Received: 22 January 2025 | Revised: 3 June 2025 | Accepted: 4 June 2025
DOI: 10.1111/jfb.70120

REGULAR ARTICLE

JOURNAL OF FISH BIOLOGY fsbi

Spatial variation in otolith elemental chemistry of *Stegastes arcifrons* (Pomacentridae) reflects environmental patchiness at the Galápagos archipelago

Juan Manuel Alava-Jurado[1,2,3] | **Margarita Brandt**[2,4,5] | **Michael J. Kingsford**[2,3]

[1]Universidad San Francisco de Quito USFQ, Colegio de Ciencias Biológicas & Ambientales COCIBA, Programa de Maestría en Ecología, Quito, Ecuador

[2]Galápagos Science Center, Universidad San Francisco de Quito USFQ & University of North Carolina at Chapel Hill UNC, Puerto Baquerizo Moreno, San Cristóbal, Ecuador

[3]Marine Biology and Aquaculture, The College of Science and Engineering, James Cook University, Townsville, Queensland, Australia

[4]Universidad San Francisco de Quito USFQ, Colegio de Ciencias Biológicas & Ambientales COCIBA, Quito, Ecuador

[5]Extensión Galápagos, Universidad San Francisco de Quito USFQ, San Cristóbal, Ecuador

Correspondence
Juan Manuel Alava-Jurado, Marine Biology and Aquaculture, The College of Science and Engineering, James Cook University, Townsville, Queensland, 4811, Australia.
Email: juanmanuel.alavajurado@my.jcu.edu.au

Funding information
Centre of Excellence for Coral Reef Studies, Australian Research Council

Abstract

In marine ecosystems, environmental conditions shape important ecological processes. The equatorial Galápagos Marine Reserve (GMR) is known for great spatial variation in the upwelling of cold nutrient-rich waters and the input of warm Panamanian waters. Differences in oceanography influence the structure of benthic communities. There is, however, a paucity of knowledge on the spatial scales of exposure to cool and warmer waters. Here we analysed the elemental chemistry of otoliths in the territorial yellow-tail damselfish (*Stegastes arcifrons*) to identify patterns of elemental signals across a gradient from warm to upwelled waters. Contrasting patterns of elemental ratios (Ba/Ca, Mg/Ca, Mn/Ca and Sr/Ca) were found in whole otoliths of adult fish at spatial scales of kilometres to 10 s of kilometres; there was also high variation among fish within some sites. A positive correlation was detected between temperature and Sr/Ca ratios. We conclude that variation in environmental conditions influenced fish elemental incorporation into otoliths, highlighting the oceanographic heterogeneity of shallow rocky reef environments in the Galápagos.

KEYWORDS
damselfish, elemental chemistry, otoliths, spatial variation, upwelling gradient

1 | INTRODUCTION

In natural ecosystems, the prevailing environmental conditions shape local ecological processes. Changes in water temperature and food provisioning affect organismal physiology and life-history patterns for marine organisms (Macpherson et al., 2009; Sponaugle et al., 2006; Walther et al., 2010). Upwellings, the flow of cold, nutrient-rich deep waters to the photic zone via surface winds or currents (Sigman & Hain, 2012), can have an important influence on marine communities. Worldwide, upwelling systems are considered among the most biologically productive regions (Thomas et al., 2004), supporting approximately 5% of global marine primary production and 20% of global marine fisheries (Messié & Chavez, 2015). In addition, there are several studies that highlight the importance of the effects of nutrient supply by different upwelling intensities on intertidal communities (Menge et al., 2003; Menge & Menge, 2013), fish assemblages (Ritter, 2009) and fish growth (Fuentes et al., 2017).

The eastern tropical Pacific Ocean is one of the most productive areas in the world because both coastal upwelling along eastern boundaries and oceanic upwelling along offshore divergences occur in this region (Chavez & Messié, 2009; Fiedler et al., 1991). The Galápagos Islands are located at the equator in this region where the confluence of several major cold and warm water oceanic currents occurs (Schaeffer et al., 2008; Sweet et al., 2007). The warm Panamá current flows from the northeast and affects the northern and central islands. In addition, cool water flows from east to west carried by the South Equatorial Current. This current is influenced by the Panamá current in the northeast and by the Humboldt Current in the southeast, the latter is generated in the Peru upwelling zone, affecting the central and southern areas of the Galápagos. Additionally, the eastward-flowing subsurface Equatorial Undercurrent (EUC, also known as the Cromwell current), brings cold, nutrient-rich waters to the surface by means of topographically induced upwelling and mainly affects the western section of the archipelago (Palacios, 2004), with some influence in the central archipelago as well (Witman et al., 2010). These currents vary in intensity with El Niño Southern Oscillation (ENSO) events (Tarakanov & Borisova, 2013). Furthermore, they show great seasonal variability and short-term variability (days to weeks) and are influenced by trade winds and other atmospheric processes that change the water mass properties in terms of salinity, pH and temperature (Fiedler & Lavín, 2017; Sweet et al., 2007). These distinctive geographic and oceanographic settings around the archipelago make these oceanic islands unique in terms of diversity and endemism, where tropical and subtropical/temperate species can be found, sometimes near one another (Edgar et al., 2004; Schaeffer et al., 2008). Species composition for macroinvertebrates and reef fish differs in areas with contrasting oceanographic conditions (Edgar et al., 2004).

Several studies in the Galápagos suggest that sites that support high upwelling intensity are very important as a frequent source of nutrients and food availability, which shows a strong linkage between oceanographic conditions and ecosystem dynamics, both in intertidal rocky shores (Vinueza et al., 2014) and subtidal ecosystems (Krutwa, 2014; Witman et al., 2010). Further, these studies show great spatial variation in environmental conditions at sites located within the same biographic region or even around the same island. Understanding how the higher productivity due to upwelling supports local diversity and ecological processes has been studied mostly for benthic organisms; however, the importance of upwelling and warm water intrusions on the ecology of most reef fish remains understudied in the Galápagos. Some studies have demonstrated different demographic patterns for reef fish living in different regions of the islands (Ruttenberg et al., 2005) and differences in reef fish assemblages with contrasting levels of upwelling and warm water input (Kingsford et al., 2023).

Vessel-based measurements of oceanographic conditions (water flow, temperature, in situ chlorophyll-α and dissolved oxygen concentrations) can be complemented with satellite imagery of chlorophyll-α concentrations and sea surface temperature (SST) over broader spatial scales. Although satellite-derived ocean colour observations have transformed our interpretation of oceanic productivity (Thengade & Agale, 2014), metrics from satellite detection are limited to surface waters. Accordingly, images are likely to provide only approximate estimates of environmental conditions that impact local communities below the surface, especially where the water column is highly stratified (Kingsford et al., 2023). Living organisms can also provide time-integrated records of historical environmental conditions. Many sessile organisms, such as scleractinian corals and bivalves, produce carbonate skeletons that are useful for reconstructing temporal and spatial variation in environmental conditions in marine systems (Walther et al., 2013).

Teleost fishes have aragonite otoliths located in the inner ear cavity that are used for balance and hearing (Campana, 1999; Campana & Thorrold, 2001). New material is deposited periodically to the exterior surface of this structure forming annual increments of opaque and translucent zones (Campana, 1999; Fowler, 1990). Otoliths are acellular and metabolically inert; therefore, once ions are incorporated into the calcareous material, they are not subject to reabsorption, which means the chemical composition of each layer remains constant over time (Campana & Thorrold, 2001; Walther & Thorrold, 2006). Furthermore, environmental variables such as temperature, salinity and water chemistry influence how elemental incorporation takes place (Elsdon & Gillanders, 2002; Elsdon & Gillanders, 2004). This allows the use of some elements as natural tags (Elsdon et al., 2008), which are likely to offer an accurate indicator of the chemical and physical properties of the water mass. However, there has been only a limited number of studies that used otolith elemental chemistry in the Galápagos (Cavole et al., 2020; Ruttenberg & Warner, 2006).

Territorial reef fish are ideal for detecting environmental variation at a specific location because they stay within a small area as juveniles and adults (Kingsford et al., 2009). The focus of our study was the yellow-tail damselfish *Stegastes arcifrons* (Heller & Snodgrass 1903), an abundant territorial species that has a widespread distribution in the Galápagos archipelago's shallow reefs (Allen et al., 2010; Allen & Woods, 1980). In addition to being territorial species, *S. arcifrons* was particularly useful for this study because it is relatively long-lived (25+ years), and signals of environmental events, such as the 1982–1983 El Niño event, have been found in their otoliths (Meekan et al., 1999), strongly suggesting that environmental conditions have a significative effect on these structures. However, Meekan et al. (1999) did not measure temporal or spatial variation in elemental ratios. *S. arcifrons* inhabits shallow waters in all the bioregions (Edgar et al., 2004; Kingsford et al., 2023) that experience contrasting temperatures and food availability within and among bioregions. This variation in environmental conditions has the potential to influence patterns of the elemental chemistry of otoliths.

The main goal of this study was to determine how time-integrated (years) elemental chemistry of *S. arcifrons* otoliths varied among sites in areas with different environmental conditions. A mensurative sampling design was used to determine how elemental loads in otoliths of fish vary among sites across a temperature gradient.

2 | MATERIALS AND METHODS

2.1 | Selection of study sites, sample design and collection of specimens

We predicted that patterns of elemental chemistry would vary among sites located in waters of different temperatures and historical accounts

TABLE 1 Sites where adult *Stegastes arcifrons* were collected in the Galápagos Marine Reserve, arranged based on sea surface temperature (SST) in ascending order.

				SST (°C)			
	Site	**Island**	**Bioregion**	**Mean**	**Range**	**10% percentile**	**Upwelling regime**
1	Punta Mangle	Fernandina	Western	22.74	18.07–28.43	19.98	High
2	La Botella	Floreana	Central-southeastern	22.95	17.84–28.02	19.99	High
3	North Tijeretas	San Cristóbal	Central-southeastern	23.21	17.63–28.25	20.49	High
4	Punta Suárez	Española	Central-southeastern	23.41	17.96–28.59	20.66	High
5	Cerro Brujo	San Cristóbal	Central-southeastern	23.51	18.74–27.84	20.98	Intermediate
6	Champion	Floreana	Central-southeastern	23.53	18.58–28.49	20.69	Low
7	Pinzón west	Pinzón	Central-southeastern	23.59	18.18–28.34	21.03	Intermediate
8	Pinzón east	Pinzón	Central-southeastern	23.61	18.51–29.40	21.02	Intermediate
9	Bahía Gardner	Española	Central-southeastern	23.62	18.02–28.72	20.81	Intermediate
10	North Baltra	Baltra	Central-southeastern	23.88	18.79–28.78	21.37	High
11	Bahía Cartago	Isabela	Central-southeastern	23.92	18.87–28.52	21.26	Intermediate
12	Beagle Rocks	Santiago	Central-southeastern	23.92	19.30–28.95	21.38	Low
13	Cabo Chalmers	Pinta	Northern	24.30	17.63–28.52	21.85	Low
14	Cabo Ibbetson	Pinta	Northern	24.48	19.43–29.09	21.91	Low

Note: 10% = mean of the lowest 10% of all values. Upwelling regime categorization was based on studies that measured upwelling events (Witman et al., 2010), and established patterns were based on satellite imagery over time (Kingsford et al., 2023; Liu et al., 2013; Palacios, 2004; Schaeffer et al., 2008; Sweet et al., 2007).

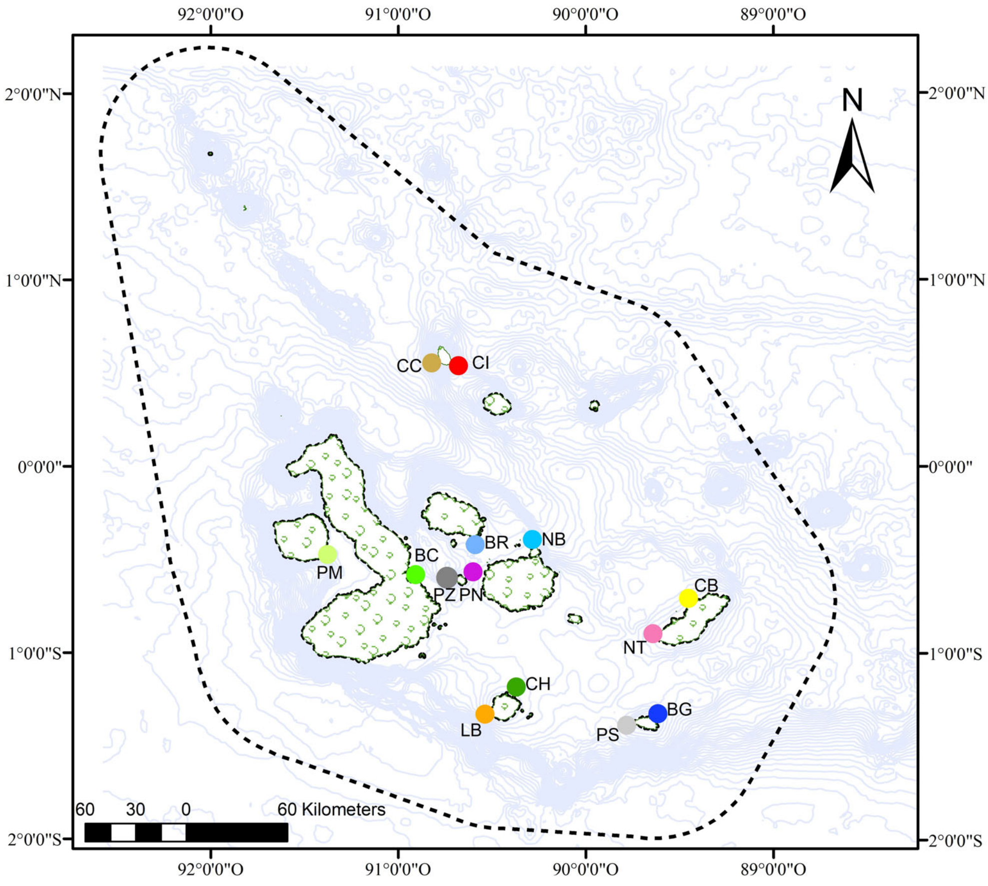

FIGURE 1 Study sites in alphabetical order: Bahía Cartago (●BC), Bahía Gardner (●BG), Cabo Chalmers (●CC), Cabo Ibettson (●CI), Cerro Brujo (●CB), Champion (●CH), La Botella (●LB), Pinzón east (●PN), Pinzón west (●PZ), Punta Suárez (●PS), North Baltra (●NB), Punta Mangle (●PM), Beagle Rocks (●BR) and North Tijeretas (●NT) in the Galápagos Marine Reserve (GMR). External broken line shows the 40-nm boundary of the protected area. Bathymetry is shown in 100-m intervals; darker colouration around islands shows shallow waters.

of upwelling. Fourteen sites in the Galápagos Marine Reserve (GMR) were chosen based on the average environmental conditions that varied based on the level of upwelling and warm water intrusion. Additional consideration with site choice included known areas of upwelling regimes and satellite imagery of SST (Schaeffer et al., 2008; Sweet et al., 2007; Witman et al., 2010; Table 1; Figure 1).

TABLE 2 Mean age and standard length of *Stegastes arcifrons* for a subsample group corresponding to eight sites.

			Age (years)			Standard length (mm)		
	Site	Island	Mean	Range	SE	Mean	Range	SE
1	Punta Mangle	Fernandina	7.4	3–12	0.83	113.2	99–125	2.37
2	La Botella	Floreana	12.11	8–23	1.50	121.2	110–127	2.23
3	North Tijeretas	San Cristóbal	8.55	5–16	1.06	120.5	107–133	2.06
4	Cerro Brujo	San Cristóbal	6	4–9	0.71	120.4	110–129	1.89
5	Champion	Floreana	6.9	4–16	1.18	110.7	103–119	1.66
6	North Baltra	Baltra	6.13	3–8	0.61	122.9	116–128	1.46
7	Beagle Rocks	Santiago	9.4	4–19	1.74	118.9	114–124	1.28
8	Cabo Ibbetson	Pinta	6.73	3–10	0.69	104.7	80–119	3.57

Abbreviation: SE, standard error.

Fish were collected in May and October 2015 using hand spears; all fish were in the adult size range [>100 mm standard length (L_S) ($n = 10$ fish per site, Table 1). Fish were only aged from eight sites [La Botella (LB), Punta Mangle (PM), Cerro Brujo (CB), North Baltra (NB), North Tijeretas (NT), Champion (CH), Cabo Ibettson (CI), Beagle Rocks (BR)], but these sites captured the full range of temperature variation in the archipelago (Table 2). All aged fish were in the adult size range of 102–166 mm L_S [x ± standard error (SE) = 145.62 ± 0.87 years, $n = 76$], and their ages ranged from 3 to 23 years (x ± SE = 7.9 ± 0.43 years, $n = 76$). The mean age at the eight sites ranged from 6 to 9.4 with one outlier at 12.11 years. Age did not confound our interpretation of spatial variation in Ba/Ca and Sr/Ca, as there were no significant relationships for all fish between both Ba/Ca and Sr/Ca and age (Ba/Ca $r^2 = 0.05$), analysis of variance (ANOVA) for slopes $df = 15$, $F = 0.56$, NS; Sr/Ca $r^2 = 0.06$, ANOVA for slopes $df = 15$, $F = 0.27$, NS.

Specimens were processed as soon as possible after collection, either on the boat or stored in ice and processed in the laboratory on the same day. Fish were collected with the support of research permit PC-47-15 granted by the Galápagos National Park Authority. All fish were euthanized as soon as they were collected.

2.2 | Otolith extraction

For extracting the otoliths, we followed the methods of the following studies: Kingsford et al. (2009); Sih & Kingsford (2015): *Pomacentrus amboinensis*; and, Walther et al. (2010): *Acanthochromis polyacanthus*. Before dissection, all fish were measured for standard length (L_S), fork length (L_F) and total length (L_T) to the nearest millimetre. Then, the largest pair of otoliths (sagittae) was removed, cleaned with Milli-Q water to remove any tissue left, dried and placed into 1.5-mL Eppendorf tubes. They were transported to James Cook University (Townsville, Australia) where otolith preparation and chemical analyses took place.

2.3 | Otolith preparation

One sagittal otolith was used for ageing the fish, from 76 randomly selected individuals from eight sites with a range of SST values (Table 1). Sagittae were sectioned transversally, placed in Crystalbond resin on a glass microscope slides, grounded and polished with lapping film. Mounted otoliths were viewed under a Leica DMLB compound microscope using a cold light source. Images were taken with the attached Leica DC300 camera and processed using IM50 software. The pictures were used for ageing the fish (Campana & Thorrold, 2001; Kingsford et al., 2019).

Sectioned otoliths were examined at 200×, and annual increments (composed of opaque and translucent zones) were identified and counted from the nucleus to the edge of the sagittae. One reader made three readings of every otolith, with an interval of 5 days between readings. The identification and size of each fish were unknown to avoid potential bias when interpreting the otolith. The three readings were recorded independently and compared. In the cases where readings did not match, a second reader made at least two independent readings before age was determined, and a consensus was reached between the two readers. Otoliths (5%) were rejected if no consensus could be made.

2.4 | Elemental chemistry analysis with all adult fish

One otolith from each pair was randomly selected and weighed using a Sartorius Genius microbalance to the nearest 0.00001 g. Otoliths were then cleaned in 1% HNO_3 (65% Merck Suprapure) for 5 to 10 s, rinsed thrice with Milli-Q water and allowed to dry inside a positive-flow Class-100 laminar flow cabinet (AS 1807). Samples were dissolved in 500 μL of HNO_3 (20%), and the solution was then made up to a final volume of 5 mL with Milli-Q water; otoliths were previously partitioned into groups by weight category for appropriate dilution factor. Samples were analysed using a Varian 820 inductively coupled plasma mass spectrometer (ICP-MS). Blank samples (without otoliths) were prepared in the same fashion and were used for 'blank corrections' to calculate the limits of detection (Kingsford et al., 2009). We focused our study based on the elemental concentration of Ba/Ca, Mg/Ca, Mn/Ca and Sr/Ca.

2.5 | Statistical analyses

2.5.1 | Otolith elemental chemistry of adult fish (mensurative design)

It was hypothesised that individual elemental loads would vary among sites. Variation among sites was tested with a one-way ANOVA using the procedures of Underwood (1997). Raw data were tested for homogeneity of variances with a Cochran test; in the few cases where Cochran's was significant and data were heterogeneous, the analysis was completed as ANOVA is robust to the heterogeneity of variances (Underwood, 1997). In most cases, this Cochran's tests were not significant. Some of the otoliths were lost due to poor quality; in these cases, the lost replicates of the original 10 fish were replaced with the mean of remaining values to maintain a balanced design; a degree of freedom was subtracted for each loss, a maximum two per site. A principal component analysis (PCA) was used to compare elemental fingerprints. The elemental values for each fish were based on those above the detection limits for Ba137/Ca43, Mg25/Ca43, Mn55/Ca43 and Sr88/Ca43.

To determine how elemental loads related to the spatial spread of sites, time-averaged temperatures, highly accurate estimates of SST were obtained from NASA's Giovanni platform (https://giovanni.gsfc.nasa.gov/giovanni). Mean surface temperature (SST) values for each site were derived from square of 4 × 4 km pixels. Monthly averages were used to estimate a grand mean by year for the period of 2002–2015 (92.8% of fish were less than 13 years old). Values for each month included those collected both day and night. Other satellite data were available for longer periods from IRI/LDEO Climate Data Library (http://ingrid.ldgo.columbia.edu) but had a much larger pixel size, and therefore did not provide the spatial resolution required for site comparison.

Where regressions have been presented, we provide the goodness of fit (r^2) and the results of ANOVA to determine if the slopes were significantly different from zero. The data are presented as the grand mean and range for 13 years along with the average of the lowest 10% of values. The latter was to allow for short-term variation in temperature change. Satellite imagery only detects temperatures in surface layers, which is a weakness if the water column is stratified (e.g., Kingsford et al., 2023). However, our fish were generally sampled in less than 6 m of water. SST data are the only spatially explicit data available at the Galápagos over multiple years. Minitab Statistical Software 17.0 was used for all statistical analysis and plots.

3 | RESULTS

3.1 | Whole otolith elemental chemistry

All elements showed significant differences among sites (Ba/Ca, Mg/Ca, Mn/Ca and Sr/Ca). These reflected strong spatial variation in environmental conditions (Figure 2; Table 3). Clear patterns relating to a positive temperature gradient were found for Mn/Ca and Sr/Ca, whereas more variable patterns were found for Ba/Ca and Mg/Ca. Relationships (r^2) generally explained more variation when the age of fish was known (Table 4).

There was a significant relationship between SST and mean values of Ba/Ca, which was for all 14 sites but improved greatly where fish were aged (Table 4). Ba/Ca ratios varied among sites with cool water [i.e., PM to Punta Suárez (PS), Figure 2]. At PM, the values were low, whereas at LB, known for EUC upwelling (Whitman et al., 2010), the values were higher (means = 3.47 vs. 15.38 μmol/mol) but still well below values at warmer sites. Further, Cabo Chalmers (CC) and CI, two sites in the northern region, bathed by warm, nutrient-poor waters, had the highest loads of Ba/Ca (means 39.30 and 48.09 μmol/mol, respectively). Similarly, CH, classified as a low upwelling regime (Krutwa, 2014; Witman et al., 2010), exhibited a high mean Ba/Ca load (mean = 39.61 μmol/mol). High spatial variation in Ba/Ca was observed at some sites within the same island, including Española [Bahía Gardner (BG) and PS] and two sites in San Cristóbal (CB and NT). At some sites, there was high variation among replicate fish from the same site (e.g., NT, PS and CI).

Spatial variation for Mg/Ca was also considerable (Table 3). In contrast to Ba and Sr, there were no significant relationships with SST (Table 4). The highest mean loads were found at Pinzón, although with great variation among individuals [Pinzón east (PN), Pinzón west (PZ), means 130.7 and 209.6 μmol/mol, respectively]. The spatial variation of Mg/Ca load was also evident between sites for other islands such as Española (BG and PS, means 49.16 and 58.07 μmol/mol, respectively). In contrast, the sites in Pinta had similar mean values (means: CC: 94.5; CI: 91.26 μmol/mol). Particularly high variation was found among fish from Pinzon west (Figure 2).

Mn/Ca ratios also varied significantly among sites (Table 3), with a positive but variable relationship between temperature and loading of Mn/Ca; again the relationship was strongest where fish were aged (Table 4). The highest ratios were found in the two northern sites in warm waters at Pinta (Figure 2) followed by the sites in Pinzón (PZ: $x = 2.64$ μmol/mol; PN: $x = 2.64$ μmol/mol). The sites in Floreana had contrasting loads; however, sites in Española and San Cristóbal were similar. Differences among replicate fish within sites were sometimes high [e.g., Bahía Cartago (BC)].

There were significant differences in Sr/Ca among sites (Table 3; Figure 2). With a positive relationship between SST and elemental load but variable for Sr/Ca ratios, the relationship explained more variation at the sites where the age of fish was

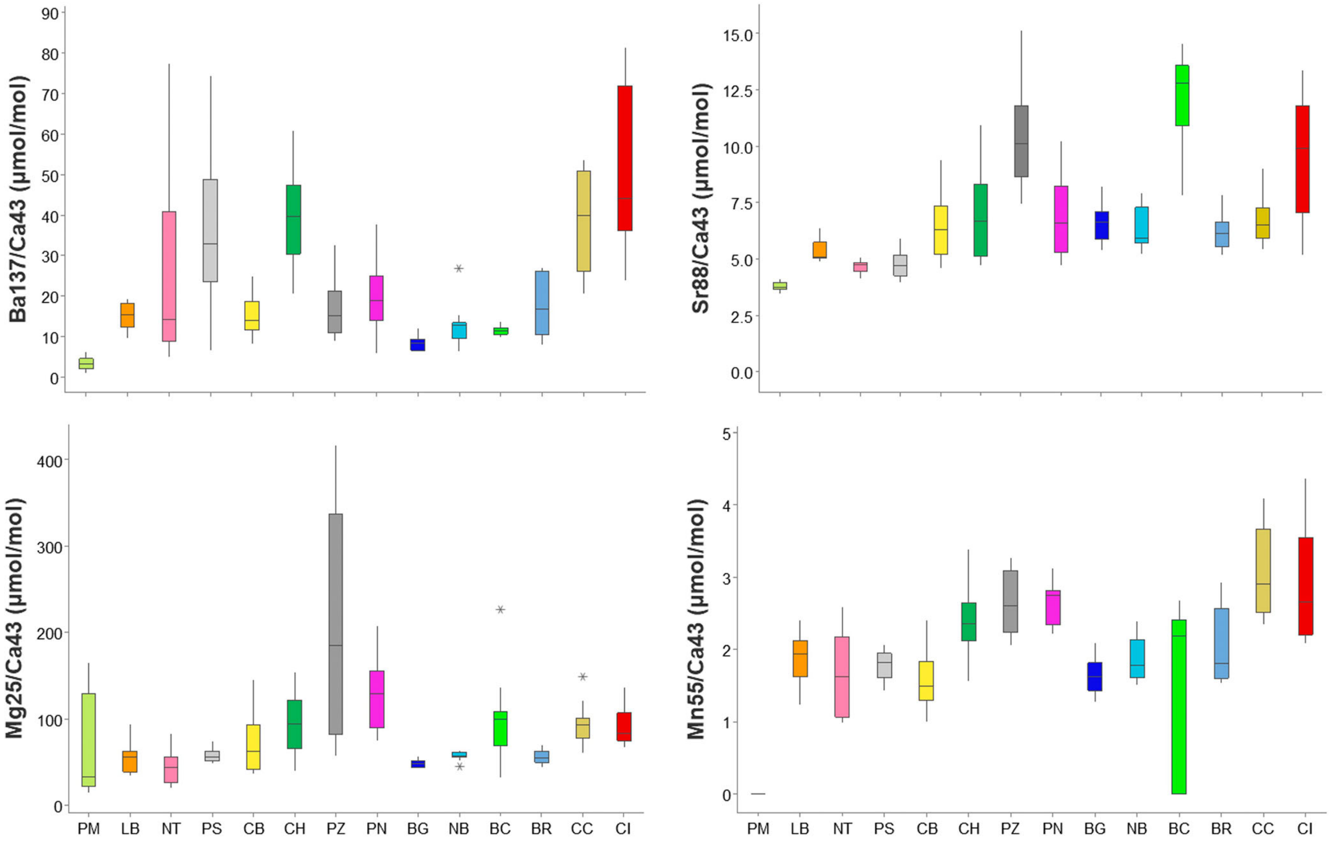

FIGURE 2 Variation in metal-to-calcium ratios in otolith of adult fish (with standard error bars) at 14 sites in the Galápagos Marine Reserve (GMR), from left to right, Punta Mangle (PM), La Botella (LB), North Tijeretas (NT), Punta Suárez (PS), Cerro Brujo (CB), Champion (CH), Pinzón west (PZ), Pinzón east (PN), Bahía Gardner (BG), North Baltra (NB), Bahía Cartago (BC), Beagle Rocks (BR), Cabo Chalmers (CC) and Cabo Ibettson (CI); the order of sites corresponds with the mean sea surface temperature of each site from lowest to highest. For Mn55/Ca 43, there was not a detectable amount by the inductively coupled plasma mass spectrometer (ICP-MS) at PM. Asterisks represent outliers.

TABLE 3 One-way analysis of variance (ANOVA) for elemental ratios in otoliths of adult *Stegastes arcifrons*.

	Ba137/Ca43				**Mn55/Ca43**			
Source	***df***	**MS**	***F***	***p***	***df***	**MS**	***F***	***p***
Site	13	1959.9	12.10	**0.000****	13	5.59	25.04	**0.000****
Error	105	161.9			105	0.22		
Total	118				118			
	Mg25/Ca43				**Sr88/Ca43**			
Source	***df***	**MS**	***F***	***p***	***df***	**MS**	***F***	***p***
Site	13	18,753.1	6.98	**0.000****	13	55.61	24.56	**0.000****
Error	105	2686.3			105	2.26		
Total	118				118			

Note: Statistically significant values are presented in bold.

known (Figure 3; Table 4). The four coolest sites had the lowest values of Sr/Ca and the lowest variation among replicate fish within sites (Figures 2 and 3). For some islands there was high spatial variation between sites, as evident for Pinzón and Pinta. Further, at most sites where the average SST was above 23.5°C, there was high variation among replicate fish.

3.2 | Elemental fingerprints

There was great variation in the elemental fingerprints based on the combination of elements for each fish among individual fish within sites (Figure 4). PC1 explained 44.7% of the variation and was characterised by a high contribution of Mn/Ca and Sr/Ca values. PC2

TABLE 4 Relation between element concentration and average sea surface temperature (SST).

	14 sites				8 sites			
Element	R^2	*F*	*p*	Trend	R^2	*F*	*p*	Trend
Ba137/Ca43	0.18	29.51	**0.000****	Positive	0.37	42.6	**0.000****	Positive
Mg25/Ca43	0.17	2.43	0.122	Positive	0.05	3.94	0.051	Positive
Mn55/Ca43	0.34	71.85	**0.000****	Positive	0.42	71.85	**0.000****	Positive
Sr88/Ca43	0.28	54.17	**0.000****	Positive	0.49	70.04	**0.000****	Positive

Note: The eight sites refer to those where fish were aged, and age was related to SST data for those years only. Statistically significant values are presented in bold.

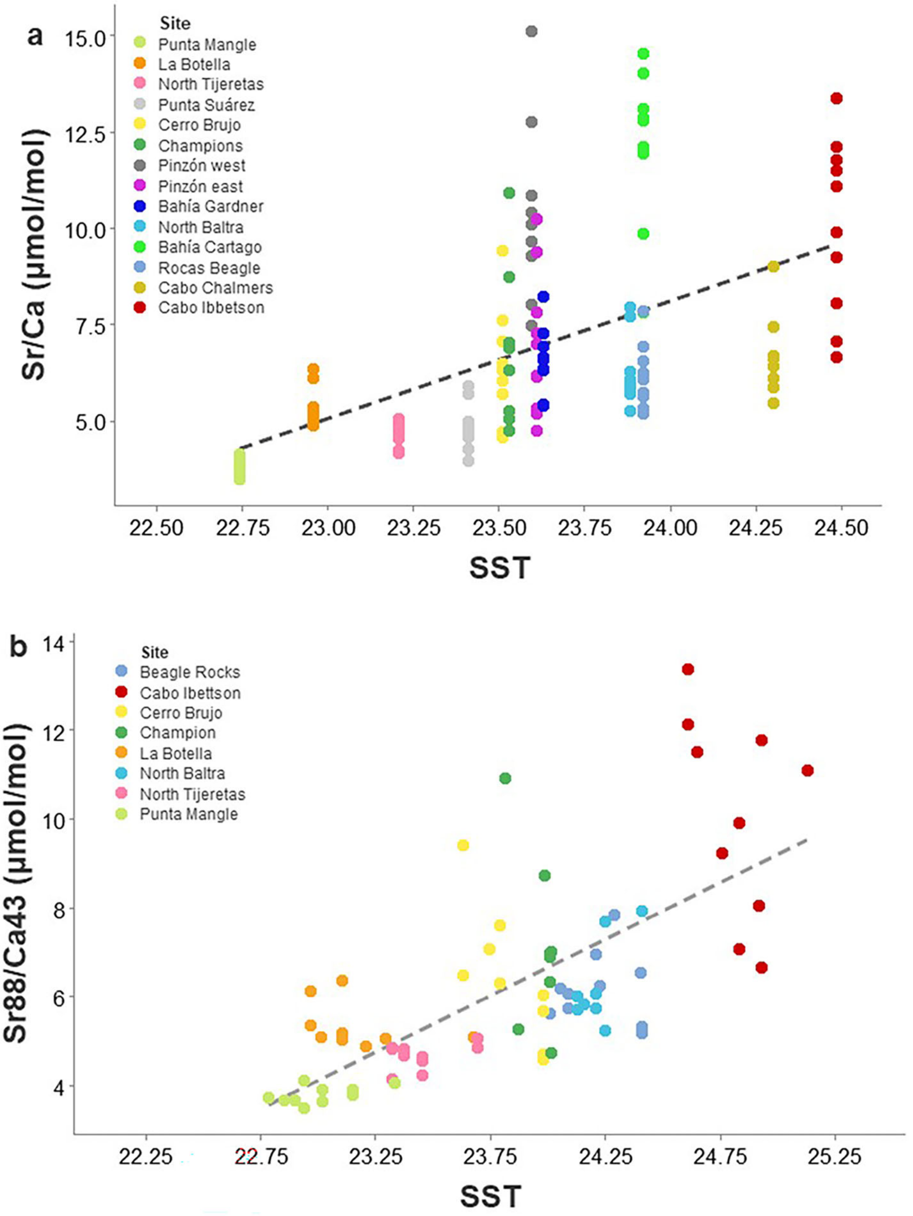

FIGURE 3 Correlation between sea surface temperature (SST, averaged over from 2002 to 2015) and Sr/Ca ratios of otoliths of adult fish: (a) ($r^2 = 0.28$) at 14 sites and (b) ($r^2 = 0.49$) at eight sites where fish were aged, and age was related to SST data for those years only. All samples were from the Galápagos Marine Reserve (GMR).

accounted for 24.2% of the variation and presented high positive Ba/Ca values and high Mg/Ca negative loads. The sites with the coolest waters, including PM (Fernandina), LB, NT and PS, clustered together with negative values of PC1. In contrast, warmer sites, such as CI (Pinta), had higher values for both PC1 and PC2.

4 | DISCUSSION

Our time-integrated elemental ratios effectively determined fish's lifetime environmental exposure. We have provided evidence that fishes collected at sites with great variation in environmental conditions

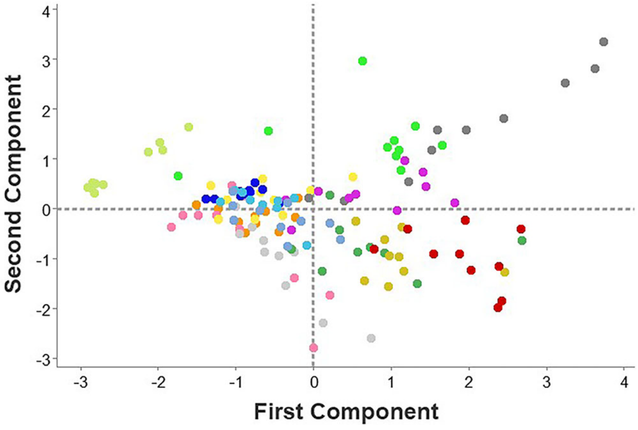

FIGURE 4 Principal components analysis score plot of elemental loads in otoliths of adult fish pooled by site. Each point represents an otolith from a single fish. PC1 loads are (from higher to lower) 0.563 Mn55/Ca43, 0.520 Sr88/Ca43, 0.488 Mg25/Ca430 and 0.418 Ba137/Ca43, whereas PC2 ratios are −0.719 Ba137/Ca43, −0.260 Mn55/Ca43, 0.355 Sr88/Ca43 and 0.537 Mg25/Ca43. Study sites are in alphabetical order: Bahía Cartago(● BC), Bahía Gardner (● BG), Cabo Chalmers (● CC), Cabo Ibettson (● CI), Cerro Brujo (● CB), Champion (● CH), La Botella (● LB), Pinzón east (● PN), Pinzón west (● PZ), Punta Suárez (● PS), North Baltra (● NB), Punta Mangle (● PM), Beagle Rocks (● BR) and North Tijeretas (● NT) in the Galápagos Marine Reserve (GMR).

have different patterns of elemental chemistry of their otoliths. These conclusions were based on a broad-scale mensurative sampling design that included large (10–100 s of kilometres) and small spatial scales (<10 km). Generalised knowledge of patterns of upwelling and warm currents (especially the Panama current) could partly explain the patterns we found. The most robust patterns for elemental chemistry versus average SST were for Sr/Ca where the lowest values were found in cool waters and the highest in warm waters. More of the variation in the relationship was explained when elemental ratios were calibrated to the age of fish. These spatial differences suggest that small-scale variations in temperature affect elemental concentration in the water column. The fish themselves, therefore, were sentinels of environmental change in that strong inference on the environmental regime that fish experienced could be deduced from time-integrated elemental chemistry without site-specific historical environmental measurements. Variation in SST at the Galapagos is generally a good predictor of warm tropical currents and/or upwelling (Liu et al., 2013). Elemental chemistry therefore is another tool for predicting local oceanographic conditions. In contrast to cool water sites, there was great variation within and between sites within islands, especially where SSTs were highest. At cool water sites, variation among individuals was low. When all elements above the detection limits were included in a multivariate comparison, differences were also detected among fish from sites that varied in SST.

4.1 | Elemental chemistry

Throughout the archipelago, different current systems cause great spatial variation in oceanographic conditions (Liu et al., 2013), and thus we suggest that the use of elemental chemistry in territorial fish can provide a useful predictive tool to identify areas with contrasting temperature and related primary productivity regimes. Shallow rocky reefs in the Galápagos experience high spatial variability in environmental conditions that can affect habitat structure (Kingsford et al., 2023) and in our case environmental signals in fish. Our results contrast with another study that analysed elemental chemistry in juveniles of two predator species (*Lutjanus argentiventris* and *Mycteroperca olfax*) in mangrove areas in different islands of the archipelago where no significative differences in elemental loads were detected, although differences in elemental loads were found for *L. argentiventris*, when the Galápagos was compared to distant Baja California (Cavole et al., 2020). Patchiness in elemental signatures on different scales from hundreds to tens of kilometres has been found in other studies. In French Polynesia, the elemental signatures were significantly different between islands and within sites, and such differences were evident in sites 200 m apart. Mn concentrations were the stronger predictor of site identity (Lo-Yat et al., 2005). On the Great Barrier Reef, Kingsford et al. (2009) found that variation in elemental chemistry for *A. polyacanthus* was largely explained by variation at the site level: higher Ba/Ca ratios among sites related to upwelling. In contrast, in the GMR, there was no simple relationship between Ba/Ca ratios and cool upwelled waters. Our findings concur, to some extent, with the experiment conducted by Walther et al. (2010), where they reported significant interactive effects between life-history stage, temperature and food quantity. *A. polyacanthus* reared with low-quality food had higher Ba/Ca concentrations than those with a high-quality diet. We suggest that poorer feeding conditions (i.e., low algal biomass and perhaps composition) at areas with high SST (e.g., Kingsford et al., 2023) and low chlorophyll-a concentrations, like the sites in Pinta or CH (identified as a low productivity site), could explain this. This pattern is likely to be responsible for the high variation in Ba/Ca ratios we found among individuals that could be explained by competitive interactions between these territorial herbivores where food is limited (e.g., Holbrooks & Schmitt, 1989). In areas with abundant fish and scarce resources, herbivorous fish may consume less-optimal food than those in productive waters with better-quality sources (Catano et al., 2014). In Galápagos rocky reefs, high fish densities likely intensify interspecific competition, forcing territorial fish to consume available resources. We propose that competition drives elemental chemistry variation among replicate fish within a site. Low upwelling areas, characterised by warm waters and habitats dominated by short filamentous algae, support high herbivore numbers (Kingsford et al., 2023). Vinueza et al. (2014) described a strong top-down effect on algal cover in low-productivity intertidal zones, where high-quality algae are scarce. This mechanism is likely to occur in the shallow subtidal zone, increasing resource-based competition.

Furthermore, we found a positive trend between Ba/Ca ratios and temperature at the two extremes of our temperature gradient. Our findings partly align with research on juvenile *Acanthopagrus butcheri*, where Ba/Ca concentrations increased with temperature but the upper and lower temperature treatments showed no significant differences (Elsdon & Gillanders, 2002). Considering that upwelled waters in the Galápagos and incursions of the warm Panama current, our results suggest that the environmental conditions at a local level are quite heterogeneous contributing to the elemental and habitat patchiness (Kingsford et al., 2023). Spatial patterns of elemental ratios were not confounded by the age of fish, as we did not detect any significant relationships between Ba/Ca and Sr/Ca and age.

A positive relationship between Sr/Ca and temperature explained 48% of the variation in our study. This concurs with studies on corals (Fallon et al., 2003), but the relationship can be more complex among species of fishes. For juvenile black bream (*A. butcheri*) Sr/Ca ratios were significantly greater at low (12°C and 16°C) and high (28°C) temperatures, respectively (Elsdon & Gillanders, 2002), whereas significant interactions between stage and food were observed for Sr/Ca in *A. polyacanthus* (Walther et al., 2010). Barnes et al. (2013) demonstrated experimentally that the incorporation of Sr varied based on the interactive effects of genetics, salinity and temperature, whereas the incorporation of Ba varied with salinity and the genetics. These more complex interactions may influence the incorporation of elements and could also affect the variation we found at the individual level, but in the Galapagos, individual-based variation within sites was lowest in coolest waters.

Variation in otolith elemental composition is thought to reflect physiological controls, likely modulated by ambient temperature (e.g., European plaice *Pleuronectes platessa*; Sturrock et al., 2015). Strong environmental signals have been found in otoliths of rockfish (*Sebastes caurinus*, *Sebastes flavidus* and *Sebastes melanops*). Wheeler et al. (2016) determined that changes in Ba/Ca and Sr/Ca ratios were proportionally similar to the elemental concentrations in seawater being at a minimum during upwelling and increased when relaxation and weak upwelling conditions were present. Our study aligns in that Ba/Ca and Sr/Ca ratios were highest at sites with warmer waters.

When evaluating the combined effects of ambient water concentration, salinity and temperature on elemental chemistry incorporation in the otoliths of juvenile *Dicentrarchus labrax*, it was reported that Sr/Ca and Ba/Ca values were positively correlated with water density (Sigma-t), where both temperature and salinity appeared to have positive effects (Reis-Santos et al., 2013). We had no data on salinity at the relevant spatial scales; however, variation in salinity is only a few milligrams per litre at the Galápagos, the Cromwell current has been described as a cold and salty water mass (Schaeffer et al., 2008; Sweet et al., 2007), whereas the coastal waters of the islands are not prone to large input of freshwater where great changes in salinity would equate with the findings of the *D. labrax* study (10, 20 and 30 mg L^{-1}).

In conclusion, we demonstrated there were major differences in single element and multielement chemistry in olotiths from fish among sites throughout the Galápagos archipelago, where individuals had experienced contrasting regimes of temperature that likely relates to the input of tropical waters via the Panama current and upwelling. Differences for individual elements and elemental fingerprints sometimes varied between sites located at the same island, most likely indicating small-scale differences in exposure to cold and warmer waters and diet. This may explain the habitat patchiness of many reefs, for which the Galápagos are known. Strong time-integrated environmental signals in whole otoliths can assist in prediction and the identification of localised areas with different temperatures.

AUTHOR CONTRIBUTIONS

Michael J. Kingsford, Margarita Brandt and Juan Manuel Alava-Jurado designed the study. Juan Manuel Alava-Jurado and Michael J. Kingsford conducted data collection in the field, prepared the samples, performed statistical analyses, interpreted the data and prepared the figures. Juan Manuel Alava-Jurado wrote the manuscript text with input from all authors.

ACKNOWLEDGEMENTS

We thank Carlos Mena and all the people at the Galápagos Science Center for logistical support and Mark O'Callaghan from James Cook University for technical support with otoliths. We are grateful to the Crews of Valeska Yamilé and Queen Mabel for all the help during field research. We also thank the Galápagos National Park Authority for granting us the permit PC-47-15 to carry out the research, collect and export samples. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

This project was funded by an ARC Centre of Excellence Grant to Michael J. Kingsford with support from the Galápagos Science Center, Universidad San Francisco de Quito.

CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflict of interest.

ORCID

Juan Manuel Alava-Jurado https://orcid.org/0000-0001-9509-5572

Margarita Brandt https://orcid.org/0000-0002-9786-0490

Michael J. Kingsford https://orcid.org/0000-0003-1704-6198

REFERENCES

Allen, G. R., Robertson, R., Rivera, R., Edgar, G., Merlen, G., Zapata, F., & Barraza, E. (2010). *Stegastes arcifrons*. In *IUCN Red List of Threatened Species*. Version 2015.1. Available at https://www.iucnredlist.org/species/183530/8129476 (last accessed 10 June 2016).

Allen, G. R., & Woods, L. (1980). A review of the damselfish genus *Stegastes* from the eastern Pacific with description of a new species. *Records of Western Australia Museum*, *8*, 171–198.

Barnes, T. C., Gillanders, B. M., & Rose, K. (2013). Combined effects of extrinsic and intrinsic factors on otolith chemistry: Implications for environmental reconstructions. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*, 1159–1166. https://doi.org/10.1139/cjfas-2012-0442

Campana, S. E. (1999). Chemistry and composition of fish otoliths: Pathways, mechanisms and applications. *Marine Ecology Progress Series*, *188*, 263–297. https://doi.org/10.3354/meps188263

Campana, S. E., & Thorrold, S. R. (2001). Otoliths, increments, and elements: Keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 30–38. https://doi.org/10.1139/f00-177

Catano, L. B., Shantz, A. A., & Burkepile, D. E. (2014). Predation risk, competition, and territorial damselfishes as drivers of herbivore foraging on Caribbean coral reefs. *Marine Ecology Progress Series*, *511*, 193–207. https://doi.org/10.3354/meps10921

Cavole, L. M., Miller, J. A., Salinas-de-León, P., Aburto-Oropeza, O., Jarrin, J. R. M., & Johnson, A. F. (2020). The role of extrinsic variation cohabiting juvenile fish species exhibit similar otolith elemental signatures. *Marine Ecology Progress Series*, *646*, 109–125. https://doi.org/10.3354/meps13394

Chavez, F. P., & Messié, M. (2009). A comparison of eastern boundary upwelling ecosystems. *Progress in Oceanography*, *83*, 80–96. https://doi.org/10.1016/j.pocean.2009.07.032

Edgar, G., Banks, S., Fariña, J., Calvopiña, M., & Martínez, C. (2004). Regional biogeography of shallow reef fish and macro-invertebrate communities in the Galapagos archipelago. *Journal of Biogeography*, *31*, 1107–1124. https://doi.org/10.1111/j.1365-2699.2004.01055.x

Elsdon, T. S., & Gillanders, B. M. (2002). Interactive effects of temperature and salinity on otolith chemistry: Challenges for determining environmental histories of fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 1796–1808. https://doi.org/10.1139/f02-154

Elsdon, T. S., & Gillanders, B. M. (2004). Fish otolith chemistry influenced by exposure to multiple environmental variables. *Journal of Experimental Marine Biology and Ecology*, *313*, 269–284. https://doi.org/10.1016/j.jembe.2004.08.010

Elsdon, T. S., Wells, B. K., Campana, S. E., Gillanders, B. M., Jones, C. M., Limburg, K. E., Secor, D. H., Thorrold, S. R., & Walther, B. D. (2008). Oceanography and marine biology: an annual review. In *Otolith chemistry to describe movements and life-history parameters of fishes: Hypotheses, assumptions, limitations and inferences* (Vol. 46, pp. 297–330). CRC Press. https://doi.org/10.1201/9781420065756.ch7

Fallon, S. J., McCulloch, M. T., & Alibert, C. (2003). Examining water temperature proxies in Porites corals from the great barrier reef: A cross-shelf comparison. *Coral Reefs*, *22*, 389–404. https://doi.org/10.1007/s00338-003-0322-5

Fiedler, P. C., & Lavín, M. F. (2017). Oceanographic conditions of the eastern tropical Pacific. In P. Glynn, D. Manzello, & I. Enochs (Eds.), Coral Reefs of the World, *Coral reefs of the eastern tropical Pacific* (Vol. 8, pp. 59–83). Springer. https://doi.org/10.1007/978-94-017-7499-4_3

Fiedler, P. C., Philbrick, V., & Chavez, F. P. (1991). Oceanic upwelling and productivity in the eastern tropical Pacific. *Limnology and Oceanography*, *36*, 1834–1850. https://doi.org/10.4319/lo.1991.36.8.1834

Fowler, A. J. (1990). Validation of annual growth increments in the otoliths of a small, tropical coral reef fish. *Marine Ecology Progress Series*, *64*, 25–38. https://doi.org/10.3354/meps064025

Fuentes, E. N., Zuloaga, R., Almarza, O., Mendez, K., Valdés, J. A., Molina, A., & Pulgar, J. (2017). Upwelling-derived oceanographic conditions impact growth performance and growth-related gene expression in intertidal fish. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, *214*, 12–18. https://doi.org/10.1016/j.cbpb.2017.09.001

Holbrook, S. J., & Schmitt, R. J. (1989). Resource overlap, prey dynamics, and the strength of competition. *Ecology*, *70*, 1943–1953.

Kingsford, M. J., Brandt, M., & Alava-Jurado, J. M. (2023). Levels of upwelling are important to consider for conservation. In S. Walsh & C. Mena (Eds.), *Island ecosystems: Challenges to sustainability* (pp. 271–289). Springer-Verlag.

Kingsford, M. J., Hughes, J. M., & Patterson, H. M. (2009). Otolith chemistry of the non-dispersing reef fish Acanthochromis polyacanthus: Cross-shelf patterns from the central great barrier reef. *Marine Ecology Progress Series*, *377*, 279–288. https://doi.org/10.3354/meps07794

Kingsford, M. J., Welch, D., & O'Callaghan, M. (2019). Latitudinal and cross-shelf patterns of size, age, growth, and mortality of a tropical damselfish Acanthochromis polyacanthus on the great barrier reef. *Diversity*, *11*(67). https://doi.org/10.3390/d11050067

Krutwa, A. (2014). Small-scale Differences in Tropical Subtidal Rocky Reef Communities of Floreana Island, Galápagos. PhD Dissertation, University of Bremen. http://nbn-resolving.de/urn:nbn:de:gbv:46-00104182-14

Liu, Y., Xie, L., Morrison, J. M., & Kamykowski, D. (2013). Dynamic downscaling of the impact of climate change on the ocean circulation in the Galápagos archipelago. *Advances in Meteorology*, *2013*, 1–18. https://doi.org/10.1155/2013/837432

Lo-Yat, A., Meekan, M., Munksgaard, N., Parry, D., Planes, S., Wolter, M., & Carleton, J. (2005). Small-scale spatial variation in the elemental composition of otoliths of Stegastes nigricans (Pomacentridae) in French Polynesia. *Coral Reefs*, *24*, 646–653. https://doi.org/10.1007/s00338-005-0047-8

Macpherson, E., Hastings, P. A., & Robertson, D. R. (2009). Macroecological patterns among marine fishes. In J. D. Witman & K. Roy (Eds.), *Marine macroecology* (pp. 122–152). University of Chicago Press.

Meekan, M., Wellington, G., & Axe, L. (1999). El Niño-southern oscillation events produce checks in the otoliths of coral reef fishes in the Galápagos archipelago. *Bulletin of Marine Science*, *64*, 383–390.

Menge, B. A., Lubchenco, J., Bracken, M., Chan, F., Foley, M., Freidenburg, T., Gaines, S. D., Hudson, G., Krenz, C., Leslie, H., Menge, D. N., Russel, R., & Webster, M. S. (2003). Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 12229–12234. https://doi.org/10.1073/pnas.1534875100

Menge, B. A., & Menge, D. N. (2013). Dynamics of coastal meta-ecosystems: The intermittent upwelling hypothesis and a test in rocky intertidal regions. *Ecological Monographs*, *83*, 283–310. https://doi.org/10.1890/12-1706.1

Messié, M., & Chavez, F. P. (2015). Seasonal regulation of primary production in eastern boundary upwelling systems. *Progress in Oceanography*, *134*, 1–18. https://doi.org/10.1016/j.pocean.2014.10.011

Palacios, D. M. (2004). Seasonal patterns of sea-surface temperature and ocean color around the Galápagos: Regional and local influences. *Deep Sea Research Part II: Topical Studies in Oceanography*, *51*, 43–57. https://doi.org/10.1016/j.dsr2.2003.08.001

Reis-Santos, P., Tanner, S. E., Elsdon, T. S., Cabral, H. N., & Gillanders, B. M. (2013). Effects of temperature, salinity and water composition on otolith elemental incorporation of Dicentrarchus labrax. *Journal of Experimental Marine Biology and Ecology*, *446*, 245–252. https://doi.org/10.1016/j.jembe.2013.05.027

Ritter, A. F. (2009). Regional variation in oceanographic conditions influences intertidal fish assemblage structure. *Limnology and Oceanography*, *54*, 1559–1573. https://doi.org/10.4319/lo.2009.54.5.1559

Ruttenberg, B. I., Haupt, A. J., Chiriboga, A. I., & Warner, R. R. (2005). Patterns, causes and consequences of regional variation in the ecology and life history of a reef fish. *Oecologia*, *145*, 394–403. https://doi.org/10.1007/s00442-005-0150-0

Ruttenberg, B. I., & Warner, R. R. (2006). Spatial variation in the chemical composition of natal otoliths from a reef fish in the Galápagos Islands. *Marine Ecology Progress Series*, *328*, 225–236. https://doi.org/10.3354/meps328225

Schaeffer, B. A., Morrison, J. M., Kamykowski, D., Feldman, G. C., Xie, L., Liu, Y., Sweet, W., McCulloch, A., & Banks, S. (2008). Phytoplankton biomass distribution and identification of productive habitats within the Galapagos marine reserve by MODIS, a surface acquisition system, and in-situ measurements. *Remote Sensing of Environment*, *112*, 3044–3054. https://doi.org/10.1016/j.rse.2008.03.005

Sigman, D. M., & Hain, M. P. (2012). The biological productivity of the ocean. *Nature Education Knowledge*, *3*, 1–16.

Sih, T. L., & Kingsford, M. J. (2015). Near-reef elemental signals in the otoliths of settling *Pomacentrus amboinensis* (Pomacentridae). *Coral Reefs*, *35*(1), 303–315. https://doi.org/10.1007/s00338-015-1376-x

Sponaugle, S., Grorud-Colvert, K., & Pinkard, D. (2006). Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida keys. *Marine Ecology Progress Series*, *308*, 1–15. https://doi.org/10.3354/meps308001

Sturrock, A. M., Hunter, E., Milton, J. A., Johnson, R. C., Waring, C. P., & Trueman, C. N. (2015). Quantifying physiological influences on otolith microchemistry. *Methods in Ecology and Evolution*, *6*, 806–816. https://doi.org/10.1111/2041-210X.12381

Sweet, W., Morrison, J., Kamykowski, D., Schaeffer, B., Banks, S., & McCulloch, A. (2007). Water mass seasonal variability in the Galápagos archipelago. *Deep Sea Research, Part I: Oceanographic Research Papers*, *54*, 2023–2035. https://doi.org/10.1016/j.dsr.2007.09.009

Tarakanov, A. O., & Borisova, A. V. (2013). Galapagos indicator of El Niño using monthly SST from NASA Giovanni system. *Environmental Modelling & Software*, *50*, 12–15. https://doi.org/10.1016/j.envsoft.2013.08.011

Thengade, A., & Agale, S. A. (2014). Satellite image classification and Content-Base image retrieval using Type-2 fuzzy logic. *IOSR Journal of Computer Engineering*, *16*, 74–78. https://doi.org/10.9790/0661-16647478

Thomas, A. C., Strub, P. T., Carr, M. E., & Weatherbee, R. (2004). Comparisons of chlorophyll variability between the four major global eastern boundary currents. *International Journal of Remote Sensing*, *25*, 1443–1447. https://doi.org/10.1080/01431160310001592418

Underwood, A. J. (1997). *Experiments in ecology: Their logical design and interpretation using analysis of variance*. Cambridge University Press.

Vinueza, L. R., Menge, B. A., Ruiz, D., & Palacios, D. M. (2014). Oceanographic and climatic variation drive top-down/bottom-up coupling in the Galápagos intertidal meta-ecosystem. *Ecological Monographs*, *84*, 411–434. https://doi.org/10.1890/13-0169.1

Walther, B. D., Kingsford, M. J., & McCulloch, M. T. (2013). Environmental records from great barrier reef corals: Inshore versus offshore drivers. *PLoS One*, *8*, e77091. https://doi.org/10.1371/journal.pone.0077091

Walther, B. D., Kingsford, M. J., O'Callaghan, M. D., & McCulloch, M. T. (2010). Interactive effects of ontogeny, food ration and temperature on elemental incorporation in otoliths of a coral reef fish. *Environmental Biology of Fishes*, *89*, 441–451. https://doi.org/10.1007/s10641-010-9661-6

Walther, B. D., & Thorrold, S. R. (2006). Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. *Marine Ecology Pregress Series*, *311*, 125–130. https://doi.org/10.3354/meps311125

Wheeler, S. G., Russell, A. D., Fehrenbacher, J. S., & Morgan, S. G. (2016). Evaluating chemical signatures in a coastal upwelling region to reconstruct water mass associations of settlement-stage rockfishes. *Marine Ecology Progress Series*, *550*, 191–206. https://doi.org/10.3354/meps11704

Witman, J. D., Brandt, M., & Smith, F. (2010). Coupling between subtidal prey and consumers along a mesoscale upwelling gradient in the Galapagos Islands. *Ecological Monographs*, *80*, 153–177. https://doi.org/10.1890/08-1922.1

How to cite this article: Alava-Jurado, J. M., Brandt, M., & Kingsford, M. J. (2025). Spatial variation in otolith elemental chemistry of *Stegastes arcifrons* (Pomacentridae) reflects environmental patchiness at the Galápagos archipelago. *Journal of Fish Biology*, *107*(4), 1237–1247. https://doi.org/10.1111/jfb.70120