A synthesis of studies of South African sardine population structure

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Overview

A substantial amount of research over the past decade has documented spatial (regional) differences in a variety of biological traits of sardine around the South African coast. These include differences in (i) life history strategies such as distribution patterns, spawning and nursery areas and their environmental characteristics, and reproductive seasonality; (ii) meristic characteristics such as gill raker number and vertebral number; (iii) morphometric characteristics such as gill raker length, and body and otolith shape; (iv) the prevalence and abundance of a digenean parasite biotag; and (v) otolith elemental composition and muscle metallic element composition. These results, together with observations that marine species around South Africa tend to be subdivided into regional populations associated with distinct biogeographic provinces, had suggested the existence of three sardine populations (hereafter stocks) around the country, on the West, South and East coasts, respectively. The eastern stock was thought to comprise fish that mix with southern stock sardines during summer, but then separate from them during autumn/winter to travel toward their East Coast spawning grounds during the KZN sardine run. Although management of the purse-seine fishery for sardine has incorporated this hypothesized spatial structure by developing a 2-stock (western and southern) assessment model and setting region-specific catch levels in recent years, previous genetic studies that examined microsatellite and mitochondrial DNA did not support the multi-stock hypothesis.

Most recently, thousands of genetic markers from across the genomes of hundreds of sardines captured around the SA coast were analysed to test the hypothesis that sardines participating in the KZN sardine run are genetically distinct. A suite of genetic markers with a signal of adaptation to water temperature showed regional genetic differences within the species' temperate core range and only two stocks; one associated with South Africa's cool-temperate West Coast and the other with the warm-temperate South Coast. The strong affiliation with water temperature suggests that thermal adaptation maintains these patterns because each stock is adapted to the temperature range that it experiences in its native region. Surprisingly, sardines participating in the sardine run on the East Coast were not genetically distinct and showed a clear affiliation with the cool-temperate stock, indicating that the former were migrants that originate from the cool-temperate Atlantic.

The genomic results have confirmed the existence of two sardine stocks off South Africa, each of which has adapted to different water temperatures and would experience reduced fitness and lower survival when outside their preferred temperature ranges. The revision of current stock assessment models to incorporate these new results is currently underway. This document provides a synthesis of the multiple method approach of stock discrimination applied to South African sardine by listing and synthesizing studies that have tested for significant spatial variability in phenotypic, genotypic, and other characteristics (Table 1). Whereas most of those studies examined spatial variability in a single (*e.g.* parasite bio-tag loads) or a few (e.g. gill raker length and number) characteristics of individual sardine, and collectively constitute a multi-method approach, one study assessed spatial variability in multiple characteristics collected from the same individual fish.

Table 1: Main findings of studies that have tested for significant spatial variability in phenotypic, genotypic, and other characteristics of sardine around the South African coast (W=West, S=South and E=East coasts, respectively).

Category and characteristic	Main findings and reference/s
Distribution patterns	1. Consistent break between Cape Agulhas and Mossel Bay (Central Agulhas Bank) in the distribution of sardine at low and medium biomass levels and contraction into refugia at low biomass levels typical of small pelagic fishes (Coetzee *et al*., 2008).
Spawning, areas, characteristics, and seasons	2. Widely-separated and discrete spawning areas on the W and S coasts, separated by the Central Agulhas Bank and with different environmental characteristics (e.g. preferred spawning SSTs are 14-18.5°C on the W coast and 18-22°C on the S coast; van der Lingen, 2011; Mhlongo *et al*., 2015); spawning off the E coast during the KZN sardine run (Coetzee *et al*., 2010; Connell, 2010; Fréon *et al*., 2010). 3. Relative gonad size (standardized gonad mass) of immature and female sardine is significantly higher for sardine on the W compared to S coast (van der Lingen *et al.*, 2006). 4. Female sardine on the S coast mature at a larger size than those on the W coast (van der Lingen, 2011). 5. Different peak spawning seasons of sardine around the coast, being spring-summer (Sep-Feb) on W but winter-spring (Jun-Nov) on S and E coasts (Connell, 2010; van der Lingen and McGrath, 2017).
Nursery areas and natal characteristics	1. Coupled 3D hydrodynamic-individual based models indicate three spawning-nursery area/recruitment systems: (i) eggs spawned on the W coast are retained on the W coast and recruit there; (ii) eggs spawned on the S coast are retained on the S coast and recruit there; and (iii) some eggs spawned on the S coast are transported to the W coast and recruit there (Miller *et al.*, 2006; McGrath *et al*., 2020). 2. Analyses of otolith oxygen isotope ratios and microstructure indicate that fish on the W coast experience cooler (by around 4°C) natal temperatures and show slower early (first 100 days) than those on the S and E coasts (Sakamoto *et al*., 2020).
Meristic characteristics	1. The number of vertebrae does not differ between fish from the W and S coasts (Groenewald *et al*., 2019), but fish from the E coast have significantly fewer vertebrae (van der Lingen *et al*., 2010). 2. The number of gill rakers is significantly different between juvenile (but not adult) fish from the W and S coasts (Idris *et al*., 2016).
Morphometric characteristics	1. There are significant differences in body shape between sardine from the W and S coasts (Groenewald *et al*., 2019), and between fish from the W, S and E coasts (van der Lingen *et al*., 2010). 2. There are significant difference in otolith shape between fish from the E coast and those from W and S coasts (which are not different from each other; Hampton, 2014). 3. There are significant differences in gill arch length between sardine from the W, S and E coasts (Idris *et al*., 2016)

Other characteristics	1. Prevalence-at-length and infection-at-length curves for the digenean parasite bio-tag are significantly different for fish off the W, S and E coasts (Weston *et al*., 2012; van der Lingen *et al*., 2015; van der Lingen, 2021). 2. Sardine otolith elemental composition shows significant spatial variability, but this is not temporally stable (Hampton *et al*., 2016). 3. The metallic composition of muscle tissue is significantly different between sardine from the W and S coasts (Uren *et al*., 2020).
Multiple-method approach	1. An overall classification accuracy (of sardine into western or southern stocks) of >80% by two multi-variate analyses (Classification Tree Analysis and Random Forest models) that used the number of gill rakers, gill arch length, gill raker gap, two otolith shape indices (circularity and form factor), the number of vertebrae and the abundance of the digenean parasite bio-tag, all recorded from the same individual fish (Ukomadu, 2017).
Genetic characteristics	1. Substantial haploid diversity but no significant spatial structuring using mitochondrial and microsatellite DNA (Hampton, 2014). 2. Two distinct genomic stocks: (i) cool temperate sardine observed predominantly on the W coast and also the E coast; and (ii) warm temperate sardine observed predominantly off the south coast (Teske *et al*., 2021).

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