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Evaluating tools for the spatial management of fisheries

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Abstract

1. The ability to define the spatial dynamics of fish stocks is critical to fisheries management. Combating illegal, unreported and unregulated fishing and the regulation of area-based management through physical patrols and port side controls are growing areas of management attention. Augmenting the existing approaches to fisheries management with forensic techniques has the potential to increase compliance and enforcement success rates.
2. We tested the accuracy of three techniques (genotyping, otolith microchemistry and morphometrics) that can be used to identify geographic origin. We used fish caught from three fishing grounds, separated by a minimum of 5 km and a maximum of 60 km, to test the accuracy of these approaches at relatively small spatial scales.
3. Using nearest-neighbour analyses, morphometric analysis was the most accurate (79.5%) in assigning individual fish to their fishing ground of origin. Neither otolith microchemistry (54.0%) or genetic analyses (52.4%) had sufficient accuracy at the spatial scales we examined.
4. *Synthesis and applications.* The combination of accuracy and minimal resource requirements make morphometric analysis a promising tool for assessing compliance with area-based fishing restrictions at the scale of kilometres. Furthermore, this approach has promising application, in small-scale fisheries through to community-based management approaches where technical and financial resources are limited.

KEYWORDS

fisheries tools, fishing restrictions, genetics, morphometrics, *Ocyurus chrysurus*, otoliths, small-scale fisheries, spatial management

1 | INTRODUCTION

Fisheries management aims to manage exploited fish populations, based on estimating maximum sustainable yield or maximum economic yield, and setting catch limits around these targets to maximize catches and profits (Christensen, 2010). The financial investment and technical expertise required to conduct fish stock assessments is significant as are the resources required to implement harvest control rules and effectively limit total allowable catch. Therefore, the majority of the world's fish stocks remain unassessed and largely unmanaged. To address declines in fish stocks, managers have a suite of input and output controls over fishing activities, including limiting entry, empirical harvest control rules and area-based management approaches, such as marine

protected areas (MPA's), no-take zones (NTZ's) and territorial user rights fisheries (TURFs; Selig et al., 2017). MPA's and NTZ's aim to reduce or eliminate fishing pressure across defined areas, which allow fish populations to increase and then potentially spill-over into surrounding waters to replenish the exploited areas and/or populations (Gaines, White, Carr, & Palumbi, 2010). TURF's link area-based management to explicit access rights of a geographically defined fishing area or areas to which an individual fisher or fishing community have been granted exclusive access (Nguyen, Quynh, Schilizzi, Hailu, & Iftekhar, 2017). A combination of increased compliance and effective enforcement of regulations is required to effectively manage MPA's, NTZ's and TURF's and combat illegal, unreported and unregulated (IUU) fishing. Current top-down enforcement strategies focus on physical patrols, onboard monitoring and port side measures. However, these can be prohibitively expensive to conduct routinely (Arias, Pressley, Jones, Alvarez-Romero, & Cinner, 2014; Dhanjal-Adams, Mustin, Possingham, & Fuller, 2016). Additionally, fishers have been observed to alter their behaviour when they know patrols are in operation or when enforcement vessels come into view, resulting in diminishing returns of physical patrols (Dhanjal-Adams et al., 2016). Shortfalls in enforcement personnel and financial stability have been identified as primary factors that undermine the effectiveness of area-based management (Gill et al., 2017). Alternative cost-effective tools are required to help improve management efficacy. We evaluated the potential of three approaches currently used to identify the geographic origin of individual fish; microsatellite genetic analysis, otolith elemental analysis, and morphometric analysis, all of which have successfully been used to delineate fish stocks (Cadrin, 2000). The ability to assign individual fish to their fishing ground of origin using forensic methods could provide evidence to either confirm compliance or identify fishing infractions, e.g. fishing within an NTZ or in an area outside a fisher's designated fishing area, providing an additional tool to fisheries managers to verify origin or identify illegal fishing activity. Additionally, the ability to independently verify the origin of landed catch is key for fisheries management. Fishing grounds are often shared among multiple communities, each of which have individual names for their fishing ground (personal observations), therefore local and regional management plans may underestimate fishing pressure at fishing grounds. Here we examine three methods for identifying origin and compared them in terms of accuracy, cost, time versus technical difficulty and applicability at small spatial scales—kilometres to tens of kilometres.

1.1 | Genetic analysis

Previous studies have used this approach at large spatial scales (10s–100s kilometres). However, many reserves and community-based management approaches often established under a TURF system, and managed access initiatives operate at smaller scales (smaller than 10s km). Many of these fisheries are also relatively low value and any management operates under severe resource constraints. Genetics analysis uses the variation of allele frequencies within and among sample groups to identify stocks or populations. Microsatellites (simple sequence repeats) produce comparable estimates of population structure to other molecular markers (Nybom, 2004; Powell et al., 1996). Microsatellites offer some specific advantages over other markers, which include the selective neutrality of loci (Meloni, Albanese, Ravassard, Treilhou, & Mallet, 1998), and very high levels of allelic polymorphism (Bhargava & Fuentes, 2010). High levels of allelic polymorphism is useful when assessing species that exhibit very low levels of variation (Bhargava & Fuentes, 2010), and thus may be more indicative when sampling at fine spatial scales (less than 100 km). Microsatellite markers have important applications in fisheries management and conservation strategies (Abdul-Muneer, 2014) and have successfully been used to discriminate fish stocks at spatial scales varying from 100s to 1,000s km (e.g. Gold, Saillant, Ebelt, & Lem, 2009; Saillant, Renshaw, Cummings, & Gold, 2012).

1.2 | Microchemistry

Otoliths provide an archive of environmental conditions of fish habitats through elemental deposits. Otoliths are acellular and metabolically inert; elements constantly accrete onto the growing (outer) surface from surrounding waters throughout the life cycle of the fish, and dietary derived inorganic elements are minimal (Hoff & Fuiman, 1995). The accreted elements provide a permanent record of the environment which they inhabit (Campana & Neilson, 1985), and can be used to identify and classify individuals to specific stocks or populations. Otolith microchemistry can be analysed through laser ablation inductively coupled plasma mass spectrometry, which is costly and time-consuming. Otolith element signatures have successfully distinguished fish stocks across different geographies and spatial scales of 10s–1,000s km (e.g. Bickford & Hannigan, 2005; Sohn, Kang, & Kim, 2005; Wells, Rooker, & Prince, 2010).

1.3 | Morphometrics

Morphometric analysis uses a series of standard anatomical features to create a truss network, which provides a representation of an individual fish's body shape using interlandmark distances (Strauss & Bookstein, 1982). Several environmental variables can influence fish morphology, including diet (Wimberger, 1992), water temperature (Lõhmus, Sundström, Björklund, & Devlin, 2010), predation pressure (Scharnweber et al., 2013), habitat structure (Willis, Winemiller, & Lopez-Fernandez, 2005), depth (Mwanja et al., 2011) and water currents (Franssen, Stewart, & Schaefer, 2013). These environmental differences can vary geographically. Morphometric analyses have been used successfully to discriminate fish populations at spatial scales of 100s–1,000s km (e.g. Turan, 2004; Vasconcellos, Vianna, Paiva, Schama, & Sole-Cava, 2008).

Here, we compared the accuracy of genetic, otolith and morphometric analyses at assigning individual fish to three fishing grounds separated by 5–60 km, using the yellowtail snapper (*Ocyurus chrysurus*) as a model species. Yellowtail snapper is an important fishery within the Wider Caribbean especially for small-scale fisheries

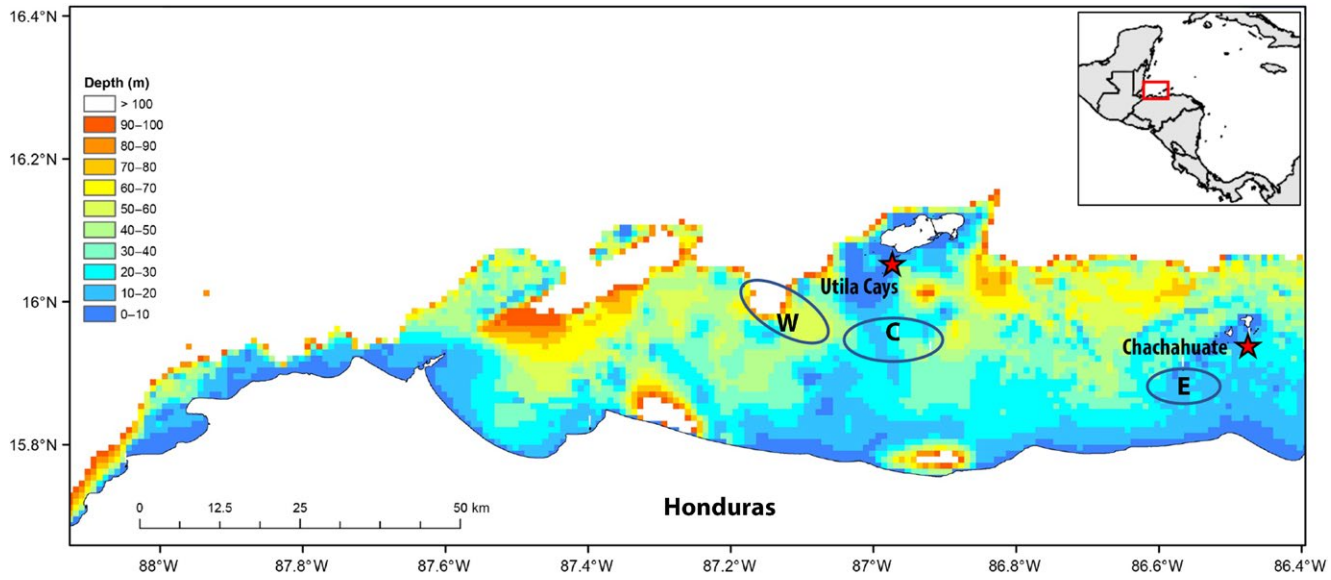

FIGURE 1 Map of the Honduran north shore, highlighting the fishing communities of the Utila Cays and Chachahuate, Cayos Cochinos, and the eastern (E), central (C) and western (W) fishing grounds. Colour is the depth profile produced from an interpolation of Gebco data (Bathymetric map created by Iliana Chollett). Inset map is of Central America, highlighting area of interest in this study

(Claro, Sadovy de Mitcheson, Lindeman, & Garcia-Cagide, 2009). Our model fishery was the Honduran small-scale fishery, where yellowtail snapper contributes substantially to the total catch of local fishing communities (Box & Canty, 2010).

2 | MATERIALS AND METHODS

Our study was based on samples from three distinct fishing grounds, separated by 5–60 km, and fished by communities based on the Utila Cays (N16.06°; W086.96°) and Chachahuate (N15.96°; W086.47°), Honduras (Figure 1). A total of 149 individuals, 93 adults (≥250 mm fork length [FL]) and 56 juveniles (150–249 mm FL) from the fishery, caught by local fishers were collected (Summary statistics in Figure 2). Sampling was conducted from August 2011 to March 2012, and fish were caught using hook and line and the fishing ground georeferenced. For complete descriptions of methodologies of genetic and otolith analyses see Appendix S1.

2.1 | Fishing grounds

The eastern fishing ground is part of the Chachahuate small-scale fishery, located within the Cayos Cochinos archipelago, and the central and western fishing grounds are part of the Utila Cays small-scale fishery (Figure 1). Each of the fishing grounds are associated with different bathymetries, and terrestrial and oceanic inputs (Table 1). We assume these will have a differential effect on otolith element signatures and morphometrics of fish found within each of the fishing grounds. Despite the close proximity of two of the fishing grounds (5 km), we assume that deep water (60–70 m) separating the shallow banks would preclude the mixing of individuals across the

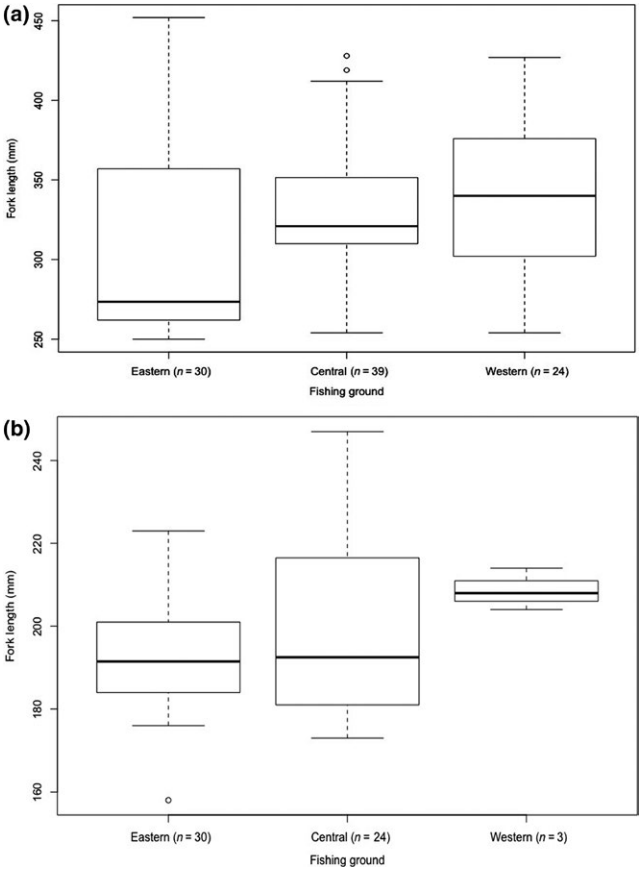

FIGURE 2 Summary statistics of adult (a) and juvenile (b) yellowtail snapper used in the testing of genetic, otolith microchemistry and morphometric analyses

different fishing grounds, due to the association of yellowtail snapper with reef habitats.

TABLE 1 Abiotic characteristics of the three fishing grounds within the Honduran small-scale fishery

	Fishing grounds		
	Eastern	Central	Western
Depth range (m)	1–30	10–60	60–100
Depth profile[a]	Shallow	Medium	Deep
Distance to mainland (km)	12.7	19.7	28.6
Terrestrial input[a]	High	Medium	Low
Distance to continental shelf drop-off (km)	15.1	16.0	0.0
Oceanic input[a]	Medium	Medium	High

[a]Relative scales in respect to characteristics of the three fishing grounds.

2.2 | Genetic analysis

All 149 fish were used in the genetic analyses. A 1 cm^2 caudal fin clip was taken from each individual and stored in alcohol at −20°C prior to DNA extraction, which was conducted using a Qiagen DNeasy Blood and Tissue Kit. We used 15 previously described microsatellite markers; seven for yellowtail snapper (*och2*, *och4*, *och6*, *och9*, *och10*, *och13*, *och14*), five for lane snapper (*lsy2*, *lsy5*, *lsy7*, *lsy11*, *lsy13*) and three for mutton snapper (*lan3*, *lan5*, *lan11*), all of which have been validated as polymorphic and easy to score for yellowtail snapper (Renshaw, Karlsson, & Gold, 2007), we used the scored genotypes for statistical analyses.

2.3 | Otolith elemental analysis

Only adults (≥250 mm FL) were used in the otolith elemental analyses. Only 71 individual otoliths were analysed due to breakages during sectioning and the cost associated with laser ablation. Otoliths were sent to the British Antarctic Survey for sectioning prior to elemental analysis at the British Geological Society. A total of 15 elements: strontium, manganese, barium, lithium, boron, sodium, magnesium, potassium, copper, tin, lead, aluminium, iron, zinc and rubidium, were measured, with ^{42}Ca used as the internal standard to correct for ablation volume differences. The elemental signatures of the outer two ablations, which we consider to be the most recent accretions by the adult fish, produce a mean elemental ratio which comprised the signature for each otolith.

2.4 | Morphometric analysis

Only adults were used in the morphometric analyses (n = 93). Juveniles were not included in the morphometric analysis due to allometric growth differences (Huxley, 1932). Additionally, individuals that have not fully recruited to the fishing ground would not have been subjected to the environmental conditions that influence fish morphology, and therefore may not have a true signal for the ground.

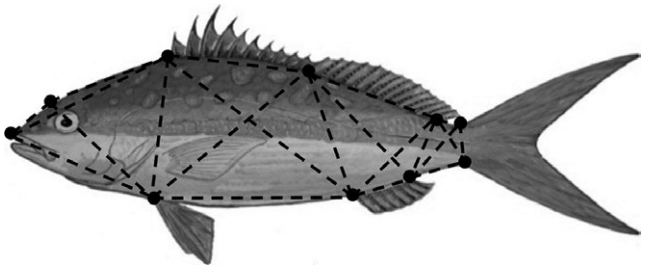

FIGURE 3 Ten morphometric truss points overlaid on a yellowtail snapper used for the canonical correspondence analysis (adapted from Strauss & Bookstein, 1982; portrait of yellowtail snapper by Javier Maradiaga)

Ten truss points, which provided a truss network with 21 discrete measurements, were used in the morphometric analysis (Strauss & Bookstein, 1982; Figure 3). Measurements were taken with callipers of 1.0 mm precision, using methods adapted from Vasconcellos et al. (2008). Each measurement was transformed to a proportion of the total length of the individual to remove bias of size differences, making interlandmark measurements directly comparable among individuals.

2.5 | Statistical analysis

We conducted pairwise permutational analyses of variance (PERMANOVA) tests between the fishing grounds using the ADONIS function in the R-package VEGAN, using 999 permutations. The PERMANOVA test does not assume that the data are normally distributed. We conducted nearest neighbour analyses, a nonparametric test, on microsatellite genotypes, otolith elemental signatures and morphometric truss ratios, using the R-package kknn. Data were normalized along a scale of 0–1, where 0 is the minimum value and 1 the maximum value of a variable, to reduce bias associated with large numbers. Original K values were assigned based on the square root of the number of observations. However, once the model was run an optimal K value was provided by the model, this value was subsequently selected for each permutation of the model (Table 2). Each model was trained using 10% of the associated dataset, which was randomly selected for each of the 100 iterations of the model, from which we calculated a mean assignment accuracy for each of the tools.

Sample sizes were relatively small, particularly for otolith analyses (n = 71). However, our sample sizes are comparable with those for discrete sampling sites in similar studies that used microsatellite genetic analyses (e.g. Davies, Gosling, Was, Brophy, & Tysklind, 2011) and otolith analyses (e.g. Carlson, Fincel, & Graeb, 2016). Our sample size conformed to minimum samples sizes recommended for morphometric analyses (Cardini, Seetah, & Barker, 2015; Kocovsky, Adams, & Bronte, 2009). We therefore consider our sample sizes sufficient to provide robust statistical analyses.

2.6 | Tool comparisons

We tabulated the different steps required to get from initial sampling to data interpretation for each of the tools we tested. We

TABLE 2 Management tool nearest neighbour analysis parameters and assignment accuracies to their correct fishing ground

Management tool	*N*	Initial K	Optimal K	Assignment accuracy		
				Minimum	Maximum	Mean[a]
Microsatellite genotypes	149	11	7	26.7%	80.0%	52.4%
Otolith chemical signatures	71	8	5	12.5%	87.5%	54.0%
Morphometric truss ratios	93	9	8	50.0%	100.0%	79.5%

[a]Mean is calculated from 100 permutations.

constructed a relative scale for the expertise, a time requirement and a cost per sample to conduct each of the analyses, based on obtaining initial samples (i.e. genetic material, otoliths, and truss measurements) through to data interpretation (usable data outputs). We assumed that fishers would provide access to fish for genetic and morphometric measurements free of charge, while due to the otolith extraction process the purchase of individual fish is required for otolith analyses. For each of the analyses we reviewed the costs associated for each analysis that are required to fulfil each procedural step. However, we did not include the costs of basic equipment (e.g. thermocycler, mass spectrometer, calipers), nor did we include estimates of labour costs.

3 | RESULTS

Of the three techniques morphometric analysis was the most accurate. Pairwise PERMANOVA analyses of morphometric truss ratios identified highly significant differences between all pairs of fishing grounds (eastern and central, $F = 10.29$, $p = 0.001$; eastern and western, $F = 6.63$, $p = 0.001$; central and western, $F = 9.37$, $p = 0.001$). Significant differences of genotypes were observed between all three fishing grounds (eastern and central, $F = 4.06$, $p = 0.014$; eastern and western, $F = 5.46$, $p = 0.009$; central and western, $F = 5.31$, $p = 0.004$). With otolith microchemistry, significant differences were only observed between central and western fishing grounds ($F = 5.67$, $p = 0.011$), and no significant differences were observed between central and eastern ($F = 1.17$, $p = 0.31$) or eastern and western fishing grounds ($F = 1.58$, $p = 0.183$; Table 3).

Nearest neighbour assignment accuracy was greatest for morphometric truss ratios, with a mean accuracy of 79.5%. The mean assignment accuracies for otolith element signatures and microsatellite genotypes were 54.0% and 52.4%, respectively (Table 2).

Morphometric truss ratio analysis requires a lower level of technical expertise, has the fastest turnaround time from data collection to interpretation, and the lowest cost per sample. Microsatellite genotyping and otolith chemical signature analyses require high levels of technical expertise and an average turnaround time of 2 months from data collection to data interpretation. Of these two laboratory analyses-based approaches microsatellite genotyping was cheaper than otolith chemical signature analysis (Table 4).

TABLE 3 Fishing ground pairwise PERMANOVA analyses of microsatellite alleles, otolith chemistry signatures and morphometric truss ratios

	F-static	*p*
Microsatellite genotypes ($n = 149$)		
Eastern–Central	4.06	**0.016**
Eastern–Western	5.46	**0.009**
Central–Western	5.31	**0.004**
Otolith chemical signatures ($n = 71$)		
Eastern–Central	1.58	0.183
Eastern–Western	1.17	0.310
Central–Western	5.67	**0.011**
Morphometric truss ratios ($n = 93$)		
Eastern–Central	10.29	**0.001**
Eastern–Western	6.63	**0.001**
Central–Western	9.37	**0.001**

Significant results are highlighted in bold.

4 | DISCUSSION

We found that measuring the truss points of a fish and using those to provide a morphometric profile provided the highest accuracy of assigning individual fish to their fishing ground of origin (79.5%), at spatial scales of 5–60 km compared with laboratory-based microchemistry or genetic approaches. Importantly, measuring fish post capture has low cost other than labour, with no specialized equipment or installations required. Results are available within a day, requiring a medium level of technical expertise and analyses. The low cost and high accuracy of morphometric analyses make it an appropriate method for use by fisheries managers, and also accessible to management groups focused on low value, or community-based fisheries. In addition to minimal equipment requirements, data analyses are simple and the short turnaround time from sampling to results, make morphometric nearest neighbour analyses a powerful tool and relatively easy to adopt. Forensic methods can augment physical patrols, with sampling possible at fish landing sites or at sea. To improve the accuracy of the tool a greater number of individuals should be used to provide the baseline morphometric signature of each fishing ground. Based on the current accuracy level, morphometric analysis is best paired with physical patrols, the tool can

TABLE 4 Processes required for each of the three analyses tested, including level of expertise and time required to conduct each analysis and a typical cost per sample

Processes	Microsatellite genotyping	Otolith chemical signatures	Morphometric truss ratios
1	Tissue collection	Otolith removal	Fish measurements
2	DNA extraction	Sectioning and mounting	Data analysis
3	PCR reactions	Laser ablation	Data interpretation
4	Sequencing	Data analysis	
5	Data analysis	Data interpretation	
6	Data interpretation		
Technical expertise and specialized equipment	High	High	Medium
Time requirement	2 months	2 months	Hours
Typical cost per sample[a]	US$ 20	US$ 35	US$ 0

[a]Costs were based on processing costs only, i.e. reagents and costs of running specific equipment. The purchase of any specialized equipment and/or labour was not included in the cost estimate.

be used to support in situ observations of fishing infractions. While tested on the yellowtail snapper, there is the potential for morphometric analyses to be appropriate for other fisheries, for example groupers (Serranidae), snappers (Lutjanidae), grunts (Haemulidae) and spiny lobsters (Palinuridae). However, applicability of this methodology to species within these families requires explicit testing. An important caveat is morphometric analyses is not a "one size fits all" management tool. It may not be a useful tool for fish species with large home ranges, low residency rates or in regions with homogeneous environmental conditions. However, the potential for morphometric analyses to be a useful management for species with high residency times and in areas where the spatial unit of management is tens of kilometres.

Otolith element signatures and microsatellite genotypes assignment accuracies were low (54.0% and 52.4% respectively). Significant genetic differences were observed between the three grounds. However, these differences were not sufficient to accurately assign individuals to their fishing ground of origin. Significant differences in otolith element signatures were only observed between central and west fishing grounds. Fishing ground assignment accuracy for otolith measures were slightly greater than for the genetic analyses. However, the range of assignment accuracy was highly variable. We therefore do not consider otolith element signatures and microsatellite genotypes suitable tools to assist in fisheries management for this species at these spatial scales. Assignment accuracy could be improved by the analysis of additional elements for otolith element signatures, testing genomic analyses (single-nucleotide polymorphisms), and increasing sample size. Additionally, pairwise analyses of genetic, otolith and morphometric analyses could have increased assignment accuracy. However, the high costs of laboratory-based tools and the slow turnaround time from sample collection to final analysis reduces the utility of both otolith and genetic analyses for fisheries managers with limited resources and therefore the adoption of the management tool. Nevertheless, both genetic and otolith analyses have important roles in fisheries management (e.g. Ferguson, Ward, & Gillanders, 2011; Truelove et al., 2017). None of the tools examined in this study are stand-alone tools, they constitute options that need to be incorporated where appropriate into fisheries management and monitoring strategies.

Our findings suggest the presence of three distinct body shapes of yellowtail snapper, each distinct to one of the three fishing grounds and detectable over small spatial scales (5–60 km). Our results do not, however, show where the boundaries between these differences occur or explain causation. Vasconcellos et al. (2008) had similar findings within the yellowtail snapper fisheries of Brazil, but at larger scales. In their study, morphometric analyses differentiated yellowtail snapper among four areas separated by hundreds of kilometres where genetic analyses lacked discriminatory power. We hypothesize that the environmental conditions at each of the three fishing grounds in our study influenced the body shape of individuals which provides additional evidence of a limited home range of yellowtail snapper (Farmer & Ault, 2011). Medina, Brêthes, and Sévigny (2008) identified morphometric differences in the African hind (*Cephalopholis taeniops*) that were directly correlated with geographical distance of sampling sites and depth. Bathymetry of each of our sampling sites suggest a range of depth gradients, thus depth could be an environmental driver of morphology within the Honduran yellowtail snapper fishery. Local hydrology may also be a driver of morphometric differences. For example, differences have been observed in the northern pike (*Esox lucius*) as a result of flow variations in different streams (Senay, Harvey-Lavoie, Macnaughton, Bourque, & Boisclair, 2017). There are likely to be differences in local hydrological conditions at each of the fishing grounds in this study based on their proximity to the continental shelf and Honduran mainland where riverine inputs will impact hydrological patterns, salinity and sediment load. Local hydrology and bathymetry influence water temperature, which is another known driver of body shape (Lõhmus et al., 2010). Additional research is required to untangle which environmental factor or factors are driving the morphology of yellowtail snapper in the Honduran fishery, and to identify the extent of similar morphology on a continuum.

5 | CONCLUSIONS

Accurate and robust tools to support evidence-based management are critical to achieving sustainable fisheries. Expensive and highly technical management tools are constrained in their applicability through financial and technical limitations. Morphometric analyses offer a cost-effective and accurate tool to assist in site based management approaches, with the potential application to fisher compliance of NTZs and/or TURFs. Importantly, it would be possible to automate this approach using off the shelf digital technology and a digital image of the sampled fish. Incorporating these data into user-friendly systems with outputs that are easily interpreted by mangers, fishers and other stakeholders can increase the availability of data for decision-making.

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AUTHORS' CONTRIBUTIONS

S.W.J.C. conducted research design, fieldwork, statistical analyses and provided the main input into the writing of the manuscript; N.K.T. conducted genetic analyses through allele scoring, wrote relevant methods section and provided editorial input; R.F.P. assisted with genetic and statistical analyses, and provided editorial input; S.C. and M.A.S.H. conducted the laser ablation of otoliths, wrote the relevant methods section and provided editorial input; S.J.B. conducted research design and provided editorial input. All authors have given their approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.1n51337 (Canty et al., 2018).

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REFERENCES

Abdul-Muneer, P. M. (2014). Application of microsatellite markers in conservation genetics and fisheries management: Recent advances in population structure analysis and conservation strategies. *Genetics Research International*, *2014*, 691759. https://doi.org/10.1155/2014/691759

Arias, A., Pressley, R. L., Jones, R. E., Alvarez-Romero, J. G., & Cinner, J. E. (2014). Optimizing enforcement and compliance in offshore marine protected areas: A case study from Cocos Island, Costa Rica. *Oryx*, *50*, 1–9. https://doi.org/10.1017/S0030605314000337

Bhargava, A., & Fuentes, F. F. (2010). Mutational dynamics of microsatellites. *Molecular Biotechnology*, *44*(3), 250–266. https://doi.org/10.1007/s12033-009-9230-4

Bickford, N., & Hannigan, R. (2005). Stock identification of walleye via otolith chemistry in the Eleven Point River, Arkansas. *North American Journal of Fisheries Management*, *25*(4), 1542–1549. https://doi.org/10.1577/m04-189.1

Box, S., & Canty, S. (2010). The long and short term economic drivers of overexploitation in honduran coral reef fisheries due to their dependence on export markets. *Proceedings of the 63rd Gulf and Caribbean Fisheries Institute*, *63*, 43–51.

Cadrin, S. X. (2000). Advances in morphometric identification of fishery stocks. *Reviews in Fish Biology and Fisheries*, *10*, 91–112.

Campana, S. E., & Neilson, J. D. (1985). Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*, 1014–1032.

Canty, S. W. J., Truelove, N. K., Preziosi, R. F., Chenery, S., Horstwood, M. A. S., & Box, S. J. (2018). Data from: Evaluating tools for the spatial management of fisheries. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.1n51337

Cardini, A., Seetah, K., & Barker, G. (2015). How many specimens do I need? Sampling error in geometric morphometrics: Testing the sensitivity of means and variances in simple randomized selection experiments. *Zoomorphology*, *134*(2), 149–163. https://doi.org/10.1007/s00435-015-0253-z

Carlson, A. K., Fincel, M. J., & Graeb, B. D. S. (2016). Otolith microchemistry reveals natal origins of walleyes in Missouri river reservoirs. *North American Journal of Fisheries Management*, *36*(2), 341–350. https://doi.org/10.1080/02755947.2015.1135214

Christensen, V. (2010). MEY = MSY. *Fish and Fisheries*, *11*(1), 105–110. https://doi.org/10.1111/j.1467-2979.2009.00341.x

Claro, R., Sadovy de Mitcheson, Y., Lindeman, K. C., & Garcia-Cagide, A. (2009). Historical analysis of Cuban commercial fishing effort and the effects of management interventions on important reef fishes from 1960–2005. *Fisheries Research*, *99*(1), 7–16. https://doi.org/10.1016/j.fishres.2009.04.004

Davies, C. A., Gosling, E. M., Was, A., Brophy, D., & Tysklind, A. (2011). Microsatellite analysis of albacore tuna (*Thunnus alalunga*): Population genetic structure in the North-East Atlantic Ocean and Mediterranean Sea. *Marine Biology*, *158*(12), 2727–2740. https://doi.org/10.1007/s00227-011-1772-x

Dhanjal-Adams, K. L., Mustin, K., Possingham, H. P., & Fuller, R. A. (2016). Optimizing disturbance management for wildlife protection: The enforcement allocation problem. *Journal of Applied Ecology*, *53*(4), 1215–1224. https://doi.org/10.1111/1365-2664.12606

Farmer, N. A., & Ault, J. S. (2011). Grouper and snapper movements and habitat use in Dry Tortugas, Florida. *Marine Ecology Progress Series*, *433*, 169–184. https://doi.org/10.3354/meps09198

Ferguson, G. J., Ward, T. M., & Gillanders, B. M. (2011). Otolith shape and elemental composition: Complementary tools for stock discrimination of mulloway (*Argyrosomus japonicus*) in southern Australia. *Fisheries Research*, *110*, 75–83. https://doi.org/10.1016/j.fishres.2011.03.014

Franssen, N. R., Stewart, L. K., & Schaefer, J. F. (2013). Morphological divergence and flow-induced phenotypic plasticity in a native fish from anthropogenically altered stream habitats. *Ecology and Evolution*, *3*(14), 4648–4657. https://doi.org/10.1002/ece3.842

Gaines, S. D., White, C., Carr, M. H., & Palumbi, S. R. (2010). Designing marine reserve networks for both conservation and fisheries management. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(43), 18286–18293. https://doi.org/10.1073/pnas.0906473107

Gill, D. A., Mascia, M. B., Ahmadia, G. N., Glew, L., Lester, S. E., Bames, M., … Fox, H. E. (2017). Capacity shortfalls hinder the performance of marine protected areas globally. *Nature*, *543*, 665–669. https://doi.org/10.1038/nature21708

Gold, J. R., Saillant, E., Ebelt, N. D., & Lem, S. (2009). Conservation genetics of gray snapper (*Lutjanus griseus*) in U.S. Waters of the Northern Gulf of Mexico and Western Atlantic Ocean. *Copeia*, *2009*(2), 277–286. https://doi.org/10.1643/CI-08-071

Hoff, G. R., & Fuiman, L. A. (1995). Environmentally induced variation in elemental composition of red drum (*Sciaenops ocellatus*) otoliths. *Bulletin of Marine Science*, *56*(2), 578–591

Huxley, J. S. (1932). *Problems of relative growth*, *text*. London: Methuen & Co.

Kocovsky, P. M., Adams, J. V., & Bronte, C. R. (2009). The effect of sample size on the stability of principal components analysis of truss-based fish morphometrics. *Transactions of the American Fisheries Society*, *138*(3), 487–496. https://doi.org/10.1577/T08-091.1

Lõhmus, M., Sundström, L. F., Björklund, M., & Devlin, R. H. (2010). Genotype-temperature interaction in the regulation of development, growth, and morphometrics in wild-type, and growth-hormone transgenic coho salmon. *PLoS ONE*, *5*(4), e9980. https://doi.org/10.1371/journal.pone.0009980

Medina, A., Brêthes, J. C., & Sévigny, J. M. (2008). Habitat fragmentation and body-shape variation of African hind *Cephalopholis taeniops* (Valenciennes) in an archipelago system (Cape Verde, eastern Atlantic Ocean). *Journal of Fish Biology*, *73*(4), 902–925. https://doi.org/10.1111/j.1095-8649.2008.01986.x

Meloni, R., Albanese, V., Ravassard, P., Treilhou, F., & Mallet, J. (1998). A tetranucleotide polymorphic microsatellite, located in the first intron of the tyrosine hydroxylase gene, acts as a transcription regulatory element in vitro. *Human Molecular Genetics*, *7*(3), 423–428. https://doi.org/10.1093/hmg/7.3.423

Mwanja, M. T., Muwanika, V., Nyakaana, S., Masembe, C., Rutasire, J., & Mwanja, Wilson. W. (2011). Population morphological variation of the Nile perch (*Lates niloticus*, L. 1758), of East African Lakes and their associated waters. *African Journal of Environmental Science and Technology*, *5*, 941–949. https://doi.org/10.5897/AJEST11.197

Nguyen, C., Quynh, T., Schilizzi, S., Hailu, A., & Iftekhar, S. (2017). Territorial user rights for fisheries (TURFs): State of the art and the road ahead. *Marine Policy*, *75*, 41–52.

Nybom, H. (2004). Comparison of different nuclear DNA markers for estimating intraspecific genetic diversity in plants. *Molecular Ecology*, *13*(5), 1143–1155. https://doi.org/10.1111/j.1365-294X.2004.02141.x

Powell, W., Morgante, M., Andre, C., Hanafey, M., Vogel, J., Tingey, S., & Rafalski, A. (1996). The comparison of RFLP, RAPD, AFLP and SSR (microsatellite) markers for germplasm analysis. *Molecular Breeding*, *2*(3), 225–238. https://doi.org/10.1007/BF00564200

Renshaw, M. A., Karlsson, S., & Gold, J. R. (2007). Isolation and characterization of microsatellites in lane snapper (*Lutjanus synagris*), mutton snapper (*Lutjanus analis*), and yellowtail snapper (*Ocyurus chrysurus*). *Molecular Ecology Notes*, *7*(6), 1084–1087. https://doi.org/10.1111/j.1471-8286.2007.01785.x

Saillant, E. A., Renshaw, E. A., Cummings, N. J., & Gold, J. R. (2012). Conservation genetics and management of yellowtail snapper, *Ocyurus chrysurus*, in the US Caribbean and South Florida. *Fisheries Management and Ecology*, *19*, 301–312. https://doi.org/10.1111/j.1365-2400.2011.00840.x

Scharnweber, K., Watanabe, K., Syvaranta, J., Wanke, T., Monaghan, M. T., & Mehner, T. (2013). Effects of predation pressure and resource use on morphological divergence in omnivorous prey fish. *BMC Evolutionary Biology*, *13*, 132. https://doi.org/10.1186/1471-2148-13-132

Selig, E. R., Kleisner, K. M., Ahoobim, O., Arocha, F., Cruz-Trinidad, A., Fujita, R., … Villasante, S. (2017). A typology of fisheries management tools: Using experience to catalyse greater success. *Fish and Fisheries*, *18*, 1–28. https://doi.org/10.1111/faf.12192

Senay, C., Harvey-Lavoie, S., Macnaughton, C. J., Bourque, G., & Boisclair, D. (2017). Morphological differentiation in northern pike (*Esox lucius*): The influence of environmental conditions and sex on body shape. *Canadian Journal of Zoology*, *95*(6), 383–391. https://doi.org/10.1139/cjz-2016-0159

Sohn, D., Kang, S., & Kim, S. (2005). Stock identification of chum salmon (*Oncorhynchus keta*) using trace elements in otoliths. *Journal of Oceanography*, *61*(2), 305–312. https://doi.org/10.1007/s10872-005-0041-3

Strauss, R. E., & Bookstein, F. L. (1982). The truss: Body form reconstructions in morphometrics. *Systematic Zoology*, *31*(2), 113–135. https://doi.org/10.1093/sysbio/31.2.113

Truelove, N. K., Box, S. J., Aiken, K. A., Blythe-Mallet, A., Boman, E. M., Booker, C. J., … Stoner, A. W. (2017). Isolation by oceanic distance and spatial genetic structure in an overharvested international fishery. *Diversity and Distributions*, *23*, 1–9. https://doi.org/10.1111/ddi.12626

Turan, C. (2004). Stock identification of Mediterranean horse mackerel (*Trachurus mediterraneus*) using morphometric and meristic characters. *ICES Journal of Marine Science*, *61*, 774–781. https://doi.org/10.1016/j.icesjms.2004.05.001

Vasconcellos, A. V., Vianna, P., Paiva, P. C., Schama, R., & Sole-Cava, A. (2008). Genetic and morphometric differences between yellowtail snapper (*Ocyurus chrysurus*, Lutjanidae) populations of the tropical West Atlantic. *Genetics and Molecular Biology*, *31*(1), 308–316.

Wells, R. J. D., Rooker, J. R., & Prince, E. D. (2010). Regional variation in the otolith chemistry of blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) from the western North Atlantic Ocean. *Fisheries Research*, *106*(3), 430–435. https://doi.org/10.1016/j.fishres.2010.09.017

Willis, S. C., Winemiller, K. O., & Lopez-Fernandez, H. (2005). Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. *Oecologia*, *142*(2), 284–295. https://doi.org/10.1007/s00442-004-1723-z

Wimberger, P. H. (1992). Plasticity of fish body shape. The effects of diet, development, family and age in two species of Geophagus (Pisces: Cichlidae). *Biological Journal of the Linnean Society*, *45*, 197–218.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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