, 1985). The range of *S. longiceps* does not include the Philippines; however, the range of a morphologically similar species, *S. lemuru*, does. The Bali sardinella *Sardinella lemuru* occurs from southern Japan, throughout Taiwan, the Philippines, across Indonesia to its southern limit in western Australia. This range was correctly listed in Munroe et al. (1999). Its westernmost limit is the Andaman Sea, a potential region of overlap with *S. longiceps*. *Sardinella longiceps* and *S. lemuru* can be distinguished from all other Indo-Pacific species of *Sardinella* primarily by the presence of nine pelvic-fin rays [one unbranched, eight branched] and subsequently by the combination of high counts of lower gillrakers, absence of a black spot at the dorsal-fin origin, presence of a black spot at the posterior opercular margin, and a faint gold stripe down the flanks preceded by a faint gold spot at the operculum (Whitehead, 1985). Apart from their near-geographic separation, distinguishing between *S. lemuru* and *S. longiceps* relies on two features: gillraker counts on the lower limb of the gill arch [77–188 in *S. lemuru*, 150–253, but typically 180–253 in *S. longiceps*] and the differences in their head lengths [26–29% of SL in *S. lemuru*, 29–35% of SL in *S. longiceps*] (Whitehead, 1985).

Here we set out to correctly and conclusively identify the most abundant species of *Sardinella* occurring in the Philippines using a combination of morphological and meristic characters and molecular genetics tools. Our study included samples from throughout the Philippines and a location in Indonesia near the type locality of the Bali sardinella. It is our intention that these findings be applied to current discussions regarding management of the Philippine sardine fishery.

Materials and methods

Morphological measurements and meristic values were taken from 10 specimens sampled from a municipal fish landing site

in Iloilo City, Iloilo [10°42′N; 122°35′E], YL Fishing Corporation Port, Zamboanga City, Zamboanga Sibugay [6°54′N; 122°4′E] and from 10 specimens collected at the Jimbaran fish market, Denpasar, Bali, Indonesia [8°45′S; 115°10′E] (Fig. 1). Iloilo and Zamboanga were among locations referenced in Herre's original report (1953) as where *S. longiceps* were landed. Fish were measured for twenty-five [25] diagnostic features (Table 1). Qualitative and quantitative features or standard length [SL] proportions of these features were used to ascertain similarities among fish using a Bray-Curtis similarity cluster analysis in PRIMER v6 (Clarke and Gorley, 2006).

For genetic analysis, specimens were sampled by staff of the Bureau of Fisheries and Aquatic Resources from municipal landing sites in the provinces of Albay [n = 12], Batangas [10], Iloilo [11], Leyte [10], Masbate [10], Negros Oriental [10], Sorsogon [10], Surigao del Norte [11], Zamboanga Sibugay [11] and Lanao del Sur [11] and sent to the National Fisheries Research and Development Institute (NFRDI) in Quezon City. Bali specimens [10] were handled by colleagues at the Indonesian Biodiversity Research Center, with meristics, morphological and genetic data taken using the same specimens. Fish were identified using the aforementioned diagnostic features, and tissue taken from each fish beneath the right pectoral fin was sampled and preserved in ethanol in an individually labeled 2 ml tube. DNA was extracted from tissue subsamples using 300 μl of 10% Chelex solution (BioRad) in a 1.7 ml micro tube that was vortexed, heated to 96°C for 60 min, then centrifuged at 16 000 ***g*** for 90 s. A portion of the Cytochrome *b* gene region [Heavy strand: 5′-GTGACTTGAAAAACCACCGTTG-3′; light strand: 5′-AAACTGCAGCCCCTCAGAATGATATTTGTCCTCA-3′] (Lecomte et al., 2004) was amplified using a polymerase chain reaction (PCR). Reactions consisted of 13 μl of 10× PCR Buffer, 2.0 μl of 25 mM $MgCl_2$, 2.5 μl of each 10 mM dNTP, 1.25 μl of each primer, 1 μl of BSA [10 μg μl^{-1}], 0.2 units of Taq DNA Polymerase, and 1 μl template DNA in a final volume of 25 μl. PCR parameters were an initial de-naturation at 94°C for 10 min, 38 cycles of 94°C for 30 s, 45°C for 30 s, 72°C for 45 s, and a final extension of 72°C for 10 min. The PCR product was purified for sequencing using ExoSap-It (USB Corp, Cleveland, OH) at 37°C for 30 min and 80°C for 20 min then sent to MacroGen, Inc. (Korea) for sequencing of the forward and reverse strands. Sequences of 391 bp length were proofread, assembled and aligned in SEQUENCHER v4.8 (GeneCode, Ann Arbor, MI) and MUSCLE (Edgar, 2004). Sequences for the round sardinella *Sardinella aurita* [GenBank accession number DQ197990.1] and *S. longiceps* [GenBank accession number JQ266230.1] were acquired from the public domain database GenBank for comparison. Sequences from molecular analyses of tissues of goldstripe sardinella, *S. gibbosa*, and Taiwan sardinella, *S. hualiensis,* were obtained from unpublished results of Willette et al. All sequences were aligned to the *S. longiceps* sequence from GenBank and trimmed to 391 bp. Intraspecific sequence divergence and a neighbor-joining phylogenetic tree were inferred using MEGA v5 (Tamura et al., 2011) with the Kimura two-parameter model (Kimura, 1980) with 1000 bootstrap replicates. All sequences were submitted to GenBank [Accession numbers JQ818230-JQ818251].

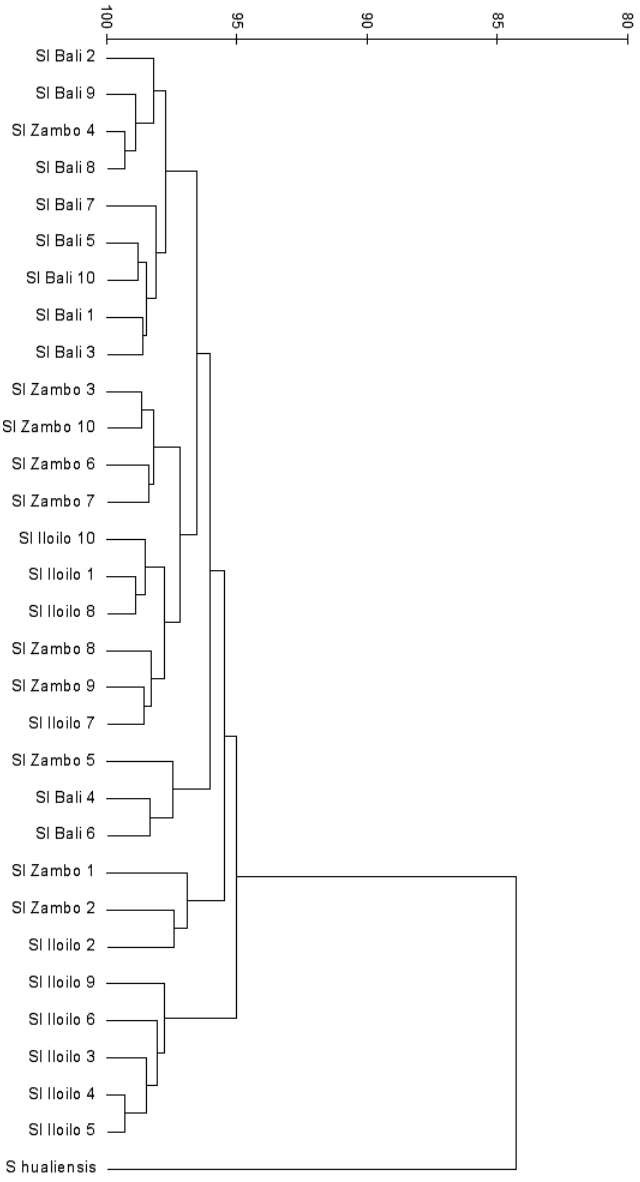

Fig. 1. Dendrogram of morphological characters and meristic values using Bray-Curtis similarity matrix. Bray-Curtis similarity results from morphological and meristic features (Table 1) of measured individuals illustrated in a dendrogram. Scale bar = percent similarity among specimens. Ten specimens each from Iloilo and Zamboanga, Philippines, and Bali, Indonesia shown with *Sardinella hualiensis* used as the out-group

Results

Morphological and meristics results of target specimens from Philippine sites were not in agreement with the diagnostic features of head length and gill raker counts for *S. longiceps*. Rather, they were in concordance with the diagnostic traits of the Bali sardinella *S. lemuru (*Whitehead, 1985; Munroe et al., 1999) and were in agreement with quantitative and qualitative features of *S. lemuru* specimens from Bali, Indonesia (Table 1). In particular, the lower gill raker counts (this study – 145–166 [± ~5 SE]; Whitehead, 1985 – 77–188) and head length (this study – 28–30% [± ~0.6%] of SL*;* Whitehead, 1985 – 26–29% of SL) of the Philippine specimens are within described ranges reported for *S. lemuru,* and are distinct from the higher values of both features for *S. longiceps*. Further, specimens from Iloilo, Zamboanga, and Indonesia demonstrate a highly heterogeneous distribution under the Bray-Curtis similarity model supportive of the specimens being the same species (Fig. 1).

Molecular data are consistent with the morphological and meristic data. Intraspecific sequence divergence for Philippine

Table 1
Morphological characters (measured in mm), meristics and pigmentation features of 10 nominal specimens of *S. lemuru* from Iloilo and Zamboanga, Philippines and Bali, Indonesia

Morphology/meristics/coloration	Iloilo *Sardinella lemuru*		Zamboanga *Sardinella lemuru*		Bali *Sardinella lemuru*		Whitehead, 1985 *Sardinella longiceps*
	Average	SE	Average	SE	Average	SE	Reported
Total length	159.40	1.62	166.30	2.11	180.10	1.55	N/D
Standard Length (SL)	126.90	1.03	131.20	1.70	144.40	1.05	150–230
Body depth/SL*	25.92	0.32	24.94	0.32	23.47	0.10	<30%
Pre-dorsal L/SL*	47.12	0.19	47.91	0.53	45.58	0.25	N/D
Pectoral-fin L/SL*	16.71	0.11	17.54	0.23	16.83	0.20	N/D
Head Length (HL)	36.80	0.49	40.00	0.63	40.20	0.42	N/D
Head Length/SL*	28.99	0.26	30.54	0.63	27.80	0.27	29–35%
Snout Length/HL*	26.62	0.50	27.53	0.32	27.12	0.40	N/D
Eye diameter/HL*	21.48	0.24	21.26	0.33	21.15	0.37	N/D
Post-orbital Length/HL*	51.90	0.50	51.21	0.49	51.73	0.54	N/D
Scutes*	32.50	0.31	32.00	0.37	32.40	0.27	N/D
Lower gillrakers	144.70	4.65	166.30	3.74	166.70	4.21	180–253
Lower gillrakers/SL*	113.98	3.43	127.00	3.50	115.46	2.84	N/D
Dorsal-fin rays*	16.40	0.16	16.10	0.28	16.50	0.22	N/D
Pelvic-fin rays*	9.10	0.10	9.00	0.00	9.00	0.00	9
Pectoral-fin rays*	15.60	0.22	15.90	0.23	15.30	0.26	N/D
Anal-fin rays*	15.40	0.22	14.90	0.23	N/D	N/D	N/D
Enlarged last 2 anal-fin rays*	Yes		Yes		Yes		Yes
Scales discontinuous striae*	Yes		Yes		Yes		Yes
Scales with few perforations*	Yes^		Yes		Yes		No
Black spot at dorsal fin origin*	No		No		No		No
Tips of caudal fin black*	No		No		No		No
Inner margin of caudal fin black*	Yes+		Yes+		Yes		N/D
Dorsal fin yellowish with black tip*	Yes		Yes'		Yes		Yes
Black spot posterior of operculum*	Yes		Yes		Yes		Yes
Faint gold stripe down flank*	Yes		Yes		Yes		Yes
Faint gold spot posterior to upper operculum*	Yes		Yes		Yes		Yes
Thin black line anterior to pectoral fin*	Yes		Yes		Yes		N/D

Numerical values report average and standard error. Qualitative features are reported as present (Yes) or absent (No) in all individuals.
*indicates quantitative and qualitative features and derived proportions used in Bray-Curtis similarity matrix analysis.
^indicates one individual was observed with no perforations;
+indicates black inner margin of caudal fin was not clearly defined and caudal fin was generally blackish in coloration. N/D for Bali *Sardinella lemuru* specimens means no data available due to irresolvable damage to anal-fin rays. Data for *S. longiceps* is all available data reported by Whitehead (1985). N/D for features of *S. longiceps* indicates no data available per source. Data for *S. longiceps* data not included in Bray-Curtis similarity matrix.

specimens morphologically identified as *S. lemuru* and Indonesian *S. lemuru* specimens was 1.0%, suggestive of a single species. Interspecific sequence divergence between *S. hualiensis*, *S. gibbosa*, and *S. longiceps* and the Philippine specimens morphologically-identified as *S. lemuru* were 20.9, 25.6, and 35.4%, respectively. These percentages are well above genetic divergence levels used to distinguish between sister fish species (Johns and Avis, 1998; Craig et al., 2009). Interspecific sequence divergence between *S. lemuru* and *S. aurita* was, however, <1.0%. The Cyt *b* neighbor-joining tree inferred a single, highly supported clade containing all Philippine specimens morphologically-identified as *S. lemuru* and the *S. lemuru* specimens from Indonesia (Fig. 2). *Sardinella aurita* was also contained within this clade. *Sardinella hualiensis* and *S. gibbosa* formed a clade sister to the *S. lemuru* clade, whereas *S. longiceps* was most distant. These results illustrate genetic separation between *S. longiceps* and Philippine specimens morphologically-identified as *S. lemuru*, the latter which are highly genetically similar to *S. lemuru* sampled from its type locality.

Discussion

Here we have conclusively shown that the Bali sardinella, *S. lemuru* is a widely-occurring species in the Philippines and is morphologically and genetically identical between and among sites in the Philippines and a site near the species' type locality in Indonesia, constituting a single species. Further, given *S. longiceps* was never morphologically or genetically-identified at any location in this study, nor in other nation-wide studies now in progress by the National Fisheries Research and Development Institute [unpublished data], we propose that *S. lemuru* has been frequently and incorrectly identified as *S. longiceps* in government and academic reporting, likely since 1908 (Seale, 1908). Interestingly, interspecific sequence divergence between the Atlantic *S. aurita* and the Philippine and Indonesian *S. lemuru* was very low, <1% difference, a level that is more reflective of intraspecific divergence. These two species are indistinguishable morphologically and it has been suggested that *S. aurita* and *S. lemuru* are merely Atlantic and Indo-Pacific forms of the same species (Whitehead, 1985). Although our molecular results support this notion, the ranges of these two nominal species are highly disjunctive (Whitehead, 1985) and unlikely for a single species; further morphological and genetic investigation is needed.

The pairing of well-established morphological methods with increasingly available genetic tools provides robust support for this study's conclusions. The findings of this study are in part a result of improved accessibility to molecular genetics tools for government-based research in the Philippines. Hence, further capacity building and combined appli-

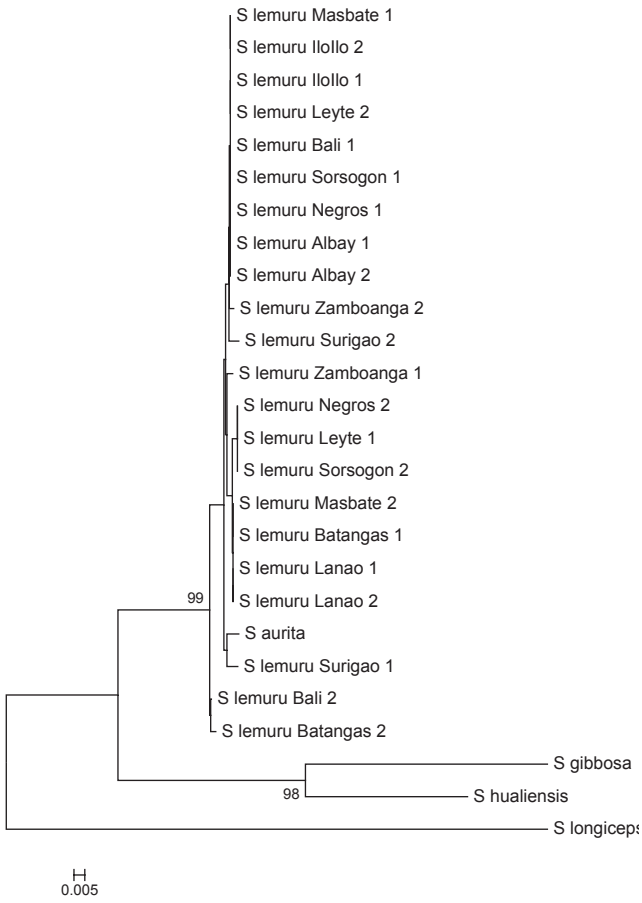

Fig. 2. Neighbor-joining phylogenetic tree of Cyt *b* sequence data Cyt *b* Kimura 2-parameter Neighbor-Joining tree with 1000 bootstrap probability replicates for Philippine specimens morphologically identified as *S. lemuru* (two representatives here), *S. lemuru* from Bali, and out-groups of *S. gibbosa* and *S. hualiensis* from unpublished data by Willette. *Sardinella aurita* and *S. longiceps* sequences from GenBank also included. Only bootstrap probability values of 90 or greater shown

cation of both morphological and molecular methods will only strengthen the efficiency and accuracy of assessing the nation's marine resources.

Results of this study have immediate implications on sardine management in the Philippines, namely correcting sardine nomenclature used in Fisheries Administrative Orders and stock assessment programs. It is noteworthy that *S. fimbriata* and *S. longiceps*, not *S. lemuru*, are the only *Sardinella* species specified for management in Philippine fisheries management policies. The use of *S. lemuru* instead of *S. longiceps* has already been included in the August 2011 Joint DA-DILG Administrative Order implementing a closed season on sardines for the East Sulu Sea, Basilan Strait and Sibuguey Bay. Implications of this study are also relevant to the commercial sardine industry regarding their need for accurate labeling of domestic and exported fishery products. Lastly, this study provides a more informed perspective on the composition of the Philippine sardine fishery. Migration behavior, timing of spawning, age of first maturity, and other life history stages, as well as Maximum Sustainable Yield, vary between and among Clupeoid species (Longhurst, 1971; Whitehead, 1985; Gaughan and Mitchell, 2000; Gonzalez and Zardoya, 2007) and inaccuracies in species identifications may lead to unintended consequences, particularly in this case, if assumptions specific to an Indian Ocean species of *Sardinella* are applied to the management of a Pacific Ocean species of this genus.

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References

Barut, N. C.; Santos, M. D.; Mijares, L. L.; Subade, R.; Armada, N. B.; Garces, L. R., 2003: Philippine coastal fisheries situation. In: 67th Worldfish center conference proceedings, pp. 1120.

Bureau of Agricultural Statistics (BAS) 2011 CountrySTAT Philippine. WorldWide Web electronic database, 2011. Available at: http://countrystat.bas.gov.ph/ (accessed on 20 November 2011).

Clarke, K. R.; Gorley, R. N., 2006: PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Conlu, P. V., 1986: Guide to Philippine flora and fauna. Natural Resources Management Center, University of the Philippines, Quezon City, pp. 485.

Craig, M. T.; Graham, R. T.; Torres, R. A.; Hyde, J. R.; Freitas, M. O.; Ferreira, B. P.; Hostim-Silva, M.; Gerhardinger, L. C.; Bertoncini, A. A.; Robertson, D. R., 2009: How many species of goliath grouper are there? Cryptic genetic divergence in a threatened marine fish and the resurrection of a geopolitical species. Endang. Species Res. **7**, 167–174.

Dalzell, P.; Corpuz, P.; Arce, F.; Ganaden, R., 1990: Philippine small pelagic fisheries and their management. Aquacult Fish Mange. **21**, 77–94.

Edgar, R. C., 2004: MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. **32**, 1792–1797.

FAO, 2011: Fishery and Aquaculture Country profiles, Philippines. In: FAO Fisheries and Aquaculture Department [online]. Rome. Updated 5 August 2004. Available at: http://www.fao.org/fishery/countrysector/FI-CP_PH/en (accessed on 25 January 2011).

Ganaden, S. R.; Lavapie-Gonzales, F., 1999: Common and local names of marine fishes of the Philippines. Bureau of Fisheries and Aquatic Resources, Philippines, pp. 385.

Gaughan, D. J.; Mitchell, R. W. D., 2000: The biology and stock assessment of the tropical sardine, *Sardinella lemuru*, of the mid-

west coast of Western Australia. Fisheries Research Report **119**, Fisheries Department, Western Australia. pp. 1–136.

Gonzalez, E. G.; Zardoya, R., 2007: Relative role of life-history traits and historical factors in shaping genetic population structure of sardines (*Sardina pilchardus*). BMC Evol. Biol. **7**, 197.

Herre, A. W., 1953: Checklist of Philippine fishes. Fish Wildl. Ser. Res. Rep. **20**, 977.

Hornell, J., 1910: Report on the results of a fishery cruise along the Malabar Coast and to Laccadives Islands in 1908. Madras Fish. Bull. **4**, 71–126.

Hornell, J.; Nayudu, M. R., 1924: A contribution to the life-history of the Indian oil sardine with notes on the plankton of the Malabar coast. Madras Fish. Bull. **17**, 129–197.

Ingles, J.; Pauly, D., 1984: An atlas of the growth, mortality and recruitment of Philippine fishes. In: 13th ICLARM Technical Report, pp. 127.

Johns, G. C.; Avis, J. C., 1998: A comparative summary of genetic distances in the vertebrates from the mitochondrial Cytochrome *b* gene. Mol. Biol. Evol. **15**, 1481–1490.

Kimura, M., 1980: A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. J. Mol. Evol. **16**, 111–120.

Lecomte, F.; Grant, W. S.; Dodson, J.; Rodriguez-Sanchez, R.; Bowen, B. W., 2004: Living with uncertainty: genetic imprints of climate shifts in East Pacific anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*). Mol. Ecol. **13**, 2169–2182.

Longhurst, A. R., 1971: The Clupeoid resources of tropical seas. Oceano. Mar. Biol. Ann. Rev. **9**, 349–385.

Munroe, T. A.; Wongratana, T.; Nizinski, M. S., 1999: Clupeidae: herrings (also sardines, shads, sprats, pilchards, and menhadens). In: FAO species identification guide for fishery purposes: the living marine resources of the West Central Pacific. Vol 3: Batoid fishes, chimaeras and Bony fishes, Part 1 (Elopidae to Linophrynidae). K.E. Carpenter, V.H. Niem (Eds). Food and Agricultural Organization of the United Nation, Rome, pp. 1775–1821.

Quilang, J. P.; Santos, B. S.; Ong, P. S.; Basiao, Z. U.; Fontanilla, I. K. C.; Cao, E. P., 2011: DNA Barcoding of the Philippine endemic freshwater sardine *Sardinella tawilis* (Clupeiformes: Clupeidae) and its marine relatives. Philipp. Agric. Sci. **94**, 248–257.

Samonte, I. E.; Pagulayan, R. C.; Mayer, W. E., 2000: Molecular phylogeny of Philippine freshwater sardines based on mitochondrial DNA analysis. J. Hered. **91**, 247–253.

Samonte, I. E.; Canlas, R. A.; Alvia, K.; Carvajal, T.; Pagulayan, R. C., 2009: Multivariate analyses of the biometric features from Philippine sardines – implications for the phylogenetic relationship of the freshwater *Sardinella tawilis* (Teleostei, Clupeomorpha). J. Zool. Syst. Evol. Res. **47**, 21–24.

Seale, A., 1908: The fishery resources of the Philippine Islands: part I, Commercial fishes. J. Philipp. Sci. **3**, 514.

Tamura, K.; Peterson, D.; Peterson, N.; Stecher, G.; Nei, M.; Kumar, S., 2011: MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol. Biol. Evol. **28**, 2731–2739.

Whitehead, P. J. P., 1985: FAO species catalogue. Vol. 7. Clupeoid fishes of the world: an annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 1 – Chirocentridae, Clupeidae and Pristigasteridae. FAO Fish Synop. **7**, 303.

Willette, D. A.; Bognot, E. D.; Mutia, T. M.; Santos, M. D., 2011a: Biology and ecology of sardines in the Philippines: a review. NFRDI Technical Paper Series. pp. 1–35.

Willette, D. A.; Santos, M. D.; Aragon, M. A., 2011b: First report of the Taiwan sardinella *Sardinella hualiensis* (Clupeiformes: Clupeidae) in the Philippines. J. Fish Biol. **79**, 2087–2094.

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