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Generic names and mislabeling conceal high species diversity in global fisheries markets

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Abstract

Consumers have the power to influence conservation of marine fishes by selectively purchasing sustainably harvested species. Yet, this power is hindered by vague labeling and seafood fraud, which may mask market biodiversity and lead to inadvertent consumption of threatened species. Here, we investigate the repercussions of such labeling inaccuracies for one of the world's most highly prized families of fishes—the snappers (Family: Lutjanidae). By DNA barcoding 300 “snapper” samples collected from six countries, we show that the lax application of this umbrella term and widespread mislabeling (40%) conceal the identities of at least 67 species from 16 families in global marketplaces, effectively lumping taxa for sale that derive from an array of disparately managed fisheries and have markedly different conservation concerns. Bringing this trade into the open should compel a revision of international labeling and traceability policies, as well as enforcement measures, which currently allow such extensive biodiversity to be consumed unknowingly.

KEYWORDS

DNA barcoding, fish, IUU fishing, mislabeling, snapper, species identification, traceability

1 | INTRODUCTION

In an era of rising seafood demand, impaired ocean health, and perturbing rates of illegal, unreported, and unregulated (IUU) fishing (Food and Agriculture Organization [FAO], 2016), consumers are increasingly urged to source species from responsibly managed fisheries (Gutiérrez et al., 2012). While there is general accord that detailed and accurate information on fishery products is crucial to empower consumer choice and promote legal and sustainable seafood trade (Barendse & Francis, 2015), these provisions have not necessarily been translated into policy. The European Union (EU) has arguably the most robust seafood labeling legislation, requiring declaration of the commercial designation, scientific name, production method, geographical origin, and fishing-gear category on retail seafood products (Reg. [EU] 1379/2013), comple-

mented with comprehensive traceability requirements (European Community [EC] Regs 178/2002; 1224/2009; Reg. [EU] 404/2011). In comparison, labeling regulations in other countries are lenient, often necessitating little more than a common name on seafood packaging (Supporting Information Table S1). Furthermore, the approved common names for fish in the seafood naming lists of different countries (Supporting Information Table S1) introduce confusion, since these lack harmonization between regions and frequently group multiple species under generic market labels. As fisheries trade expands, supply chains lengthen, and a growing number of “new” and exotic species enter world markets (Di Muri, Vandamme, Peace, Barnes, & Mariani, 2018; Watson, Green, Tracey, Farmery, & Pitcher, 2016), it becomes increasingly clear that weak and/or poorly enforced regulations promote the proliferation of seafood fraud, undermining sustainable

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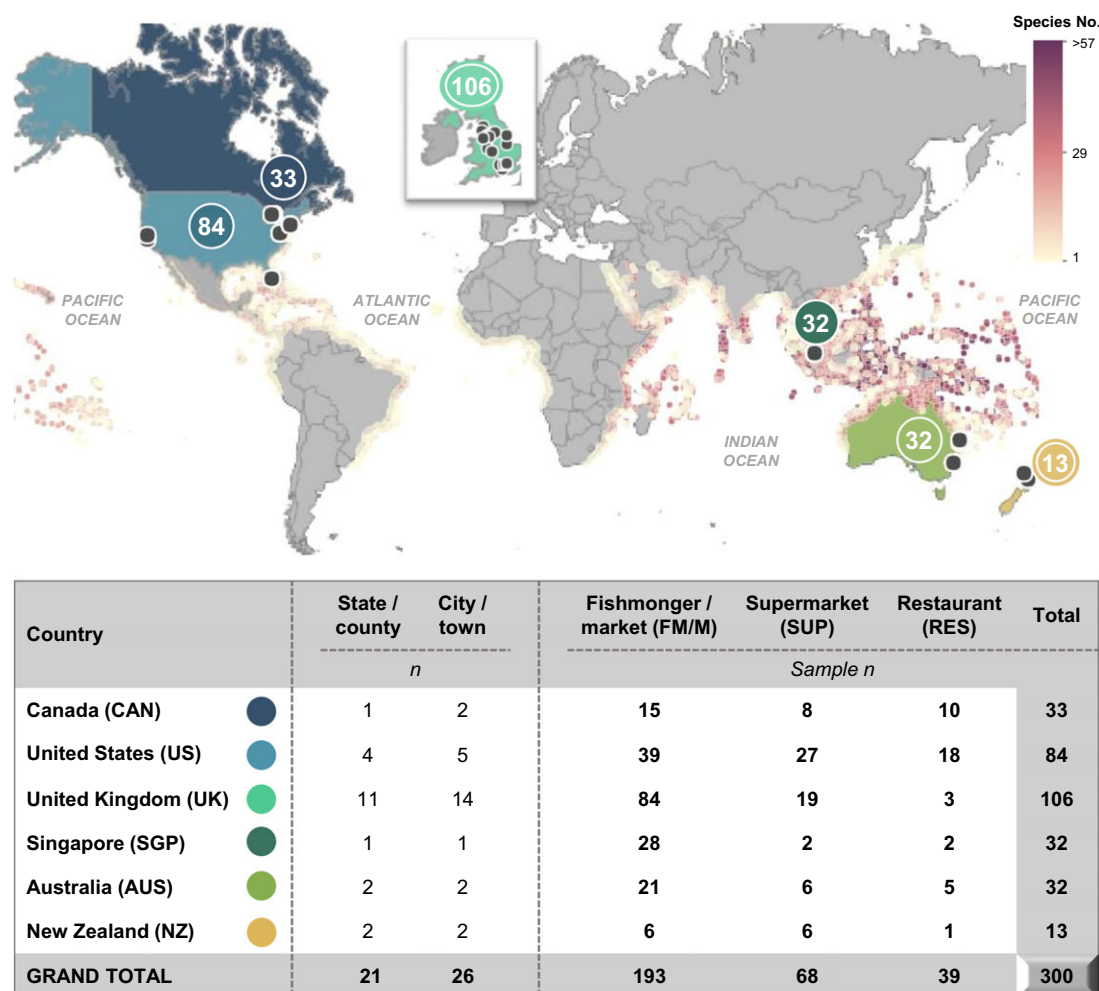


FIGURE 1 Sampling locations overlaid on the global species-richness map for the family Lutjanidae, with a breakdown of sample numbers collected per country, site, and sector. Species-richness point data (GPS coordinates) for all assessed Lutjanidae species ($n = 98$) were derived from AquaMaps (Kaschner et al., 2016) and were plotted along with GPS coordinates of individual sampling sites in ArcGIS Online (www.arcgis.com)

fisheries management and offering avenues for laundering of IUU products into legitimate marketplaces (Jacquet & Pauly, 2008). Yet, no studies have empirically tested the extent to which generic labels and noncompliance conceal market biodiversity, hamper consumer choice and potentially imperil species on a global scale.

Here, we tackle this critical issue using an iconic but diverse family of fishes as a case example—the snappers (Family: Lutjanidae). Members of this family represent major fisheries resources throughout their circumtropical range (Figure 1) and are among the world's most valued marine species (Amorim, Sousa, Westmeyer, & Menezes, 2018). However, in addition to several life-history traits that render them vulnerable to overexploitation, the taxon embodies all the complexities associated with modern seafood supply chains: caught mainly in poorly managed and data-scarce fisheries in developing countries, exported primarily to the affluent global North, and permitted to be marketed under “umbrella” terms that may mask the diversity of >100

species comprising the family, and sometimes also those from other families (Cawthorn & Mariani, 2017; Supporting Information Table S2). For instance, “snapper” can refer to 56 Lutjanid species in the United States (US; Food and Drug Administration, 2017), and 112 Lutjanid species in the United Kingdom (UK; Department for Environment, Food & Rural Affairs, 2013). Canada's “Fish List” allows 108 species to be called “snapper” or “Pacific snapper,” including both Lutjanids and *Sebastes* spp. (rockfishes) (Canadian Food Inspection Agency, 2017). In Australia, “snapper” appears in the standard names of 96 species (Australian Fish Names Committee [AFNC], 2017), whereas New Zealand's designations exclude Lutjanids altogether and rather include Sparidae (seabream) and Berycidae (alfonsino) species (Ministry for Primary Industries, 2013). Adding to this obscurity, “snappers” are exceptionally prone to market fraud (77–100%; Supporting Information Table S3), expanding the diversity under this umbrella term further.

In this most geographically widespread seafood authentication study conducted to date, we employ a forensically validated DNA barcoding technique (Dawnay, Ogden, McEwing, Carvalho, & Thorpe, 2007) to unravel the species diversity underpinning the global “snapper” trade, using the results to map patterns in labeling inconsistencies, assess the likely origins of collected “snapper” samples, and investigate the conservation impacts of “snapper” misrepresentation. Illuminating this trade, and the ripple effects on sustainability outcomes, should identify the path toward addressing the issue and oblige stakeholders to take necessary actions.

2 | METHODS

2.1 Sampling

To evaluate the variety of species sold as “snapper” on world markets, we chose six English-speaking countries for sample collection, namely Canada, US, UK, Singapore, Australia, and New Zealand. We visited multiple sites in each country, covering 21 states/counties and 26 cities/towns (Figure 1, Supporting Information Table S4). We screened 300 samples sold with “snapper” in the description, including fresh, frozen, and cooked products, ranging from portions to whole fish, obtained from fishmongers, fish markets, supermarkets, and restaurants over a 12-month period (August 2016–July 2017). The ratio of samples from different outlets and in different forms was based on availability in the given country. We submitted photographs of each sample and product-associated metadata to the Barcode of Life Database (BOLD, www.boldsystems.org), under the project “SNAP-TRACE” (Supporting Information Database S1). Duplicate tissue subsamples were excised from each sample and stored in 95%-ethanol tubes until shipping to the UK laboratory with pre-approved import permits.

2.2 | Species identification

We used a Chelex[®] resin (Sigma-Aldrich, Dorset, UK) protocol (Estoup, Largiadèr, Perrot, & Chourrout, 1996) to extract sample DNA and amplified a ~650 base-pair fragment of the cytochrome *c* oxidase I (COI) gene using the polymerase chain reaction (PCR) primers, reaction mixtures, and cycling conditions described in Cawthorn, Duncan, Kastern, Francis, and Hoffman (2015). PCR products were purified and sequenced by Macrogen (Europe) and quality-trimmed sequences were uploaded to the BOLD “SNAP-TRACE” project. Sequences were subsequently identified in GenBank (www.ncbi.nlm.nih.gov), cross-referencing results in the BOLD “Species-Level” and “Public-Records” databases. We used a similarity threshold of $\geq 98\%$ to assign sequences to potential species, as most analyzed marine fishes have intraspecific COI divergences well below 2%

(Ward, 2009). Next, we aligned all COI sequences and constructed a maximum-likelihood (ML) tree (Supporting Information File S1). For each sample, we inferred a “most likely” species from top matches across the three sequence databases and positions in the ML tree and/or BOLD “Tree-Based Identification” (TBI) tool, but also recorded possible candidate species with $<2\%$ divergence (Supporting Information Database S2). Where top matches included two or more taxa with identical sequence similarities, and where explicit identification could not be resolved from the ML tree or BOLD TBI, both/all taxa were designated “most likely” species. We considered both “most likely” species and possible candidates ($<2\%$ divergence) when evaluating “snapper” misrepresentation. However, we included only “most likely” species in downstream analyses, weighting scores equally across taxa when identifications could not be resolved.

2.3 | Market biodiversity and misrepresentation

To evaluate species diversity across countries and overall, we calculated Shannon (H') indices in PAST v 3. As a check for potential bias introduced by variations in country-specific sample sizes, we repeated the analyses using rarefaction in PAST v 3 to compare expected diversity ($E[S_n]$) in a standard subsample of 13 (i.e., smallest sample size).

We used the seafood labeling regulations and naming lists of each sample-collection country (Supporting Information Tables S1 and S2), as well as a decision tree (Supporting Information Figure S1), to define “snapper” misrepresentation on two levels, that is, “misnamed” and/or “mislabeled” by species. Samples were considered misnamed if an incorrect version of an approved common name was used at the point-of-sale, but this did not implicate another species in the relevant country's naming list. Samples were deemed mislabeled when either the declared species, or species inferred from the declared common name, did not correspond with the top genetic match or any candidate species (Supporting Information Database S2). For Singapore, where no seafood naming list exists, samples were not considered misnamed, but were considered mislabeled when identified as non-Lutjanid species. We statistically analyzed misrepresentation rates across countries and sectors using likelihood-ratio chi-squared tests with the GTest function of the R package DescTools v 0.99.24.

2.4 | Likely origin

We followed a three-step approach to trace samples to potential source fisheries, using FishBase (www.fishbase.org) to determine the FAO areas in which genetically identified species are natively distributed. Firstly, where a catch

(FAO) area was declared, we verified the occurrence of the identified species in that area and considered this the most likely geographical origin (assigned a score of 1). Where a country of origin was declared on fresh (unprocessed) samples without a catch area, we recorded only FAO areas within the declared country's exclusive economic zone in which the identified species occurs. Where no provenance information was provided, or where the declared origin was possibly the country of processing, we assumed equal probability of deriving from any FAO area in which the identified species occurs. In the latter two cases, fractional scores were equally assigned to each recorded area as proportions of 1. Scores were subsequently summed across sampling countries and areas. Last, to evaluate the state of fisheries in each area, we tabulated information on overall catch trends and percentages of overfished stocks (FAO, 2016), IUU fishing rates (Agnew et al., 2009), and snapper fisheries management (Amorim et al., 2018; FishSource [www.fishsource.org]). We nevertheless highlight that, although catch trends can be useful indicators of stock status particularly in fisheries lacking formal assessment (i.e., majority of global fisheries), declining catches may result from numerous factors, including improved management and legislation, and do not necessarily reflect abundance or mismanagement (Pauly, Hilborn, & Branch, 2013). Conversely, high IUU rates strongly correlate with weak governance and fisheries mismanagement (Agnew et al., 2009; Marine Resources Assessment Group, 2005).

2.5 | Conservation status

We evaluated the conservation status of genetically identified species using the International Union for Conservation of Nature (IUCN) Red List (IUCN, 2017), as well as scores of “intrinsic vulnerability to fishing” (IV) based on ecological and life-history traits and expressed on a scale from 1 to 100 (IV increases from 1 and is considered high at ≥ 55 ; Cheung, Pitcher, & Pauly, 2005). We chose these metrics over individual stock assessments (e.g., FAO, RAM database), since most identified species are not covered by such assessments and because catch locations required to match samples with populations/stocks were seldom declared (Supporting Information Database S1). For comparison, all valid members of the Lutjanidae family (112 species) were also evaluated. To statistically analyze IV scores, we conducted a two-way analysis of variance (ANOVA), verified acceptable normality, and used Fisher's least significant difference (LSD) post hoc testing.

3 | RESULTS

We identified at least 67 species, representing 16 families and five orders, sold as “snapper” globally (Figure 2).

Approximately one-third of all samples comprised non-Lutjanids, 32% were misnamed, and 40% were mislabeled (Figure 3). Mislabeled samples encompassed no less than 50 species, with the most common non-Lutjanid substitutes including seabreams (Sparidae spp.), rockfishes (*Sebastes* spp.), threadfin breams (*Nemipterus* spp.), tilapia (*Oreochromis* spp.), and fusiliers (*Caesio* spp.¹) (Figure 2, Supporting Information Database S2). By country, the UK samples exhibited the highest species diversity (38 species; $H' = 3.5$; $E[S_{13}] = 11.2$; Figure 2), 42% of which were non-Lutjanid spp. (Figure 3). Diversity indices were similar for the US, Canada, Singapore, and Australia ($H' = 2.0$ – 2.5 ; $E[S_{13}] = 6.9$ – 7.9), but the US had the largest proportion of Lutjanids and a high frequency of certain species within the family (e.g., *Lutjanus campechanus*). New Zealand had the lowest diversity (five species; $H' = 1.0$), with a predominance of Sparids rather than Lutjanids.

Misnaming and mislabeling rates differed by country and sector (Figure 3), although variations in sample size should be considered in proportional comparisons. The UK had the highest incidence of misnaming (67%), mostly involving samples from fishmongers and markets. Additionally, >80% of UK samples did not carry the mandatory information (scientific name, production method, geographical origin, fishing-gear category) required by EU regulations ([EU] 1379/2013; Supporting Information Figure S2). Mislabeling rates were highest in the UK and Canada (55%), followed by the US (38%), with restaurant samples most frequently implicated (Figure 3). Paradoxically, although New Zealand had the highest proportion of non-Lutjanids (85%), it had the lowest mislabeling rates, given that non-Lutjanids are permitted to be called “snapper” in the country. By designation, “red snapper” was most frequently mislabeled overall, and in the US, UK, and Canada (Figure 4).

Samples were predicted to have the highest probability of originating from the Western-Central Atlantic (FAO 31), including the bulk of Lutjanids from the US, where overall catches are declining but IUU fishing is low (Figure 5). This was followed by Indo-Pacific regions (FAO 57, 71, 61) and the Southwest Atlantic (FAO 41), where IUU fishing is exceptionally high and snapper fisheries are considered poorly managed. Non-Lutjanids appeared to mainly originate from the Southwest Pacific (FAO 81), where IUU fishing is low, although several other areas with high IUU levels were among probable sources (Figure 5). For most countries, samples were most likely to derive from surrounding areas. The UK represents an exception, with a high number of diverse likely source fisheries.

Correctly labeled Lutjanids in our study set had similar IUCN status but higher mean IV than mislabeled Lutjanids ($p = .04$), with both groups exhibiting poorer conservation status than the Lutjanidae family as a whole (Figure 6). The most notable conservation impact was observed for non-Lutjanids

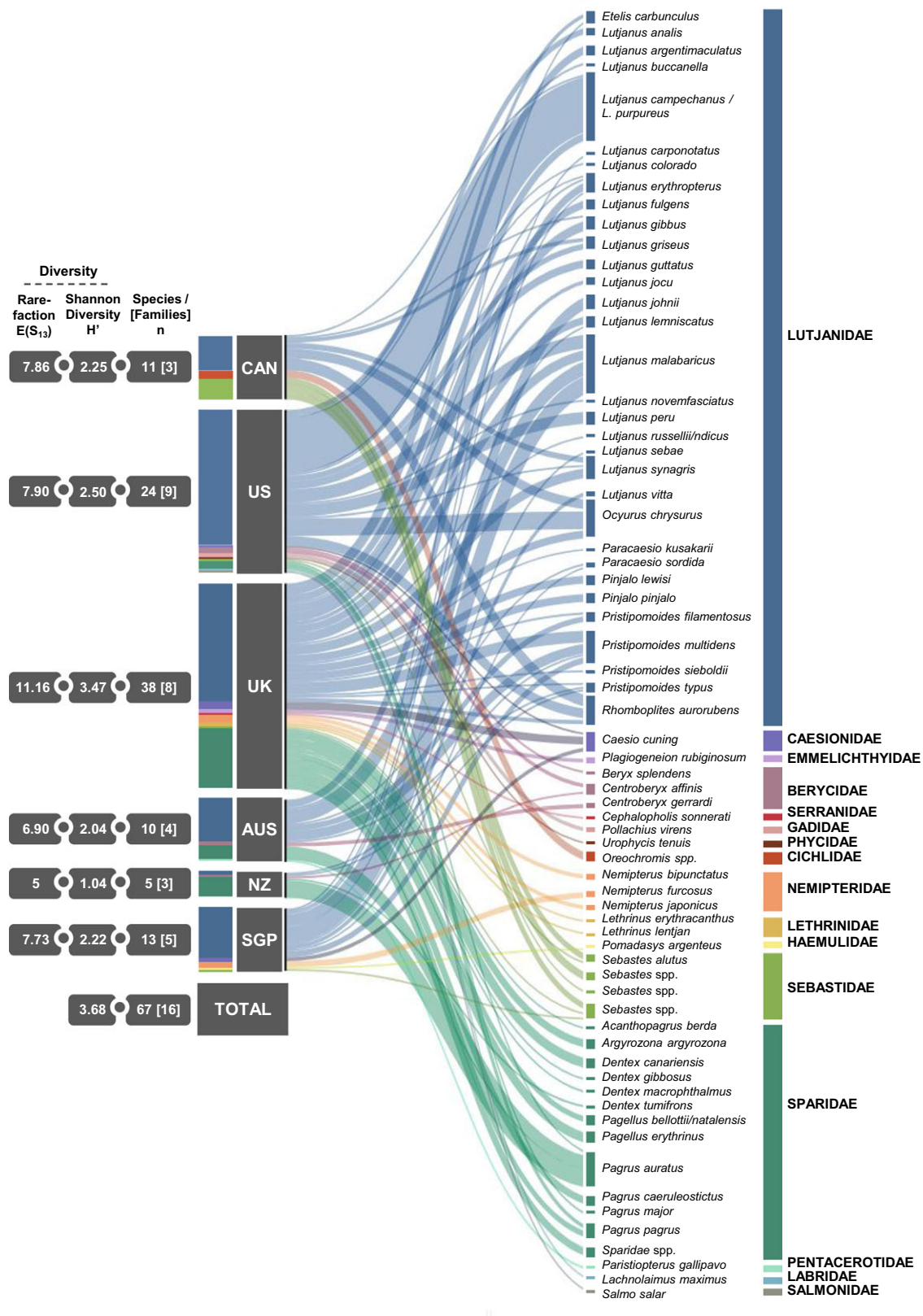


FIGURE 2 Proportional diversity of species and families identified in the global “snapper” sample set ($n = 300$; right) linked with the countries of sample collection (left), where the left panel shows the relative contributions of individual families, the number of species and families, the Shannon diversity (H') indices and expected diversity ($E[S_n]$) indices estimated by rarefaction (i.e., number of taxa expected at the smallest sample size of 13) for each country

Note. AUS: Australia; CAN: Canada; NZ: New Zealand; SGP: Singapore; UK: United Kingdom; US: United States.

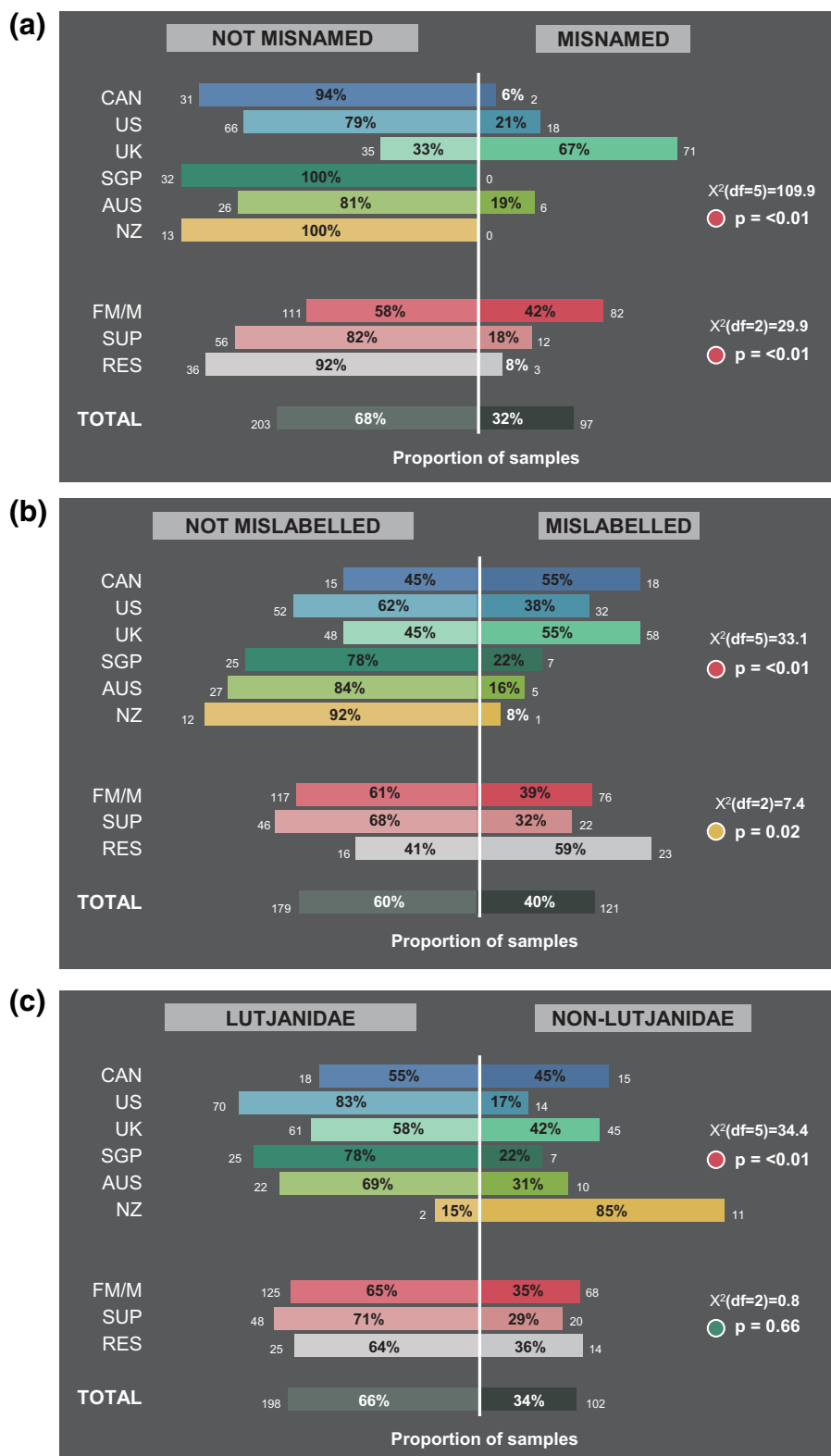


FIGURE 3 Proportions of samples (numbers and percentages) identified as being (a) correctly named vs. misnamed, (b) not mislabeled vs. mislabeled by species, and (c) Lutjanidae vs. non-Lutjanidae spp., by country, sector, and overall

Note. AUS: Australia; CAN: Canada; *df*: degrees of freedom; FM/M: fishmongers and fish markets; NZ: New Zealand; RES: restaurants; SGP: Singapore; SUP: supermarkets; UK: United Kingdom; US: United States; χ^2 : chi-squared.

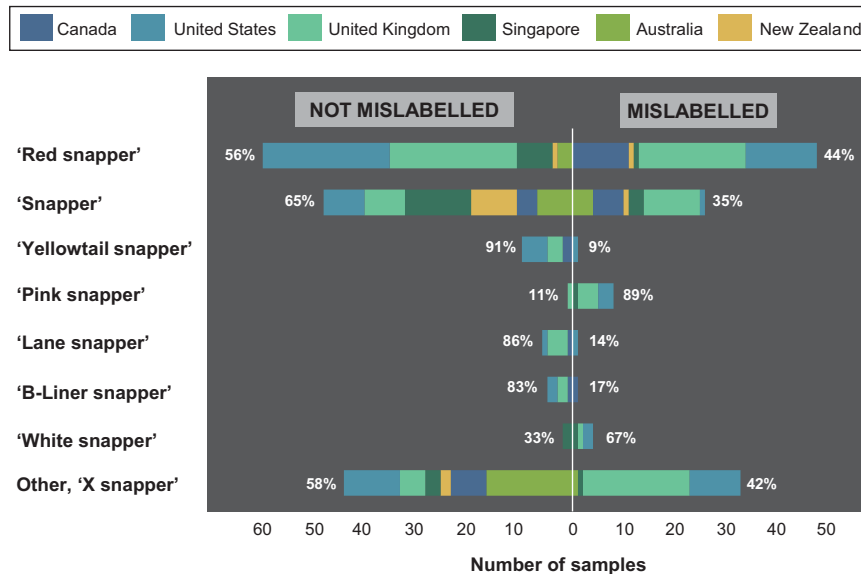


FIGURE 4 Numbers and percentages of samples not mislabeled and mislabeled according to the seafood naming lists of sample-collection countries, by designation and country

labeled in accordance with country-specific naming lists, with this group having higher mean IV (66.1) than correctly labeled Lutjanids (50.6; $p < .01$).

4 | DISCUSSION

The data presented underscore that misleading generic names and widespread mislabeling conceal substantial biodiversity in global marketplaces, with far-reaching impacts on market-based efforts to conserve wild fishes. Overall, we discovered at least 67 species from 16 families lumped under the “snapper” umbrella, potentially deriving from an array of disparately managed fisheries and having different conservation concerns. Moreover, over half of these are reef-dwelling species and are likely threatened by habitat loss/degradation, overfishing, and insufficient protection (Mouillot et al., 2016; Newton, Cote, Pilling, Jennings, & Dulvy, 2007). While inconclusive in proving intent, or assigning blame within supply chains, our study also reveals several substitutions with lower-value species (e.g., *Oreochromis* spp., *Nemipterus* spp., *Pagellus* spp., *Sebastes* spp., *Pollachius virens*), which hint at economic motives (Sumaila, Marsden, Watson, & Pauly, 2007).

Seafood naming lists are in place to reduce confusion in fish nomenclature, yet our results raise questions as to whether these are achieving their goals—which at minimum should alert consumers to a product's true nature. Members of the Lutjanidae are ecologically diverse, vary in vulnerability and value, and are frequently caught in poorly managed fisheries, with no stock assessments, and high IUU fishing rates (Amorim et al., 2018; Wagey, Nurhakim, Nikijuluw, Badrudin, & Pitcher, 2009). Even when legal, grouping these

species under single market names drastically reduces consumer power to make informed choices. Allowing members of other families to be labeled as “snapper” (Canada, Australia, New Zealand) exacerbates confusion, and may distort fisheries statistics (Cawthorn & Mariani, 2017) and promote unintentional mislabeling in importing countries (Wong & Hanner, 2008).

The high rates of “snapper” misrepresentation uncovered here indicate shortcomings in industry management and policy enforcement. This is perhaps most aptly illustrated by the UK, which follows the world's most stringent seafood labeling regulations, but where misnamed and mislabeled non-Lutjanids appeared more frequently than in a country like Singapore, with minimal labeling requirements and no seafood naming list. Beyond labeling legislation, country-specific variations in misrepresentation rates may have stemmed from various geographical, social, and economic factors. Australia, Singapore, and the US are in key Lutjanid-producing regions, which might increase local supply and familiarity with these species, and partially explain the lower mislabeling rates in at least Australia and Singapore. The US is the single largest market for “snappers,” fed primarily by imports that may derive from over 60 partner countries (Cawthorn & Mariani, 2017). The US Presidential IUU Task Force recently declared “red snapper” (*L. campechanus*) a “high-risk” species for IUU fishing and fraud (National Oceanic and Atmospheric Administration [NOAA], 2015), mandating full-chain traceability for imports of this species (NOAA, 2016), although overlooking the many species traded under other “snapper” designations. In light of this action, the current US mislabeling rates of “snapper” (38%) and specifically “red snapper” (36%) are lower than in previous studies

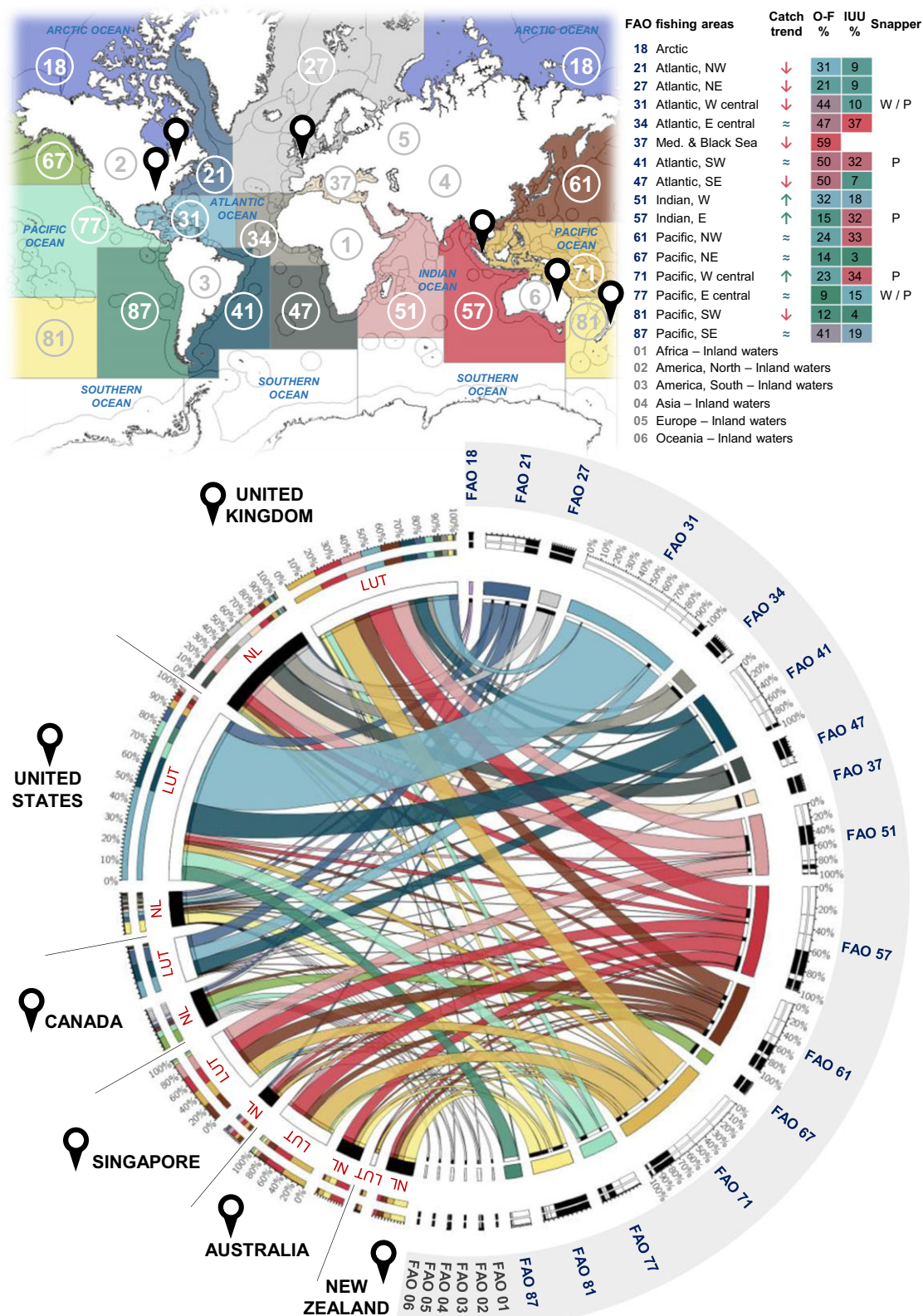


FIGURE 5 Likely geographical origins of “snapper” samples and the status of prospective source fisheries. The main circular diagram uses bands of varying width to indicate the proportions of Lutjanids (LUT, white segments) and non-Lutjanids (NL, black segments) identified from each country (left) that were linked with different FAO major fishing areas (right). The top left-hand map shows FAO area boundaries, exclusive economic zones (EEZs), and sampling locations. The top right-hand panel indicates overall fisheries landing trends, percentages of overfished (O-F) stocks, estimated rates of IUU fishing, and the status of snapper fisheries management for each FAO fishing area. The FAO boundaries map was created in ArcGIS Online (www.arcgis.com) and the circular diagram was generated with Circos software (Krzywinski et al., 2009)

Note. P: poorly managed; W: well managed.

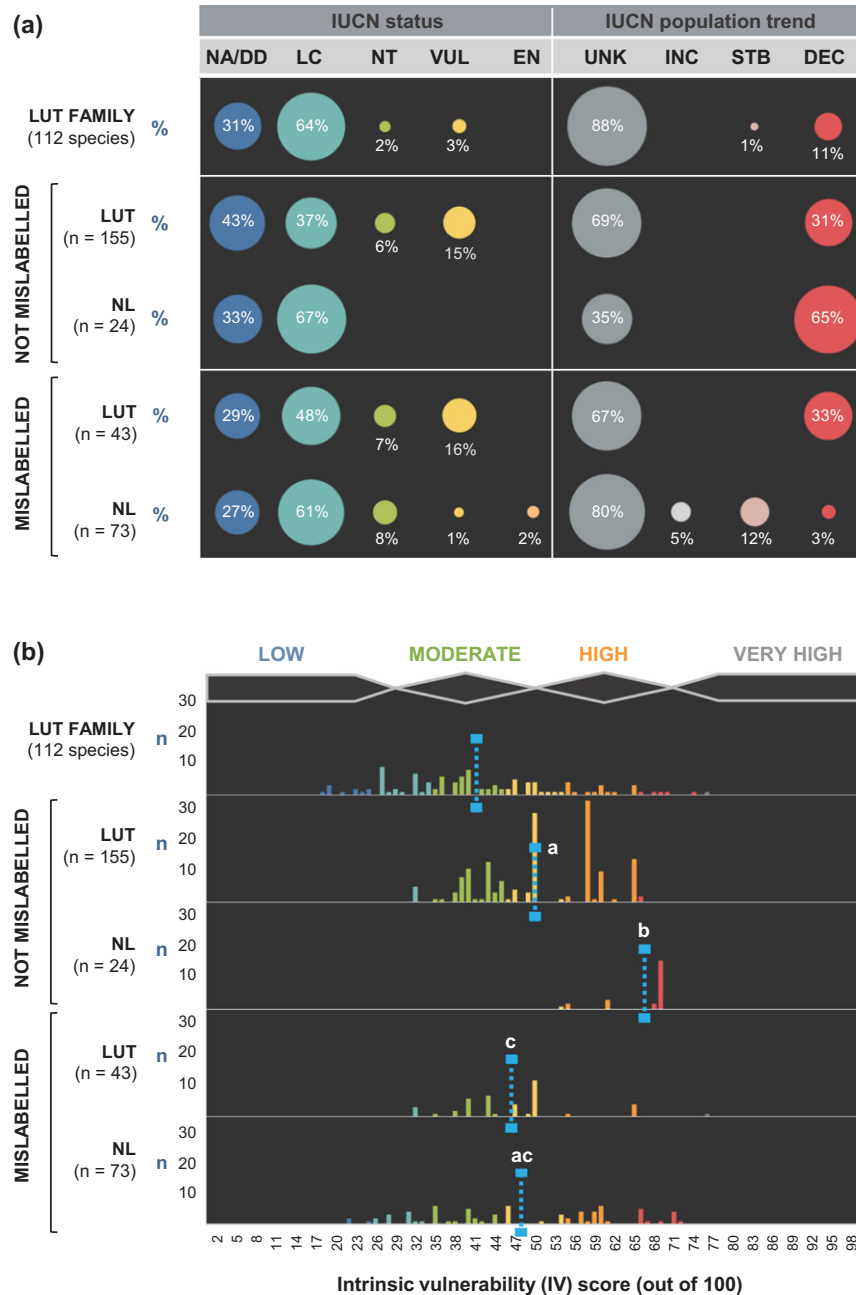


FIGURE 6 Conservation status of valid species within the Lutjanidae family (row 1) and genetically identified species (rows 2–5) inferred from IUCN ratings and “intrinsic vulnerability” scores estimated by fuzzy logic modeling; (a) shows the percentage of individuals falling into each IUCN category and (b) shows individual and mean “intrinsic vulnerability” scores (out of 100), where a significant interaction was found between “family” and “labeling status” ($F[1,291] = 22.93$, mean squared error (MSE) = 2,480.4, $p < .01$) and lower-case letters indicate differences (5% level) determined through LSD post hoc tests (between MSE = 108.17, $df = 219$). IUCN ratings indicate global extinction risk based on population trends, whereas the fuzzy logic model integrates ecological and life-history characteristics to estimate vulnerability to fishing and proxy extinction risk. Four samples identified only to family level and one sample very likely to be farmed (*Salmo salar*) were excluded from this analysis

Note. DEC: decreasing; EN: endangered; INC: increasing; LC: least concern; LUT: Lutjanidae spp.; NA/DD: not assessed/data deficient; NL: non-Lutjanidae spp.; NT: near threatened; STB: stable; UNK: unknown; VUL: vulnerable.

(Supporting Information Table S3), but remain problematic considering the volumes traded. In non-Lutjanid-producing countries like the UK and Canada, a heavy reliance on imports and lack of species familiarity potentially contributed to the high mislabeling rates (55%) observed. Additionally, our

results suggest that the UK faces momentous traceability challenges in the context of “snappers,” given the wide species diversity sold under this label, the many different likely source fisheries, and the high IUU rates in numerous source fisheries.

Considering the conservation impacts of this hidden trade more closely, we demonstrate that countries that allow non-Lutjanids to be labeled as “snappers” essentially conceal the identities of species with high vulnerability to fishing (e.g., *Pagrus auratus* [Australia, New Zealand], *Centroberyx gerardi* [New Zealand], several *Sebastes* spp. [Canada]). Logan, Alter, Haupt, Tomalty, and Palumbi (2008) have similarly shown that the permitted use of “Pacific red snapper” masks the sale of overfished *Sebastes* spp. Nonetheless, we find the repercussions arising from unauthorized mislabeling more difficult to disentangle. Whereas substitutions within the Lutjanid family might favor more resilient species, non-Lutjanid substitutes vary widely in their IUCN ratings and vulnerabilities, but may include threatened species (e.g., vulnerable *Lachnolaimus maximus*) and those from unassessed stocks from poorly managed fisheries. Moreover, even when substitutes are not endangered, mislabeling can indirectly impact conservation efforts by (1) misrepresenting the abundance of potentially dwindling labeled species, and (2) allowing overharvesting of substitute species to go unmonitored when disguised under different names (Pitcher, Watson, Forrest, Valtýsson, & Guénette, 2002). The case of “red snapper,” the most frequently marketed and mislabeled samples in this study, exemplifies the former point. Following decades of overexploitation, stocks of this highly prized taxon (*L. campechanus*) are overfished in both the US South Atlantic and Gulf (SouthEast Data, Assessment, and Review, 2015, 2017). While limited supply juxtaposed against high consumer expectations may promote substitution of red snapper, the widespread misuse of this market name likely belies the true stock status and sustains the demand. Perhaps most disconcertingly, these high mislabeling rates indicate failings in traceability systems in global snapper supply chains and, when traceability is inadequate, the chances of substitutes originating from IUU sources are vastly increased (Helyar et al., 2014).

Given the extent to which snappers are marketed globally, our findings call for a coordinated revision of international policies and practices that permit this extensive biodiversity to be consumed unknowingly. We recommend several actions to promote more transparent and sustainable snapper trade. At the national level, ambiguities in seafood naming lists might be reduced by adopting a “one species, one name” approach, as in Australia (AFNC, 2017), and by omitting references to “snapper” for non-Lutjanids. Nevertheless, recognizing the confusion with colloquial names in global marketplaces, we suggest that country-specific labeling regulations be aligned with those of the EU in requiring scientific names on seafood, as well as mandating additional criteria (geographical origin, production- and harvest-methods) to benefit consumer choice. Internationally, the Codex Alimentarius Commission (CAC) could play a leading role in establishing standards and guidelines for responsible seafood

labeling as part of its “food fraud initiative” (CAC, 2017). Along with more robust legislation, post-regulatory monitoring regimes will likely require consolidation and strengthening to overcome known barriers to enforcement, such as split or unclear governmental-agency mandates, inadequacies in agency funding, human-resource allocations, laboratory capacity, and inspection rates, corruption and bribery of officials, and minimal penalties for noncompliance (Friedman, 2017; Hofherr, Martinsohn, Cawthorn, Rasco, & Naaum, 2016). Improving supply-chain traceability is imperative and could be facilitated by emerging technologies (e.g., electronic interoperable systems, DNA-based verification), however, such measures will require co-operation from both domestic fisheries and exporting nations. Developing countries, principal suppliers of snappers, often suffer from weak governance and insufficient financial and technical resources to achieve end-to-end traceability, opening doors for illicit conduct (Cawthorn & Mariani, 2017). Fostering strategic partnerships between supply-chain actors, nongovernmental organizations, and foreign governments could assist in building infrastructure, expertise, and monitoring- and enforcement-capacity in developing-world fisheries, while preventing stricter regulations from becoming trade barriers and jeopardizing livelihoods in such nations (Willette & Cheng, 2018). Last, we recommend that all policies be complemented by appropriate public awareness campaigns on seafood sustainability, fraud, and potential substitutes, creating bottom-up pressure for transparent labeling and a marketplace less susceptible to trickery through mislabeling.

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AUTHOR CONTRIBUTIONS

DMC conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and tables, and wrote the paper. CB analyzed the data and reviewed drafts of the paper. SM conceived and designed the experiments, contributed reagents/materials, and reviewed drafts of the paper.

DNA SEQUENCE DEPOSITION

DNA sequences and accompanying metadata have been submitted to the Barcode of Life Database (BOLD, www.boldsystems.org) Barcoding Applications Campaign, under the

project “SNAP-TRACE.” Sample IDs and BOLD process IDs are included in Supporting Information Database S1.

ENDNOTES

¹ Although Caesionidae are phylogenetically nested within Lutjanidae (see Supporting Information File S1), they cannot be called “snapper” in the seafood naming lists of sample-collection countries.

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SUPPORTING INFORMATION

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

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