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Otolith chemistry indicates large-scale connectivity in Chilean jack mackerel (*Trachurus murphyi*), a highly mobile species in the Southern Pacific Ocean

Julian Ashford [a,*], Rodolfo Serra [b], Juan Carlos Saavedra [b], Jaime Letelier [b]

[a] Center for Quantitative Fisheries Ecology, Old Dominion University, 800 West 46th Street, Norfolk, VA 23508, USA
[b] Instituto de Fomento Pesquero, Blanco 839, Valparaiso, Chile

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ABSTRACT

Chemistry in material laid down prior to capture along the edges of otoliths of Chilean jack mackerel (*Trachurus murphyi*) showed strong spatial heterogeneity corresponding to hydrographic structure across putative population boundaries between (i) the western and eastern South Pacific Ocean, and (ii) Chile and Peru. Yet the chemistry of the otolith nucleus, in material laid down during early life, showed no evidence supporting the existence of these boundaries. Instead, jack mackerel from New Zealand had similar nucleus chemistry to most sampling areas off South America; and those off southern Peru showed similar nucleus chemistry to most sampling areas off Chile. Strong differences were found between southern and northern Peru, and cluster analysis indicated this was caused by a group of fish off northern Peru with chemistry found nowhere else. Most other fish grouped in two clusters, which showed properties suggesting correspondence with a major spawning zone in oceanic water off central Chile, and a smaller area in coastal water off northern Chile, characterized by similar sea surface temperature, lack of westward transport, and low kinetic energy. Rather than discrete populations separated by boundaries, these results suggest complex spatial structure defined by environmentally mediated survival and connectivity: fish caught off New Zealand may be of South American origin; the spawning zone off central Chile may supply fisheries around the South Pacific; and spawning off northern Chile may be an important source of fish caught locally and in Peru. However, northern Peru does not supply areas further south.

1. Introduction

Chilean jack mackerel, *Trachurus murphyi* (Poulin et al., 2004), support important commercial fisheries off Ecuador, Peru, Chile, New Zealand, and in international waters outside the 200 nautical miles Exclusive Economic Zone (EEZ) off Chile. Following a large increase in its abundance from the early 1970s, *T. murphyi* expanded its distribution along southwestern South America (Ecuador, Peru and Chile) toward the west, crossing the Pacific Ocean along the West Wind Drift by the mid-1980s to reach its current distribution throughout oceanic waters along the Subtropical Front; the New Zealand EEZ south of 34°S; and southeastern waters of the Australian EEZ (Bailey, 1989; Serra, 1991; Elizarov et al., 1993; Taylor, 2002). Foreign fleets in international waters off Chile have reported catches of ca. 400,000 tons. However, the fishery within the Chilean EEZ has declined to about 1.5 million tons from catches of ca. 4.2 million tons in the mid-1990s.

T. murphyi is a schooling pelagic fish adapted to both neritic and oceanic environments, and can be defined as a highly mobile species with a population structure that straddles international boundaries (Meltzer, 2005). Similarities in catch-at-length composition, recruitment dynamics and juvenile distribution between southern Peru and the north of Chile suggest that jack mackerel form a single self-recruiting population (Anonymous, 2008). Off New Zealand, few young stages have been reported and no evidence of genetic differentiation, so adult fish in the New Zealand fishery may also recruit from a South American source. Serra (1991) described a cyclic migration in which adults leave the west coast of South America to spawn in oceanic waters. Adults are highly fecund batch spawners (e.g. Anonymous, 2008): although they breed throughout most of their distribution in the Southeastern Pacific Ocean, peaking in November, by far the largest concentrations of their eggs and larvae are found during November–December in surface waters in an area of low wind intensity off Central Chile, north of the Subtropical Front (Nuñez et al., 2008) (Fig. 1). The larvae are adapted to oceanic conditions: circulation in the surface layer is wind-driven, and young of the year move eastwards with the West Wind Drift, arriving on the Chilean shelf to recruit at ca. age 1–2. They feed on smaller plankton that occur abundantly north of the

* Corresponding author. Tel.: +1 757 683 4804; fax: +1 757 683 5293.
E-mail address: jashford@odu.edu (J. Ashford).

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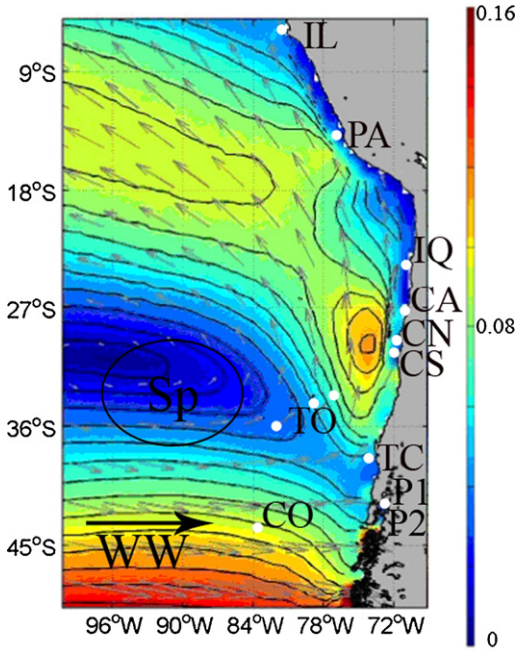

Fig. 1. Sampling areas in the southeastern South Pacific, showing mean annual wind field between 1958 and 2005 based on monthly data generated by the simulation model SODA 2.0.2–3. Color scale and grey arrows represent wind intensity ($N\,m^{-2}$) and direction respectively; black arrow, West Wind Drift (WW). Circle shows larvae distribution in November 2004 redrawn from Nuñez et al. (2008) reflecting dense concentrations up to the western boundary of the study area at 92°W. Sampling area off New Zealand not shown. IL, Islas Lobos de Afuera; PA, Paracas; IQ, Iquique; CA, Caldera; CN, north of Coquimbo; CS, Coquimbo; TC, Talcahuano coastal; TO, Talcahuano oceanic; P1 and P2, Puerto Montt; CO, Chiloé oceanic.

front, while adults migrate during summer after spawning, either onshore to feed in productive coastal waters (Serra, 1991), or south of the Subtropical Front to feed on aggregations of copepods and euphausiids (Vinogradov et al., 1991).

Reduced concentrations of eggs and larvae in the spawning zone off central Chile (Nuñez et al., 2008) may help to explain the decline in commercial catch off Chile, and could fundamentally impact fishing activity across the South Pacific Ocean if the zone supplies recruits to the fisheries in New Zealand and Peru as well (e.g. Taylor, 2002). Alternatively, however, evidence from parasite studies, catch length distributions, biomass concentrations and reproduction suggest Chilean jack mackerel caught off Peru may come from a separate self-recruiting population (Serra, 1991; Anonymous, 2008). Additionally, there has been speculation that the westward migration along the Subtropical Front may have led to another self-sustaining population established in the Southwestern Pacific (Taylor, 2002). Discrete population structure may then restrict the effect of declining egg and larvae concentrations off central Chile to coastal and oceanic fisheries in the southeastern Pacific Ocean alone.

To resolve these questions, and respond to the urgent need for research (Taylor, 2002; Anonymous, 2008), we used otolith chemistry to examine the population structure of Chilean jack mackerel throughout its distribution in the South Pacific, as part of a holistic approach (Begg and Waldmann, 1999) that included parallel studies of genetics, morphometrics, parasites and life history patterns. We compared the chemistry laid down just before capture at the otolith edge to examine empirically how otolith chemistry varies spatially across the southern Pacific Ocean. Since discrete, self-recruiting populations imply separate exposure to local environments during early life, we used chemistry laid down in the otolith nucleus to test for population differences between samples taken off Chile, Peru and New Zealand.

2. Materials and methods

2.1. Otolith analysis procedures

Observers collected adult fish from the holds of commercial purse-seiners fishing in oceanic and coastal waters off the west coast of South America, from Islas Lobos de Afuera in northern Peru as far south as Puerto Montt in southern Chile (Fig. 1). Observers also sampled catch taken by mid-water trawl east of New Zealand over the Campbell Plateau. Sampling began at the start of the spawning season in November 2007, and was completed seven months later in June 2008. Samples were taken off Paracas, Iquique, Caldera, Coquimbo, in coastal and oceanic waters off Talcahuano, and from two areas off Puerto Montt, by the end of January 2008. Further samples were collected after the spawning season in March north of Coquimbo, in April from Islas Lobos de Afuera, in May from oceanic waters off Chiloé Island, and in June from New Zealand, giving a total of twelve sample sets. Samples taken at Islas Lobos de Afuera and along the coast off Talcahuano contained more males than females, whereas those taken at Caldera, in oceanic waters off Talcahuano and Chiloé Island, and off Puerto Montt contained more females. To avoid confounding comparisons between areas, we randomly sub-sampled by sex from each sample set.

After drying, we preserved the right sagittal otolith for use in parallel morphometric analyses. In the laboratory at Old Dominion University, we removed any surface contamination by rinsing the left sagittal otoliths in Milli-Q water, placing them in 20% Ultra-Pure hydrogen peroxide for 5 min and rinsing them again in Milli-Q water. The otoliths were ground by hand from the anterior end using the grinding wheel of a HillQuist Thin Section Machine, to give a transverse surface anterior of the nucleus. Otoliths were mounted on this surface on a slide using crystalbond, previously tested to ensure it was not a source of contamination, and ground from the posterior side to reveal a transverse plane through the otolith nucleus (e.g. Ashford et al., 2010). The surface of the mounted thick section produced in this way was fine-ground and polished using a Crystalmaster 8 Machine. In a clean room, the sections were rinsed in Milli-Q water under a laminar flow hood, and lapped manually using clean plastic clamps and Mark V Laboratory polishing film. Each otolith was lapped successively on three pieces of clean 3 M film, finished on 0.3 M film, rinsed, and the surface soaked with 20% Ultra-Pure hydrogen peroxide for 5 min before rinsing again. After drying, sections from each treatment were randomly selected, removed from the slide and mounted in random order on clean petrographic slides under a laminar-flow hood using crystal bond. The mounted sections were rinsed, sonicated for 5 min, and then rinsed again, all in Milli-Q water, and left to dry.

We used a Finnegan Mat Element 2 double-focusing sector-field ICP-MS located in the Plasma Mass Spectrometry Facility at Woods Hole Oceanographic Institution (WHOI) to examine otoliths for minor and trace element chemistry. Samples were introduced in automated sequence (Chen et al., 2000) using a laser ablation system and a microflow nebulizer. Ablated otolith material from the sample cell was mixed in the spray chamber with HNO_3 aerosol introduced by the nebulizer, and the mixture was then carried to the ICP torch. For quality control, dissolved otolith reference material obtained from the National Research Council of Canada was similarly introduced to the spray chamber by the nebulizer as an aerosol, before being carried to the ICP torch. Blanks of HNO_3 aerosol also were introduced to the chamber by the nebulizer.

To control for operational variability in the laser-ICPMS, we used a randomized blocks design with each petrographic slide as the blocking factor, considered randomly drawn, with each sampling area considered a fixed treatment. One otolith from each treatment was randomly selected and mounted on each slide. Blank and refer-