

Evolution of the freshwater sardinella, *Sardinella tawilis* (Clupeiformes: Clupeidae), in Taal Lake, Philippines and identification of its marine sister-species, *Sardinella hualiensis*

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Date Submitted: 22 January, 2013.
Date Accepted: 13 June, 2013.
Available Online:

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ABSTRACT.—We identify the sister species of the world's only freshwater sardinella, *Sardinella tawilis* (Herre, 1927) of Taal Lake, Philippines as the morphologically-similar marine Taiwanese sardinella *Sardinella hualiensis* (Chu and Tsai, 1958). Evidence of incomplete lineage sorting and a species tree derived from three mitochondrial genes and one nuclear gene indicate that *S. tawilis* diverged from *S. hualiensis* in the late Pleistocene. Neutrality tests, mismatch distribution analysis, sequence diversity indices, and species tree analysis indicate populations of both species have long been stable and that the divergence between these two lineages occurred prior to the putative 18th century formation of Taal Lake.

The freshwater sardinella *Sardinella tawilis* (Herre, 1927) is endemic to Taal Lake, Philippines, a crater lake formed by the highly active Taal Volcano (Fig. 1; Herre 1927, Ramos 2002). The sardines and other Clupeiformes are predominantly marine but with many peripheral freshwater representatives (Whitehead 1985). *Sardinella tawilis* is the only freshwater representative of the 22 species in its genus. The origins of this species are enigmatic since Taal Lake putatively formed only as recently as the 18th century after a series of large eruptions of Taal Volcano (Ramos 1986, Hargrove 1991). Having erupted over 30 times since the 16th century, including several large and highly destructive events, Taal Volcano is one of the world's most active volcanoes (Torres et al. 1995, Newhall 1996). The caldera itself formed sometime from a few hundred thousand to a few tens of thousands of years ago (Ramos 2002), but Taal Lake was broadly connected to Balayan Bay until 1754 when a series of violent eruptions constricted and diverted the Pansipit River increasing the depth of the lake to its current level, 3 m above sea level (Wolfe and Self 1983, Hargrove 1991). The history of the hydrography of the lake is not well recorded although sailing ships were reported as navigating between Balayan Bay and Taal Lake prior to the 1754 eruptions (Hargrove 1991). It is also not known if the population of *S. tawilis* that now exists in the lake was previously restricted to the lake or the vicinity of the Taal caldera prior to 1754.

Several studies have sought to identify the evolutionary origin of *S. tawilis*, the most important commercial fishery of Taal Lake and a valued culinary delicacy of Filipino