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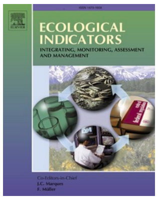

Original Articles

Fish nearshore habitat-use patterns as ecological indicators of nursery quality

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ABSTRACT

Anthropogenic factors have been identified as major stressors of nearshore environments such as estuaries, sea grass meadows and mangroves. We hypothesize that aquatic organisms functionally dependent on these habitats as nurseries respond to disturbances with subtle changes in their habitat-use patterns. We used a novel approach coupling behavioural change point analysis with fish otolith microchemistry to analyse continuous life history information independent of climate and physiological variability. Here we show that pre-industrial (1430–1640 CE) land use and fishing practices had little influence on the well synchronized migration behaviour of juvenile snapper *Chrysophrys auratus* in the Hauraki Gulf, New Zealand. In contrast, modern human disturbances have resulted in snapper spending less time in brackish nurseries and moving chaotically between habitats. Today, nearshore habitats have largely lost their nursery function for the species. Temporal comparison of habitat-use patterns is a powerful tool to evaluate past and present nursery habitat quality.

1. Introduction

Human activities have become an increasingly important factor in habitat degradation since the industrial age. Anthropogenic factors have been identified as major stressors of coastal nursery habitats affecting the biology of ecologically and commercially important aquatic organisms (Vasconcelos et al. 2007; Courrat et al. 2009; Hamilton et al. 2017; Toft et al. 2018). In particular, nurseries provide shelter and specific microhabitats that are crucial for the ontogenetic development of marine fishes (Lotze et al., 2006). When the integrity of nurseries is compromised, the productivity of entire fish populations can decline (Mumby et al. 2004). Marine fishes that are functionally dependent on these environments were therefore proposed to be highly valuable indicators of nursery habitat quality and health (Goode et al. 2020).

A high-resolution proxy method to investigate past environmental conditions involves examining the elemental imprint of waters onto otoliths, calcified structures in the fish's inner ear (Disspain et al. 2016). Although reconstructions of paleoenvironments through the study of fish otolith elemental composition is not without issues (Campana & Thorrold 2001; Izzo et al. 2018), otoliths are nevertheless extremely useful because the accretion of calcium carbonate occurs on a daily basis, thus trace elements from surrounding water are not metabolically reworked or resorbed after deposition (Thomas and Swearer, 2019). As a result, certain trace elements recorded in otoliths reflect the environments in which fish lived across their entire lifespan (Thomas et al. 2017). This characteristic makes otolith elemental composition an

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excellent chemical chronometer which can be used to retrospectively reconstruct spatial behavioural patterns such as fish migrations and habitat-use (Palumbi et al. 2003).

As fish move between environments of different concentrations of chemical tracers at various stages during their life, their otoliths record a continuous dataset in a two-dimensional space coordinated by various trace elements. Such a continuous dataset is equivalent to a time-series characterised by changes in the concentrations of these chemicals, and can be treated similar to a movement trajectory in time-series analysis. Behavioural Change Point Analysis (BCPA) is a methodology that can be employed to identify hidden shifts of the underlying parameters in the autocorrelation structure of a time-series, an approach which is rooted in the field of movement ecology (Gurarie et al. 2009). For example, when coupled with a clustering algorithm it can be utilised to infer changes in behavioural "states" of an animal's movement (Zhang et al. 2015). Like a movement trajectory, the time-series of chemical signatures extracted from otolith samples are temporally autocorrelated. This allows us to retrospectively position individual fish in space and time throughout its life and make inferences about nursery habitat-use patterns during its ontogeny.

Snapper *Chrysophrys auratus* is a seabream species widely distributed throughout the Pacific Ocean and one of the most abundant coastal fishes around New Zealand's North Island. Here, it has been fished extensively since the beginning of human colonisation (Leach & Davidson 2000). Individuals congregate between November and January to spawn in large numbers near well-established coastal nurseries, after which, settled juveniles migrate to structured brackish environments such as estuaries and seagrass meadows, before venturing

Fig. 1. The Hauraki Gulf showing archaeological midden and comparative modern sample sites.

back out to deeper marine waters when they have reached their first year in life (Parsons et al. 2014). Over the last few decades, the natural environment of the Hauraki Gulf, a large coastal embayment on the east coast of New Zealand's North Island, has changed significantly. Increasing sedimentation has had a particularly harmful impact on benthic ecology in the upper reaches of the gulf, and overall, the sand flats and tidal creeks in this region are deemed to be in poor ecological health (Hauraki Gulf Forum 2020; Drylie 2021). Although the importance of nearshore nurseries are being questioned in relation to the much lower than expected juvenile snapper abundance in these habitats (Parsons et al. 2020), the extent to which anthropogenic stressors have impacted the early life habitat-use of coastal snapper stocks is not well understood.

We hypothesized that if the nursery functions of nearshore environments are compromised, species functionally dependent on these ecosystems should respond by changes in their habitat-use patterns. More specifically, if at any time in the past human activities in the Hauraki Gulf have altered the quality of coastal habitats important for snapper ontogeny, then it is likely to have triggered subtle responses in migration behaviour. To test this hypothesis, we employ a time-series analysis approach that originates from the field of migration ecology. This approach allows us to for the first time compare archaeological and present-day otolith microchemistry independently of confounding factors to infer changes in juvenile habitat-use over time.

2. Methodology

2.1. Provenance of otolith assemblages

We sampled the archaeological and modern-day snapper otoliths used for this analysis from sites in the Hauraki Gulf, on the east coast of the North Island of New Zealand (Fig. 1). These sites are approximately 22 nautical miles (40 km) apart. For the archaeological middens, the Long Bay (AL) samples were radiocarbon dated using Bayesian modelling to between 1430 and 1485 CE, while the Omaha (AO) samples were dated to between 1530 and 1640 CE (Campbell et al. 2004, 2019). For more detailed descriptions of the archaeological middens and excavations see Campbell et al. (2021). For present-day comparison we acquired modern samples from as close as possible to the archaeological middens. Kawau Island (MO, 2016 CE) served as the closest modern comparison to the Omaha midden (surplus otoliths were sourced from Allen et al. 2018), while recreationally caught snapper outside of the current Long Bay marine reserve (ML, 2020 CE) provided samples to compare with the Long Bay midden. In total, we acquired 10 otoliths for each location (n = 40).

2.2. Trace element analysis and data processing

Laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) analysis was conducted to measure Barium (^{138}Ba) and Strontium (^{88}Sr) compositions along an ablation path though the core to the proximal tip of each otolith (Fig. 2). For each of the four sites, ten

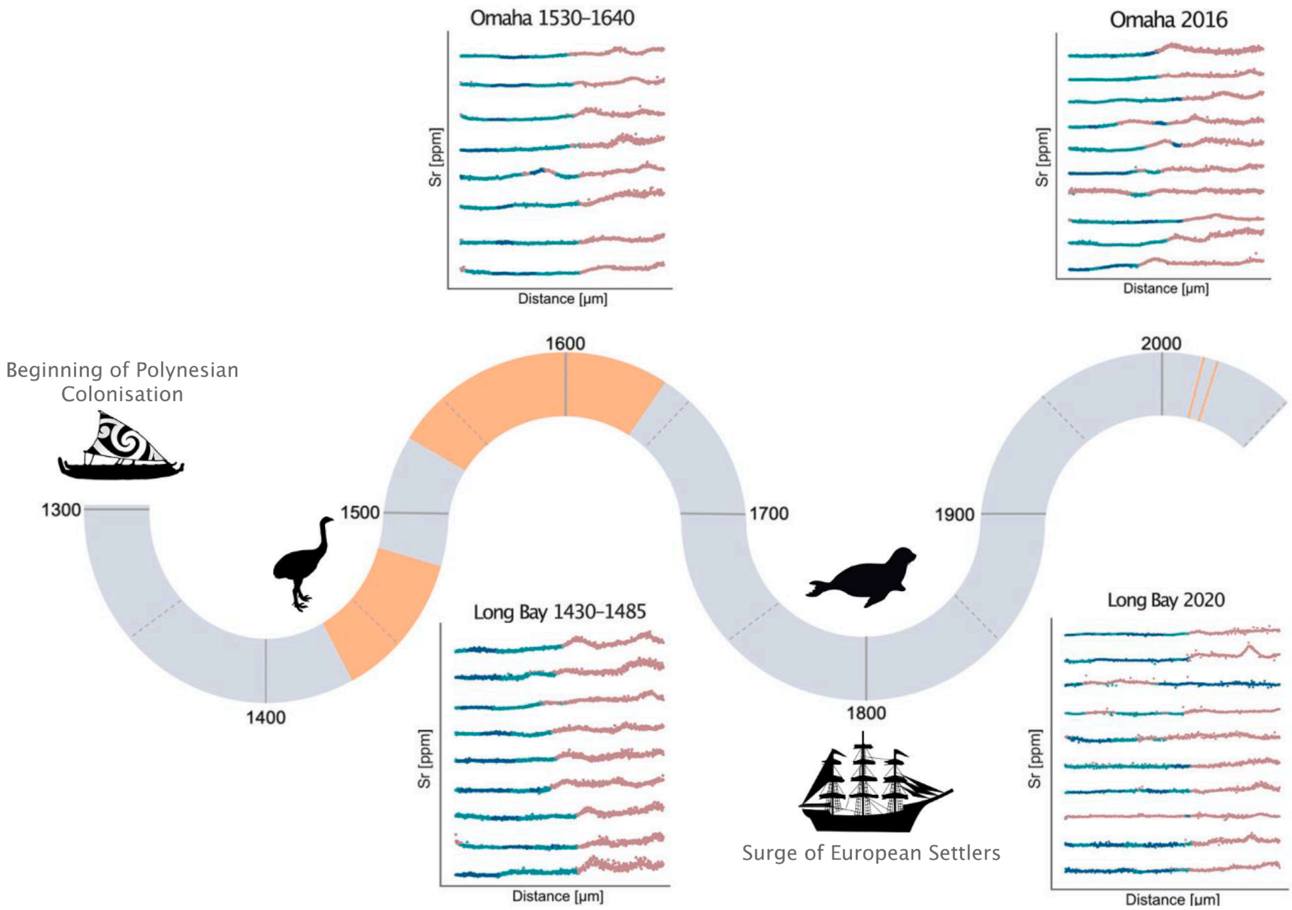

Fig. 2. Timeline illustration of sample ages (denoted in orange) and important human activities in New Zealand, including extinction of the Moa and extirpation of Seals from their natural ranges. Strontium (Sr) concentration along laser-ablated transects (1010 μm length) for each sampled New Zealand snapper *Chrysophrys auratus* otolith, represented by a curve, e.g., there are nine individual samples from Long Bay midden. Colours represent habitat types (Estuarine = Green, Riverine = Blue, Marine = Light Red) as derived by behavioural change point analysis with k-means clustering through changing trajectories in barium and strontium concentrations along the ablation path. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sagittal otoliths were transverse-sectioned and then mounted on a geological slide for laser ablation. Instrumentation was an Applied Spectroscopy RESOlution M−50 laser ablation system powered by a Coherent 193 nm ArF excimer laser and an Agilent 7900 quadrupole ICP-MS, located in the Centre for Trace Element Analysis in the Department of Chemistry, University of Otago (Dunedin, New Zealand).

Slides with mounted otoliths were placed in an ablation cell in an atmosphere of pure helium to minimize any possibilities of experiencing re-condensation of ablated materials and elemental fractionations (Eggins et al. 1998). The video imaging system had suitable magnification to identify the core and was used for mapping transect pathways. Prior to obtaining measurements the 75 μm diameter transects were pre-ablated from core to the edge of the otolith to remove surface contaminants. The spot size employed for the transects was selected as a compromise between spatial sensitivity and detection power of the overall system (Taddese et al. 2019). The ablation with a laser firing frequency of 10 Hz and an on-sample fluence of 2.5 J/cm^2 was operated along the pre-ablated transects with the sample stage moving at 10 μm/s, for determining elemental concentrations in correspondence to life cycle of the fish. The ICP-MS instrument was tuned to minimize oxide formation, double charge formation and mass fractionation. Signal intensities of Ba and Sr were maximized after carrying out gas tuning processes on software-controlled gas flows of He and N_2 along with ICP-MS controlled Ar. Standards were run regularly with NIST 610, NIST 612 and MACS-3 used for instrument calibration, verification and matrix matched quality control respectively. Data reduction of the raw count data to molar ratios (element of interest/Ca) was conducted using Iolite 3.63 (School of Earth Sciences, University of Melbourne) which subtracts gas backgrounds and corrects for any drift in instrument response (Paton et al. 2011). Accuracy and precision of the analyses were assessed using NIST 612 and the MACS-3 otolith reference material (United States Geological Survey - USGS). For the glass control precision was excellent RSD $< 3\%$ and the accuracy was within ± 5% for all elements. For the otolith reference material precision was better than 5% with recoveries percentages of 97% and 96% for Sr and Ba, respectively.

2.3. *Time-series analysis*

Three archaeological otoliths (1 AL, 2 AO) were too contaminated (presumably from fire) to be useful for analysis, and were thus disregarded. The shortest readable ablation segment from core to the edge of an otolith was 1010 μm long. This was for a two year-old snapper. Since the statistical approach only allowed for comparisons of segments of equal parallel length, we adopted an otolith core-to-edge distance of '1010 μm' as the laser ablation data length for all 37 samples.

We first identified changes in autocorrelation structures within the standardised Ba and Sr concentrations at the smallest temporal scale possible for BCPA (window size = 30). Segments of trajectories between 'change points' identified by BCPA hereon are referred to as 'bouts'. The means of Ba and Sr of output metrics were calculated and used as the units for k-means clustering analysis to further classify behavioural states. Prior to k-means clustering, the number of distinct states for the otolith time-series were determined through within-group sums of squares and serial classification of bouts, following the hierarchical cluster method of Krzanowski & Lai (1988). Individual bouts of same-state behaviour were classified into one of three mutually exclusive states based on combinations of Ba and Sr values, using the k-means clustering algorithm of Hartigan & Wong (1979) in the statistical software R (R Core Team) with the packages 'cluster' (Maechler et al. 2019). Thus, bouts identified by BCPA were assigned to behavioural states based on similarities of 'movement' patterns in the two-dimensional space of Ba and Sr concentrations. The time shares, represented by the distance on the otolith ablation transect that the snapper spent in each state, and the number of changes between states that occurred throughout the sampled transect were then calculated.

To assess the similarities and difference of the sequence of states in the otoliths both within and between assemblages (i.e. AO, MO, AL, ML), the proportion of individuals in each state at all distances measured on the otolith were calculated. For each assemblage, a new time-series was created for visual comparison of consistency in the behavioural sequences among individuals, representing by proportions of individual in each of the three states. If the timing for the appearance of a certain state was consistent among the individuals within an assemblage, then the proportion of this state will be high at that transect distance when the state occurs.

To describe the rate of transitions between the three states, we counted the changes from one behaviour state to the other for each individual transect. More specifically, we calculated not only the total transition rate of all three states, but also the transition rates for each pair separately. We compared the proportion of transect length reflecting each state and the mean values of state transition rates between archaeological and modern samples using Welch's Heteroscedastic F Test.

3. Results

Application of BCPA with k-means clustering modelling of otolith samples indicated that most snapper experienced three distinct "behavioural clusters" over the period represented by the 1010 μm long ablation transects (Supplementary Figs. 1 and 2). By calculating the mean values within these behavioural clusters, we were able to reconstruct three distinct aquatic habitat types experienced by snapper according to the diverging mean concentrations of Ba and Sr: *Riverine*: High Ba (1,717 ± 5 ppm) and low Sr (18.2 ± 0.3 ppm); *Estuarine*: Low Ba (8.01 ± 0.11 ppm) and medium Sr (1,767 ± 4 ppm); *Marine*: Low Ba (9.38 ± 0.13 ppm) and high Sr (2,603 ± 6 ppm). Henceforth we will consequently speak of "habitat types" instead of "behavioural clusters".

There was high variance within and between assemblages with regards to the succession of habitat types along the laser ablated transects. Archaeological snapper otoliths (AL and AM) showed a cyclic succession of Riverine and Estuarine habitat types along the laser ablation transect. In contrast, the distribution of these habitat types seemed to be rather random in the otolith transects of present-day snapper. At 600 μm on the laser ablation path, which when measured on all otoliths fell on the first annual ring (i.e., age one), all (except one present-day snapper) otoliths exhibited a purely Marine habitat type signature (Fig. 3).

In MO snapper otoliths the changing concentrations of Ba and Sr corresponded to a 57.60 ± 4.55% (Mean ± SD) Marine habitat type, relative to the analysed laser ablated transect length. This is higher when compared to AO otoliths, which exhibited a mean Marine habitat type occurrence of 44.87 ± 0.99% relative to transect length. Furthermore, otoliths sampled from both archaeological sites exhibited a higher proportion of the Estuarine habitat type (AL 30.89 ± 3.10%; AO 42.0 ± 2.20%) when compared to their present-day conspecifics (ML 19.80 ± 4.58%; MO 31.50 ± 5.51%). The proportion of the Marine habitat type per transect length was significantly higher in MO than in AO otoliths (Welch's Heteroscedastic F Test, $F_{(1,\ 9.84)} = 7.46$, $p = 0.02$).

The overall mean number of transitions between the three habitat types differed significantly across all assemblages as identified by the model (ANOVA, $F_{(3,\ 33)} = 9.45$, $p < 0.001$). The total number of transitions between habitats was highest in the transects of ML otoliths (31.8 ± 3.38 transitions transect^{-1}), and differed significantly from the ones of the other three assemblages (Tukey HSD, all $p < 0.001$). We recorded the second highest transition number within transects of MO otoliths (15.7 ± 3.13 transitions transect^{-1}), followed by AL (15.11 ± 2.80 transitions transect^{-1}), and AO (12.25 ± 1.58 transitions transect^{-1}). ML otoliths exhibited significantly more transitions between Estuarine and Riverine (Welch's Heteroscedastic F Test, $F_{(1,\ 13.9)} = 4.71$, $p < 0.05$) as well as between Riverine and Marine environments when compared to their conspecifics from archaeological middens (Welch's Heteroscedastic F Test, $F_{(1,\ 10.2)} = 9.86$, $p = 0.01$).

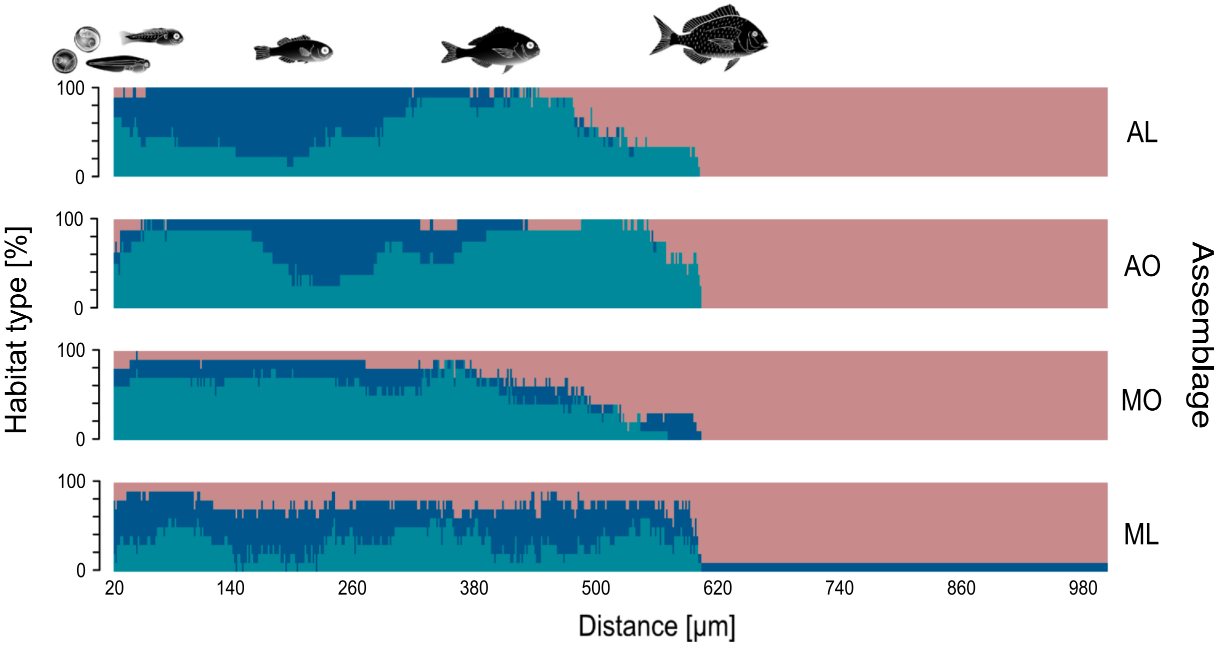

Fig. 3. The mean proportion of habitat types (Riverine = Blue, Estuarine = Green, Marine = Light Red) identified by behavioural change point analysis with k-means clustering against the laser-ablated distance (core to edge) on the otoliths of New Zealand snapper *Chrysophrys auratus* by assemblage: AL = Archaeological Long Bay (1430 – 1485 CE), AO = Archaeological Omaha (1530 – 1640 CE), MO = Present-day Omaha (2016 CE), ML = Present-day Long Bay (2020 CE). For reference, we also show drawings of snapper early life stages during ontogeny. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

The degradation of critical nursery habitats from anthropogenic factors is a major concern for fisheries management and conservation ecology. Therefore, the development of indicators to assess the quality of habitats critical for survival of marine resources is now more urgent than ever. The methodology we employed in this study has significantly enhanced the utility of otolith chemical profiles in making inferences about past and present nursery habitat quality.

Because the incorporation of Ba and Sr into fish otoliths are strongly influenced by climatic variations and physiological factors (Campana & Thorrold 2001; Izzo et al. 2018), we had to overcome this high inter-individual variability, especially in our archaeological samples that are more than a century apart in age. Using BCPA with k-means clustering, we addressed this issue by considering only concerted changes (rather than absolute values) in Ba and Sr. It is well established that relative concentrations of otolith Ba and Sr can be used to reconstruct fish life-history (Thomas et al. 2017; Thomas and Swearer, 2019). Higher Ba concentrations are generally a reflection of riverine input through terrestrial runoff (Montaggioni & Braithwaite 2009), therefore, freshwater residency of fish can be inferred from otolith Ba concentrations (Elsdon & Gillanders 2005). Higher Sr concentrations are an accurate proxy of oceanic water residency as Sr is better absorbed at higher salinities (Secor & Rooker 2000; de Vries et al. 2005; Macdonald & Crook 2010). Our identification of three habitat types (Riverine, Estuarine, Marine) matched exceptionally well with the brackish and marine aquatic environments expected to be experienced by snappers during their sampled lifespan. The approach thus allowed us to retroactively place individual fish in a specific aquatic milieu at a specific time during ontogeny - independent of climatic and physiological disrupting factors.

Population productivity is often highly dependent on the connectivity of juvenile subpopulations that utilize coastal nurseries (Fodrie et al. 2009). Furthermore, connectivity and well-timed shifts between habitats during ontogeny are generally beneficial for fish as growth and survival rates in early life stages are closely linked to predation risk and food availability, both of which are influenced by being at the right place at the right time during ontogeny (Sheaves et al. 2015). Juvenile Hauraki Gulf snapper are considered to be highly dependent on brackish near shore habitats (Parsons et al. 2014). Accordingly, historic snapper sampled from both archaeological sites spent most of their early life in a habitat we characterized as “Estuarine”. In contrast, snapper from present-day assemblages spent on average more of their early life in the Marine habitat type than in brackish environments.

Interruptions to their complex life cycle due to a lack of suitable nurseries will inevitably affect the overall fitness of the current Hauraki Gulf snapper population (Fodrie et al. 2009). Fig. 2 informs us that over several centuries, historical individuals showed well-synchronised movement patterns between Riverine, Estuarine and Marine habitats. In contrast, present-day snapper switched chaotically between these environments. It is therefore evident that early habitat movement patterns of snapper in the Hauraki Gulf have changed dramatically at some stage over the past four centuries. The higher total number of transitions between habitats in the ML snapper is somewhat perplexing, as it is not reflected in the MO samples – and especially since no significant differences in the number of transitions between individual environments were found between the two contemporary sites. This could be due to a range of present-day differences in anthropogenic stressors between the two sites, including the intensity of coastal development in Long Bay compared to Omaha and its proximity to Auckland’s densely populated urban regions. The observed lack of time spent in nursery environments and higher transition rates between habitats likely confer slower growth and condition, higher mortality, and ultimately lower recruitment chances to present-day individuals (Whitfield 2017).

New Zealand’s landscape has changed dramatically since the beginning of human settlement (ca. 1280 CE) due to extensive forest clearance for the purposes of horticulture (McWethy et al. 2014). Further, snapper have been dominant target fish for Māori with remains found in archaeological middens accounting for 50% or more of total fish catch (Leach & Davidson 2000). Still, otoliths of both historical assemblages in this study exhibited highly consistent and predictable movements between early life habitats. However, without the availability of otoliths from before human colonisation, we cannot conclusively determine whether Māori really had no impact on the habitat-use of historical snapper populations. The lack of snapper residence in Hauraki Gulf nearshore habitats by present-day individuals, however, can be linked to modern land-based stressors that have contributed significantly to the reduction in critical nursery habitats (Parsons et al. 2014; 2020). We, therefore, hold modern human disruptions of coastal environments and nurseries accountable for the changes in snapper habitat-use patterns observed in this study.

High resolution assessment of interactions between fish and habitats through otolith microchemistry coupled with behavioural change point analysis provides detailed insight into early life history and ecosystem dynamics. The novel investigative approach adopted in this study can both serve as a useful proxy of examining ancient habitat quality, and may also be used to develop indicators to assess the success of modern habitat reconstruction measures. What this study has shown is the clear association and dependency of snapper in the Hauraki Gulf on nursery habitats in the past. We therefore place high value on the conservation of these critical habitats and advocate for their concerted management.

5. Data availability statement

All data and scripts used for analysis have been deposited in a publicly accessible GitHub repository (https://jzha336.github.io/Fish-nearshore-habitat-use/) and are also available on Zenodo (http://doi.org/10.5281/zenodo.5518872).

CRediT authorship contribution statement

Conceptualization: A.S., M.C., R.W., K.W. and J.L., Data curation: J. L., J.Z., K.W., and A.S., Formal analysis: J.Z. and J.L., Funding acquisition: R.W. and A.S., Methodology: M.R., J.Z., and J.L., Project administration: R.W and A.S., Validation: J.L., J.Z., M.R., and A.S., Visualization: J.Z., J.L., M.C., Writing - original draft: JL. and A.S., Writing - review & editing: A.S., J.Z., M.C., R.W., H.A., M.R., K.W., and J.L

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108225.

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