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Improving the productivity–susceptibility analysis to assess data-limited fisheries

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ABSTRACT: Each year, millions of marine aquarium fish and invertebrates are harvested from coral reefs and enter the complex and largely unregulated marine aquarium trade (MAT). It is challenging to identify species at risk of overexploitation in this trade due to its data-limited and poorly monitored nature. We developed a new analytical approach based on a productivity–susceptibility analysis (PSA) to assess the vulnerability of wild-captured marine aquarium fish. The PSA was originally developed to assess food fisheries; however, species and operational characteristics between food fisheries and the MAT differ. Thus, we improved a prior PSA framework to assess the data-limited MAT through customization of productivity and susceptibility factors to align with the target fishery, improved data binning, calculation of susceptibility, and characterization of the vulnerability scores. Our vulnerability results align well with the most recent IUCN assessments, showing improved accuracy using this revised PSA compared to prior adaptions of the PSA to the MAT. Further, we show that this PSA approach can be used to assess species on either a global or country-specific scale. A Gaussian mixture model clustering algorithm was applied to the PSA results to objectively classify fish along a sustainability continuum. Among 32 species, a majority of species clustered as highly sustainable or sustainable indicating little management or over-harvest concern; however, the Bangaii cardinalfish *Pterapogon kauderni* and blue tang *Paracanthurus hepatus* indexed as unsustainable. This novel PSA method, and use of a clustering algorithm to classify results, provides a predictive tool for a wide range of fisheries. In addition to informing species management plans, the compilation of sustainability status data generated by our PSA can inform a consumer guide, allowing consumers and other stakeholders to make sustainable decisions when purchasing fish.

KEY WORDS: Marine aquarium trade · Productivity–susceptibility analysis · Data-limited fisheries · Sustainability · Gaussian mixture model · Ornamental fish

1. INTRODUCTION

The marine aquarium trade (MAT) is supplied by a complex network of fisheries that rely on harvesting and shipping vertebrates and invertebrates from more than 40 countries to markets in the Americas, EU, and Asia (Wood 2001, Wabnitz et al. 2003, Tissot et al. 2010, Rhyne et al. 2012, 2017b). Although aquaculture of MAT animals has become more commercially viable due to improvements in breeding techniques, the majority of species traded are still wild-caught (Tlusty et al. 2013, Pouil et al. 2020). These fisheries supply thousands of species for display in public and private aquaria (Rhyne & Tlusty 2012, Rhyne et al. 2012). Continued and increased demand for aquarium fish is a result of the rise in popularity of the private aquarium hobby coupled with more affordable and efficient technology; however, this

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demand raises concerns over the long-term sustainability of the fisheries (Tlusty 2002, Rhyne & Tlusty 2012, Tlusty et al. 2013).

The MAT is a dynamic fishery system that spans a variety of fishing rules and regulations, levels of local management and monitoring, and involves species with varying life histories and data availability (Dee et al. 2014). Due to these compounding and often opposing factors, the MAT and species within have been difficult to evaluate. Sustainability for the MAT has been defined as 'a relationship between society and reef that continually sustains and improves the net benefit to the [coral reef social–ecological system]' (Rhyne et al. 2014, p. 103). The MAT is characterized by 'artisanal' small boat fisheries collecting individual animals under limited regulations, while selection of fishes is based on desirable morphological and behavioral traits, thus comprising a fishery system with characteristics different than food fisheries (Rhyne et al. 2017a). It is important to recognize the socio-economic consequences of management decisions on fishing communities throughout the Indo-Pacific, whose livelihoods are sustained by the MAT (Rhyne et al. 2012, 2014, Perez 2019). Primary sustainability concerns of the fishery include local species population depletions from overharvesting and habitat damage due to illegal destructive fishing techniques, such as cyanide fishing. Given the specious (2300+; Rhyne et al. 2017b) and global nature of the MAT, the need to assess the impact of fishing on harvested species has been recognized. However, traditional methods of fishery assessments (i.e. Ricker Spawner–Recruit Model, age-structured models) are not suitable for the MAT. This is primarily due to (1) a lack of robust life-history data to support management plans and (2) an absence of landings data and export/import monitoring systems to document total trade volume. The semi-quantitative productivity–susceptibility analysis (PSA) is an alternative metric to determine the sustainability status of data-limited fish species in comparison to traditional stock assessments.

The modern fisheries PSA framework originated from an Australian food fishery assessment (Hobday et al. 2007) and has been applied in a variety of other studies targeting both food and marine aquarium fish (MAF) (Patrick et al. 2009, Fujita et al. 2014, Okemwa et al. 2016, Dee et al. 2019). The PSA ultimately quantifies the vulnerability of wild-caught fish. Vulnerability refers to the potential of a fish stock to be overexploited due to fishing, and is dependent on both productivity and susceptibility factors. Productivity and susceptibility are each composed of a number of model-dependent factors that are individually scored on a 1–3 (low–high) scale. These factors are quantified in a data-binning process where productivity and susceptibility are calculated separately and inputted into the Euclidean distance formula to output the vulnerability score:

$$v = \sqrt{(p-3)^2 + (s-1)^2} \quad (1)$$

where p is the mean productivity score, s is the mean susceptibility score, and v is the vulnerability score.

Following the first iteration (Hobday et al. 2007), Hobday et al. (2011) updated the methodology to be more inclusive of all fisheries by suggesting that factors are selected based on aligning appropriately with the target fishery. Additionally, they recommend that a multiplicative product replace the arithmetic mean for the calculation of susceptibility (Hobday et al. 2011). However, these important updates to the mathematical structure of the model were largely ignored by following studies, inherently limiting the accuracy of their results.

Currently, the NOAA Toolbox (Patrick et al. 2009), an adaption of Hobday et al. (2007), is the leading PSA tool for data-limited stock analysis (for comparison of PSAs, see Table 1). The PSA contained in the NOAA Toolbox has primarily been used to identify stocks at risk of overexploitation in food fisheries at a stock-specific level. Patrick et al. (2009) expanded the analysis of Hobday et al. (2007) by evaluating 22 factors instead of 13, but did not use the updated calculation for susceptibility as suggested by Hobday et al. (2011). As more factors are introduced into a model, the degree of error simultaneously increases. In a data-limited system, where a complete data set to validate individual data points is not necessarily available, error propagation by scoring extraneous factors becomes more likely. A major limitation of implementing the NOAA Toolbox to evaluate MAF is the reliance on food fish standards to assess a fishery whose catch and fishing gear are fundamentally different than that of food fisheries.

The first study to apply the NOAA Toolbox version of the PSA evaluated Indonesian reef fishes (Fujita et al. 2014), but their vulnerability results were debatable. In that study, clownfish species *Amphiprion ocellaris* and *A. clarkii* were evaluated as being highly vulnerable (v = 1.56–1.66). However, a comprehensive global study showed these species to be at low risk for population depletions due to fishing (Maison & Graham 2016). The inconsistency between these 2 reports highlights the need for improved analytical techniques. Following Fujita et al. (2014), a revised PSA introduced slight revisions to

Table 1. Comparison of productivity–susceptibility analysis methods across 7 studies: Hobday et al. (2007, 2011), The NOAA Toolbox (Patrick et al. 2009, Fujita et al. 2014), Okemwa et al. (2016), Dee et al. (2019) and this study. Productivity (*p*) and susceptibility (*s*) factors are compared. **Bold** study titles indicate an arithmetic mean was not used to calculate susceptibility. A multiplicative product was used in Hobday et al. (2011) and Okemwa et al. (2016), whereas an arithmetic mean of logarithms was used in this study.

Hobday et al. (2007)		**Hobday et al. (2011)**		Patrick et al. (2009) Fujita et al. (2014)		**Okemwa et al. (2016)**		Dee et al. (2019)		**This study**	
p	*s*	*p*	*s*	*p*	*s*	*p*	*s*	*p*	*s*	*p*	*s*
Average age at maturity	Overlap of fishing effort with species distribution	Average age at maturity	Overlap of species range with fishery	von Bertalanffy growth coefficient	Vertical overlap	von Bertalanffy growth coefficient	Vertical overlap	von Bertalanffy growth coefficient	Vertical overlap	Mean trophic level	Trade vulnerability
Average size at maturity	Encounter-ability based on: habitat and depth	Average size at maturity	Global distribution	Recruitment pattern	Value of fishery	Recruitment pattern	Modification: desirability/ market value	Recruitment pattern	Value of fishery	Maximum size	Cyanide use
Average max age	Selectivity	Average maximum age	Habitat	Population growth rate	Survival after capture and release	Replacement: Minimum population doubling time	Replacement: post capture mortality	Population growth rate	Survival after capture and release	Maximum age	Ecological niche
Average min size	Post capture mortality	Average maximum size	Depth located	Mean trophic level	Schooling and aggregation	Mean trophic level	Schooling and aggregation	Mean trophic level	Schooling and aggregation	Fecundity	Appropriate-ness
Fecundity		Fecundity	Selectivity	Maximum size	Morphology affecting capture	Maximum size	Morphology affecting capture	Maximum size	Morphology affecting capture	Breeding strategy	Encounter-ability
Reproductive strategy		Reproductive strategy	Post-capture mortality	Maximum age	Management strategy	Maximum age	Management strategy	Maximum age	Management strategy	Average larval duration	
Trophic level		Trophic level		Fecundity	Impact to essential fish habitat	Fecundity	Replacement: ecological niche	Fecundity	Impact to essential fish habitat	Average age at maturity	
				Estimated natural mortality	Geographic concentration	Estimated natural mortality	Replacement: availability	Estimated natural mortality	Geographic concentration		
				Breeding strategy	Fishing rate relative to natural mortality	Breeding strategy	Fishing rate relative to natural mortality	Breeding strategy	Fishing rate relative to natural mortality		
				Age at maturity	Biomass of spawners	Age at maturity	Biomass of spawners	Age at maturity	Biomass of spawners		
					Areal overlap		Replacement: encounter-ability		Areal overlap		
					Migration		Migration		Appropriate-ness		

the NOAA Toolbox framework and expanded the number of species evaluated (Dee et al. 2019). However, the PSA parameters in that study remained calibrated for food fishes rather than aquarium fish, and this resulted in variable accuracy of PSA vulnerability score results.

In contrast to Dee et al. (2019), a Kenya-specific MAF study (Okemwa et al. 2016) showed how the PSA could be adjusted to generate more accurate results. Okemwa et al. (2016) successfully customized the PSA to assess the MAF in the Kenyan fisheries, and its results aligned well with pre-existing expert evaluations. This study improved the PSA by including adjustments to factor weightings, using a multiplicative product to calculate susceptibility, and streamlining the factors. However, the model relied on Kenya-specific data for catch per unit effort, a metric that is unavailable for the majority of MAF species globally. However, their methodology and approach to PSA customization by fishery can be applied to global MAF.

Although the PSA model has received criticism for its false assumption that productivity and susceptibility have a linear relationship, it remains the best available framework to evaluate a wide range of fishery and species life-history factors in a single analysis (Hordyk & Carruthers 2018). The MAT is a data-limited fishery in that it lacks elements of traditional stock assessments such as catch data, species life-history data, and population abundance time series, and therefore we must develop tools to ensure long-term MAT sustainability. It is important to only use reliable, applicable data in mathematical models to limit error in the output. Our analysis differs from previous studies by eliminating PSA factors not pertinent to the MAT, using a logarithmic-based mean for susceptibility, and a simplified weighting scheme targeted toward the MAT (Table 1). The development of a more accurate PSA methodology will allow the concept of ecosystem-based management to be incorporated into the MAT by highlighting species of concern with important ecosystem functions. This analysis will help shift the industry towards enhanced management and mend the gap in data-limited fisheries assessments.

2. METHODS

2.1. Study species

We evaluated the global vulnerability status of 32 wild-caught species from more than 30 fisheries using a modified PSA model for small reef fish. The fish selected for the analysis included the top 20 species in the trade by volume from the year 2011 based on US fish import records (Rhyne et al. 2014, 2017b). An additional 12 species were selected based on overlap with prior PSA studies (Fujita et al. 2014, Dee et al. 2019). Species life-history data was sourced preferentially from peer-reviewed literature, FishBase (Froese & Pauly 2019), and finally grey literature. Data for the susceptibility factor of trade vulnerability and cyanide use were sourced from the Global Biodiversity Information Facility website (GBIF 2019) for species distribution information, and volume in trade and country of highest export was sourced from www.aquariumtradedata.org (Rhyne et al. 2015). Primary literature or FishBase data were used to assess encounterability depth and ecological niche. If a data discrepancy was observed between data in peer-reviewed literature and FishBase, the most recent citation was used. When life-history data were unavailable for a species, the average measure of that factor for species in the same genus was applied as an estimate. For all raw data scores and species-specific sources, see Supplement 2 at www.int-res.com/articles/suppl/m644p143_supp/.

2.2. PSA mathematical model

The widely used food fish PSA (Patrick et al. 2009, Hobday et al. 2011) evaluates fish stocks on 10 productivity factors and 12 susceptibility factors; from this data, vulnerability is calculated as Euclidean distance from the origin (3,1). We modified Hobday et al. (2011) and Patrick et al. (2009) by reducing the productivity and susceptibility factors used to 7 and 5, respectively. This modified PSA will be referred to as the MAF-PSA.

Given the data-deficient nature of fisheries in the MAT, productivity and susceptibility factors that were not applicable to the fishery were eliminated to reduce the probability of error. Productivity serves as an indirect measurement of a species' ability to reproduce and its resiliency to changing conditions. A high productivity score (p = 3) indicates a fish with low vulnerability to fishing, whereas low productivity (p = 1) indicates high vulnerability. Productivity was calculated based on 7 factors: maximum age, maximum size, trophic level, length at maturity, fecundity, breeding strategy, and larval duration. A weighted arithmetic mean was used to calculate the productivity score:

$$p = \frac{\sum_{i=1}^{7} x_i \times b_i}{\sum_{i=1}^{7} b_i} \quad (2)$$

where x_i is the productivity factor score and b_i is the factor weight.

Susceptibility analyzes the likelihood that a fishery will have a negative effect on a population. Consistent with prior PSAs (Patrick et al. 2009, Hobday et al. 2011, Fujita et al. 2014, Okemwa et al. 2016, Dee et al. 2019), a high susceptibly score (s = 3) indicates high vulnerability, whereas low susceptibility (s = 1) indicates low vulnerability. Susceptibility was calculated based on 5 factors: vulnerability to trade (combination of volume in trade and geographic distribution), cyanide fishing, average encounterability depth, ecological niche, and aquarium suitability. Specifically, geographic distribution was scored based on whether a species had a global, regional, or endemic distribution. A weighted mean of logarithms expressed as an exponential function with base 10 raised to the power of the weighted logarithmic mean was used to calculate susceptibility score.

$$s = 10^{\frac{\sum_{i=1}^{5} \log(y_i) \times a_i}{\sum_{i=1}^{5} a_i}} \quad (3)$$

where y_i is the susceptibility factor score and a_i is the factor weight (see mathematical proof in Supplement 1).

Following Hobday et al. (2011), raw data were binned into a score of 1, 2, or 3 (low−high). Additionally, weights of 1 or 2 were assigned to each factor. Breeding strategy and fecundity (productivity traits) and trade vulnerability (a susceptibility trait) were each given twice the weight (2) of all other factors to indicate their importance in determining the overall vulnerability score. We provide an in-depth explanation of each factor assessed in the PSA and all corresponding data bin parameters in Table S1.

Vulnerability is estimated as the Euclidean distance from the origin (see Eq. 1) as productivity is plotted in reverse order. The vulnerability scores for this PSA range from 0–2.82, where larger numbers indicate higher vulnerability to fishing.

In Hobday et al.'s (2011) PSA, they classified species as either sustainable, moderately sustainable, or unsustainable based on their vulnerability score. We maintained their sustainability bin demarcation, but present a more objective system of data classification. Patrick et al. (2009) discussed the need for a stronger mathematical basis to support vulnerability cut-off points and suggested clustering as a solution. Instead of using discrete vulnerability score benchmarks to classify high, low, and medium vulnerability scores, a Gaussian mixture model (GMM) was applied to objectively classify species vulnerability outputs into sustainability categories. The GMM was run in Python v.3.7 (https://github.com/gbaillargeon/gbaillargeon/blob/master/GMM_PSA_DataClassification.md). Due to the multimodal nature of the component data (productivity and susceptibility), a GMM was the most appropriate clustering algorithm for our data. The silhouette coefficient (SC) was evaluated for various numbers of clusters (Rousseeuw 1987); we determined that 4 clusters (SC = 0.4) was the best fit for the current MAF data set rather than the traditional 3 clusters (SC = 0.29). The cluster groupings represent the sustainability status of the fish, corresponding to highly sustainable, sustainable, moderately sustainable, and unsustainable. These sustainability labels were designated based on vulnerability scores within that cluster, and verified using well-studied benchmark species. The purpose of clustering is to group species into vulnerability bins based on similarities between their productivity and susceptibility scores. This method eliminates misclassifying data based on pre-determined vulnerability data bins that subjectively divide the PSA plot into thirds. The yellow tang *Zebrasoma flavescens*, green chromis *Chromis viridis*, clownfish species *Amphiprion* spp., and Bangaii cardinalfish *Pterapogon kauderni* have robust life-history and fishery data and were used as benchmarks to assess the accuracy of the PSA results and GMM clustering. Using qualitative and quantitative data on these species from prior risk assessments allowed us to check whether the PSA and GMM effectively assessed these species. Naturally, species with life-history and fishery traits similar to the benchmark fish would cluster into that distinct group. Using GMM clustering allows the PSA to act more effectively as a model to estimate the vulnerability of harvested fish and remain applicable to a variety of fisheries.

2.3. Management scenario and country-specific PSA

To determine whether increased management of MAF will have an effect on the sustainability of these fishes, we adjusted our PSA to include management as an additional susceptibility factor. To simulate species-specific management, all of the management scores were set at 1, indicating well-managed fisheries. The score for cyanide fishing was also set to 1, because in well-managed fisheries it is assumed that the instance of illegal and destructive fishing methods like cyanide fishing would be eliminated (Table S2).

We conducted a second, country-specific PSA that was tailored to assess a species within the country of highest export. This analysis can be applied to any country that exports MAF. The data for the country-specific PSA only comes from one country, which changes the volume in trade, geographic distribution, and cyanide use. Here, trade vulnerability was calculated as a function of volume in trade, geographic distribution (widespread, limited, or scarce) within the country assessed, and number of exporting countries (Table S3).

2.4. Model validation

A least-squares multiple linear regression was used to test the validity of the assumed linear relationship between susceptibility and productivity. Microsoft Excel v.2019 was used to run all statistical tests. The strength of the R^2-value was evaluated to determine how closely aligned productivity and susceptibility were to each other, and to vulnerability. Additionally, we ran a multivariate linear analysis to test the relationship between factors that comprise susceptibility and productivity and their respective scores. To validate the vulnerability scores and corresponding sustainability bin, we compared these values to IUCN assessments (see Table 2).

To test whether the GMM could logically cluster a highly variable data set into tiers of sustainability bins that reflect the traditional PSA structure, we combined the MAF-PSA data with a subset of 41 fish species from a NOAA data set (from Patrick et al. 2009). When plotting the combined data set of MAF-PSA data (n = 32) and the NOAA-PSA subset (n = 41; Patrick et al. 2009), the SC showed that 3 clusters was the best fit (SC = 0.51). We also compared NOAA overfished and overfishing status (for 2008) against the GMM sustainability classification for each species evaluated in the NOAA data set to further test whether our sustainability clusters aligned with external assessments of stock status (Table S4).

3. RESULTS

The analyzed fish varied in geographic distribution, volume in trade, and life-history strategies (Fig. 1). Most species were moderately to highly productive (p = 1.78–2.67) and mildly to highly susceptible to fishing (s = 1.0–2.29) (Fig. 1). The range of traits exhibited by the species throughout this analysis is common among MAF (Fig. 1). Many species scored similarly for key productivity factors: low trophic level, small length at maturity, breeding strategy of demersal egg layers, and small maximum size (Fig. 1). Therefore, maximum age, larval duration, and fecundity were largely responsible for differentiating the productivity scores (Fig. 1). For susceptibility, all of the factors had a wide scoring distribution. The cyanide-use factor was scored on a binary (1 or 3) scale, with many species scoring as 1 (not susceptible). The large standard deviation observed when calculating the average score of each factor resulted from the variety of life-history traits or fishing pressures each MAF experiences (Fig. 1).

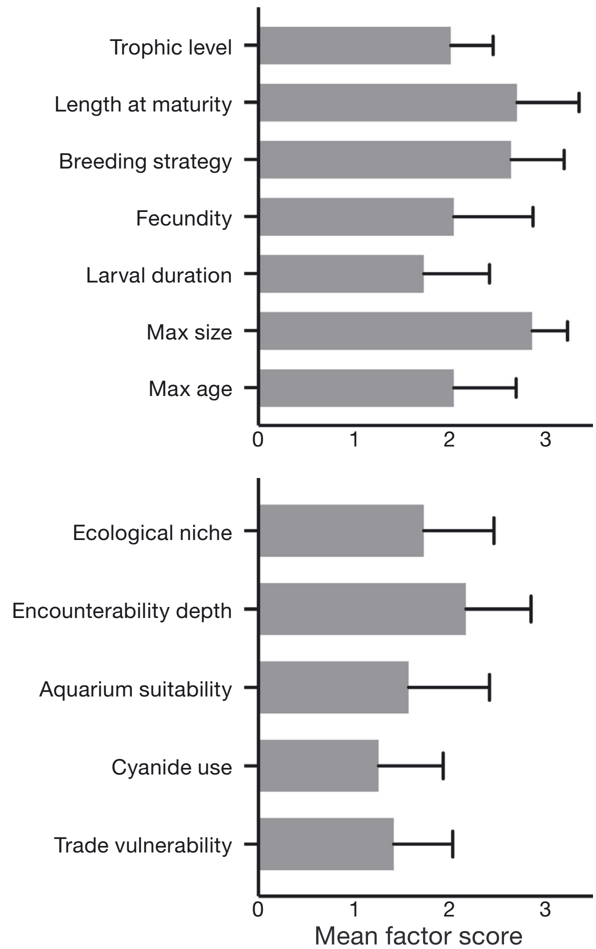

Fig. 1. The average (±SD) factor scores for all susceptibility (top) and productivity (bottom) factors (n = 32)

In terms of vulnerability score, *Dascyllus trimaculatus* scored the lowest (v = 0.42) and *Pterapogon kauderni* (v = 1.63), *Paracanthurus hepatus* (v = 1.45), and *Nemateleotris decora* (v = 1.23) scored the highest (Table 2, Fig. 2). The most sustainable fish in the PSA were *D. trimaculatus*, *Zebrasoma flavescens*, and *Centropyge bispinosa* (Table 2, Fig. 2). All of

Table 2. Comparison of current IUCN status, productivity (*p*), susceptibility (*s*), vulnerability (*v*) score, and sustainability status for each species evaluated (n = 32). Sustainability categories are: highly sustainable (HS), sustainable (S), moderately sustainable (MS), and unsustainable (U). **Bold** IUCN status indicates the last evaluation was 10+ yr ago. NE: Not Evaluated; LC: Least Concern; E: Endangered

Species	*v*	*p*	*s*	Sustainability status	IUCN
Dascyllus trimaculatus	0.42	2.67	1.26	HS	NE
Zebrasoma flavescens	0.46	2.56	1.12	HS	LC
Centropyge bispinosa	0.46	2.56	1.12	HS	**LC**
Chromis viridis	0.48	2.67	1.35	HS	NE
Centropyge loricula	0.51	2.56	1.26	HS	**LC**
Amphiprion clarkii	0.56	2.56	1.35	HS	NE
Chrysiptera hemicyanea	0.61	2.56	1.41	HS	NE
Holacanthus ciliaris	0.75	2.33	1.35	S	NE
Labroides bicolor	0.76	2.44	1.51	S	**LC**
Labroides dimidiatus	0.76	2.44	1.51	S	**LC**
Chrysiptera cyanea	0.78	2.33	1.41	S	NE
Dascyllus aruanus	0.79	2.22	1.12	S	NE
Synchiropus splendidus	0.80	2.33	1.44	S	NE
Dascyllus melanurus	0.82	2.22	1.26	S	NE
Centropyge bicolor	0.83	2.56	1.70	S	LC
Pomacanthus imperator	0.83	2.44	1.62	S	**LC**
Holacanthus passer	0.84	2.33	1.51	S	**LC**
Chrysiptera parasema	0.85	2.22	1.35	S	NE
Labroides phthirophagus	0.89	2.33	1.59	S	**LC**
Amphiprion percula	0.89	2.22	1.44	S	LC
Sphaeramia nematoptera	0.97	2.56	1.70	S	NE
Chrysiptera springeri	0.97	2.22	1.59	S	NE
Pomacanthus xanthometopon	0.99	2.33	1.73	S	**LC**
Amphiprion ocellaris	1.05	2.33	1.82	S	NE
Pseudocheilinus hexataenia	1.08	2.11	1.62	S	**LC**
Premnas biaculeatus	1.09	2.00	1.44	S	NE
Gramma loreto	1.19	1.89	1.41	S	**LC**
Nemateleotris helfrichi	1.22	1.78	1.00	MS	LC
Nemateleotris decora	1.23	1.78	1.12	MS	LC
Nemateleotris magnifica	1.23	1.78	1.12	MS	**LC**
Paracanthurus hepatus	1.45	2.33	2.29	U	LC
Pterapogon kauderni	1.63	1.78	2.08	U	E

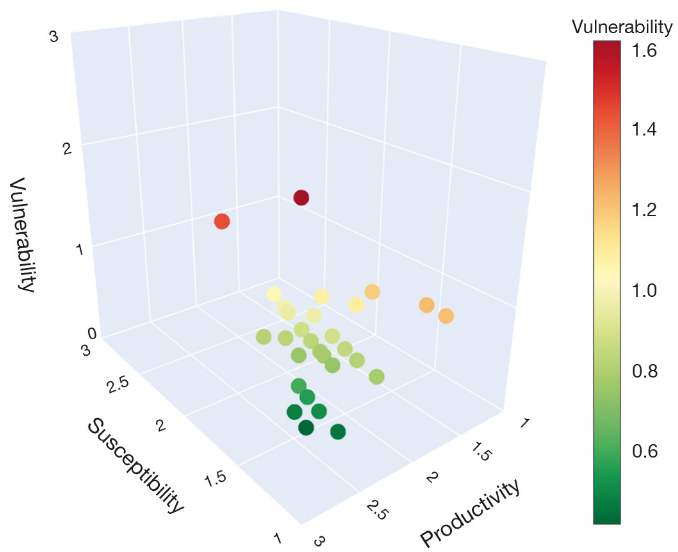

Fig. 2. Results of the productivity, susceptibility, and vulnerability score for all marine aquarium fish species evaluated (n = 32). Color gradation from green to red indicates an increase in vulnerability score

these fish exhibit very high productivity characterized by quick maturity and high fecundity, and very low susceptibility because of their wide geographic distribution, low chance of being caught with cyanide, and not occupying specialized ecological niches. *P. kauderni* is listed as Endangered by the IUCN and is the most vulnerable fish in this PSA. This high vulnerability can be attributed to their specialized reproductive strategy, high volume in the aquarium trade, and extremely narrow geographic distribution (Fig. 3).

The SCs of the GMM empirically determined that 4 clusters fit the data best based on the Mahalanobis distance (point-to-point distance) between points (Figs. 2 & 3). The 4 cluster GMM was applied to the MAF-PSA output to assess its spatial distribution and implications for management. Vulnerability scores demonstrated that 84.4% of species evaluated could be considered sustainable (Table 2). The clustering algorithm showed a highly sustainable group near the origin (7 species), a sustainable group (20 species), a moderately sustainable–special case group (3 species), and an unsustainable group (2 species) (Fig. 3). Two of the 32 (6.3%) species in this PSA, *P. kauderni* and *Paracanthurus hepatus*, were clustered together and ranked as unsustainable.

The results of our country-specific PSA demonstrated that 17 of the 32 species were less sustainable at the country level in comparison to the global analysis (Fig. 4). The shift in vulnerability score from a global to country level PSA (i.e. Δv = global − country v score) ranged from $\Delta v = 0.18$ to -0.55, where a positive change indicates increased sustainability and a negative net change indicates a decreased sustainability (Fig. 4). When comparing average vulnerability scores between the global and country-specific MAF-PSA, the average shift was towards

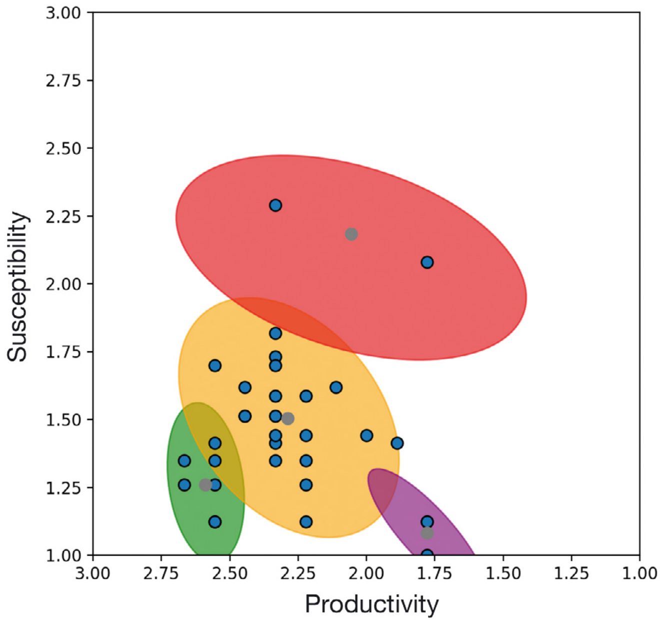

Fig. 3. Clustering output from a Gaussian mixture model with 4 clusters (silhouette coefficient = 0.4), with clustering based on productivity and susceptibility scores for all marine aquarium fish species in the analysis (n = 32). Gray points: cluster centroids. Clusters represent sustainability categories: green: highly sustainable; yellow: sustainable; purple: moderately sustainable — special case; red: unsustainable

higher vulnerability ($\Delta v = -0.13 \pm 0.20$ [SD]). Trade vulnerability scores changed based on volume in trade, geographic distribution in country, and the number of countries from which the fish were sourced. When management was introduced as a susceptibility factor in the global PSA, there was an average shift towards increased sustainability (Δv = 0–32%).

The vulnerability scores determined by this new global PSA model averaged 0.52 ± 0.41 lower (paired t-test, $t = 5.82$, n = 21, $p < 0.001$; Fig. 5 & Table S5) than the most recent PSA tailored to marine aquarium fish (Dee et al. 2019). The majority of species decreased in susceptibility score and in some cases both susceptibility and productivity scores, moving their position on the PSA plot closer to the origin (indicating increased sustainability). It was determined that changes in vulnerability score between the 2 studies were due to differences in susceptibility ($\bar{X}$ difference = 0.78, $t = 12.04$, n = 21, $p < 0.001$) and not productivity ($\bar{X}$ difference = 0.12, $t = 1.36$, n = 21, $p < 0.5$). These shifts can be attributed to using a different set of susceptibility factors, an arithmetic mean of logarithms for susceptibility, and modified data bins.

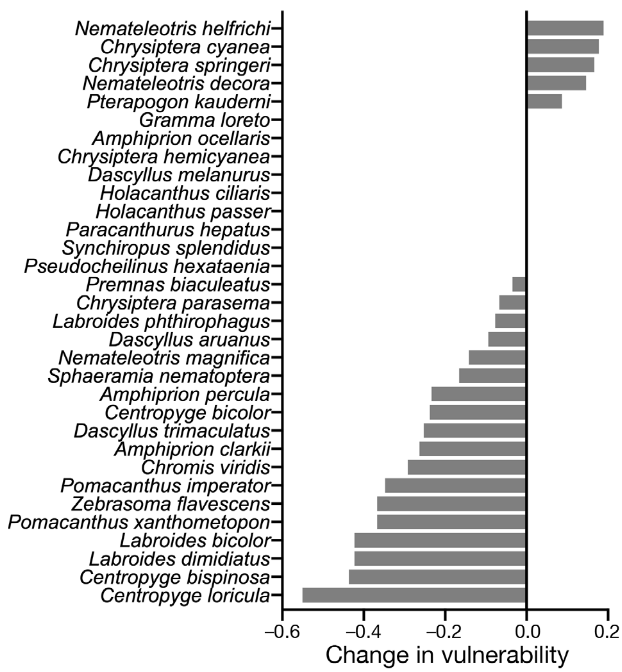

Fig. 4. Change in vulnerability score by species (n = 32) between the global and country-specific productivity–susceptibility analysis output. Positive variance indicates that the global vulnerability is greater than the country-specific vulnerability; negative variance indicates that the country-specific vulnerability is greater than the global vulnerability estimate

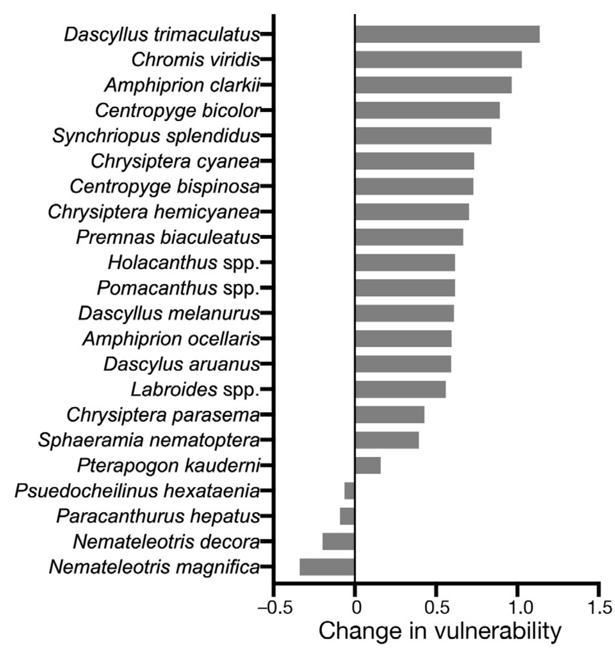

Fig. 5. Change in vulnerability score in overlapping species (n = 28) between Dee et al. (2019) and this study. Positive variance indicates that Dee et al. (2019) reported a higher vulnerability score than our study; negative variance indicates that we reported a higher vulnerability score than Dee et al. (2019)

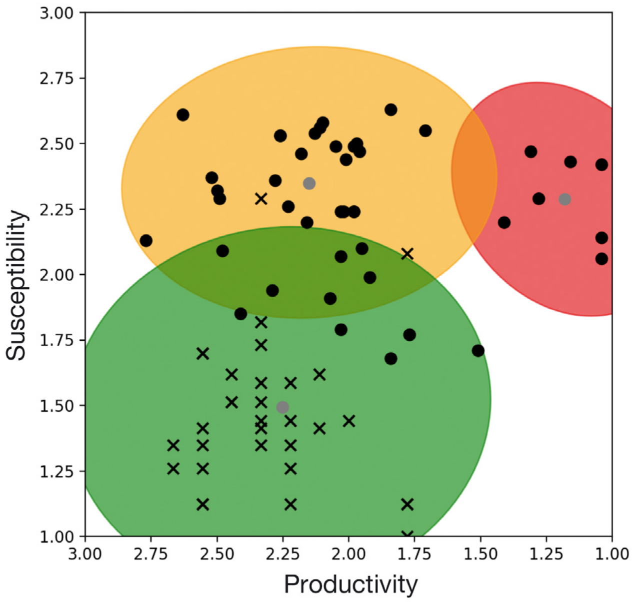

Fig. 6. Clustering output from a Gaussian mixture model with 3 clusters (silhouette coefficient = 0.51) of a combined data set composed of 2 productivity–susceptibility analysis datasets: marine aquarium fish (×) and selected NOAA data sets (Patrick et al. 2009) (●). Clustering based on productivity and susceptibility scores from each analysis for all fish species (n = 75). Gray points: cluster centroids. The clustering groups represent sustainability categories: green: sustainable; yellow: moderately sustainable; red: unsustainable

IUCN assessments and our sustainability rankings aligned well, given that 75% of fish deemed Least Concern by the IUCN also ranked as sustainable in our analysis. Excluding the unique case of the firefishes *Nemateleotris* spp., the alignment improved to 94% (Table 2). Overall, the IUCN assessments for those species evaluated and our vulnerability ratings were closely aligned. A 3 cluster GMM was applied to 75 species combining our PSA data set (32 species) with a subset of fish (43 species) from the NOAA-PSA (Patrick et al. 2009). There was a group (green in Fig. 6) with low vulnerability scores for susceptibility and productivity. A second grouping (yellow in Fig. 6) had an increased susceptibility score, while the final grouping (red in Fig. 6) had more vulnerable scores for both susceptibility and productivity. The sustainability category of the NOAA species determined by this 3 cluster GMM was in 75% alignment with the 2008 status of overfished and overfishing for each stock. It is interesting to note that the most vulnerable species (*P. kauderni* and *Paracanthurus hepatus*) in the analysis of 32 MAF clustered in the moderate group when more species were included in the analysis (Fig. 6).

4. DISCUSSION

The results of our PSA provide a semi-quantitative measure of the vulnerability and corresponding sustainability status of each of the 32 MAF evaluated. Our novel application of the GMM clustering algorithm objectively characterized the sustainability status of MAT species using the modified MAF-PSA. The customization of the PSA to the MAT fishery through alterations to the mathematical framework and factor selection allowed the vulnerability of MAF to be estimated with more accuracy than prior studies. This is demonstrated by the higher R^2 value of linear regression results when fitted to productivity and susceptibility factor scores. We demonstrated how our PSA and GMM methodology were applied to MAF and combined MAF-NOAA data sets, and that the GMM system of classification is applicable to any fishery system. Lastly, we made comparisons of the impact of global versus country-specific PSAs, and the impact of species-specific management on the vulnerability score.

4.1. GMM clustering of the PSA: a predictive tool

The sustainability of species can be better estimated by a PSA targeted towards assessing a specific fishery and then applying an objective system of classifying those data (i.e. a GMM). The use of GMM clustering can replace static vulnerability benchmarks, such as the proposed vulnerability break points used in previous studies (Patrick et al. 2009, Hobday et al. 2011). This is more in line with an adjustable sustainability benchmark suggested for fisheries that have fluctuations in yearly catch and local abundance (Worm et al. 2009, Cooke et al. 2016). Using clustering to determine sustainability groupings is a more effective and flexible means of data classification than choosing a subjective number of groupings without fitting it to the fishery-specific data set.

We observed that the GMM effectively clustered the PSA output in a spatial pattern that closely resembled that of the traditional PSA vulnerability cutoff marks; however, it more effectively grouped species with similar productivity and susceptibility scores together (Figs. 3 & 6). Given that the vulnerability score is the Euclidean distance from the origin to an x–y point (productivity, susceptibility), the location of 2 points with nearly identical vulnerability scores could be different on the PSA graph. For instance, a species with a susceptibility score of 2 and productivity score of 1 will have the same vulnerability score but different spatial representation on the PSA graph as a species with a susceptibility score of 1 and productivity score of 2. The factors that would cause either of these species to increase in vulnerability would therefore be different, and a singular management strategy could not be developed to adequately address the threats to each of these species. This situation would arise by using vulnerability score cut-off points that split the graph in equal thirds. Since the purpose of grouping the PSA output is to categorize data points based on sustainability (an index of risk), mathematically grouping points that are most similar using a GMM is the best approach.

Using the GMM clustering algorithm to characterize the PSA results creates a predictive indicator for the sustainability status of any given MAF species. Once cluster centers are calibrated, incoming data points will be clustered into one of the existing categories. Additionally, as the data set grows, the number and placement of the clusters can be re-assessed by analyzing the SC. For instance, if an arbitrary data point (productivity, susceptibility) was entered into the GMM, the model would cluster this point based on the Mahalanobis distance from that point to the nearest cluster center. In theory, every potential productivity and susceptibility score could be inputted into the GMM and a gradient of sustainability could be outputted based on realistic cluster centers generated from a comprehensive, baseline data set. Species with similar productivity and susceptibility scores would be spatially grouped on the PSA graph into clusters that have distinct management implications (Figs. 3 & 6). As the number of species in the MAF-PSA increases, the clusters should become more vertically tiered and clearly distinguish the sustainable, moderately sustainable, and unsustainable clusters.

The clustering of the combined NOAA–MAT data set demonstrated that a highly varied data set, representative of any fishery, could be logically clustered into 3 tiers of data (Fig. 3). From a mathematical and visual perspective, the pattern of GMM clustering was very similar between the combined NOAA–MAF and the MAF-only data sets, strengthening our argument that GMM clustering is a reliable way to categorize the sustainability of species. MAF appear to be less vulnerable than food fish species when the PSA is plotted with both sets of data (Fig. 6). However, the data points themselves are not comparable because they are the result of 2 different PSA approaches. Instead of making direct species vulnerability comparisons, the purpose of clustering the MAF-PSA and NOAA Toolbox PSA output together was to show that the PSA output would cluster in a characteristic, 3 tiered pattern. Our model and methods were verified by the high degree of alignment between IUCN evaluations of MAF in the MAF-PSA, and NOAA overfished and overfishing status, and their respective clusters representative of sustainability status using GMM clustering (Table S4). This clustering method demonstrates that susceptibility is the first determinant to increase a species' vulnerability, a conclusion which is supported by quantitative evidence from prior PSA studies (Hordyk & Carruthers 2018).

4.2. Sustainability trends

The PSA estimated vulnerability scores, while the GMM provided a general estimate of how the vulnerability score was interpreted. The majority of fish evaluated in our PSA could be classified as having low susceptibility and high productivity scores, deeming them sustainable. This was largely due to most fish having high productivity (average $p = 2.28$). Productivity and susceptibility scores were both used to calculate vulnerability; however, it was observed that the majority of fish share similarities in life-history traits and therefore their productivity scores fell within a narrow range ($p = 1.76$–2.67). It was the susceptibility score that distinguished fish with similar productivity scores into their distinct sustainability categories (Fig. 2). From the susceptibility perspective, the nature of the aquarium trade is to harvest fish with hand nets at shallow depths, which limits the fishery's impact on a fish population due to the constraints of the fisher's method of capture. For instance, if a fish has a varied depth distribution, the chances of it being completely fished out are low (Lindfield et al. 2014). Similarly, fish with large geographic distributions are not at risk of becoming threatened on a global scale, though localized depletions are possible (Roberts & Hawkins 1999). However, susceptibility should be looked at as the preliminary indicator of the potential long-term impacts a fishery will have on a stock, given its influence on the vulnerability score. A species with a high productivity and low susceptibility score, like many of those in the sustainable cluster, are not threatened by the MAT. A species with a high productivity and moderate susceptibility score, like those at the 'top' of the sustainable cluster, have the potential to transition into a moderately sustainable cluster if fishing pressure (measured by susceptibility) is increased. Therefore, it is recommended that these species be regularly monitored, especially those that are harvested in high numbers.

4.2.1. Sustainable fish

When analyzing the PSA outputs and GMM sustainability analysis of the MAF-only data, a few trends emerge: (1) the majority of MAF cluster as sustainable, (2) all of the firefish species cluster together, and (3) outliers are unsustainable. Within the 'highly sustainable' group (green in Fig. 3), there were several species that have long-term data or that have been fished at a high volume for a long period of time and remain abundant. Specifically, *Chromis viridis* and *Zebrasoma flavescens*, 2 species used to ground-truth our PSA results, were in this cluster. *Z. flavescens* has been monitored in Hawaii for decades and its population has remained relatively constant (Walsh 2014). *C. viridis* has a wide geographic distribution and is consistently the most traded species in the MAT (Roberts & Hawkins 1999), demonstrating that its high natural productivity makes it resilient to high fishing pressure. These 2 species share many common productivity and susceptibility traits with the other 5 species in the 'highly sustainable' cluster, justifying this classification.

4.2.2. Firefishes: special case

The grouping of the 3 firefish species as a distinct cluster was a special case. Although the placement of this grouping would suggest it be classified as moderately sustainable, by analyzing individual productivity (moderate) and susceptibility (very low) scores it can be seen that the firefishes are likely sustainable. The case of the firefish highlights an important point about how to interpret a PSA visualization (Fig. 2). Species shifted down and to the right of the central 'sustainable' cluster remain sustainable, whereas species shifted up and to the right enter the moderately sustainable to unsustainable zone. Conversely, species that are shifted down and to the left are highly sustainable while species shifted up and to the left are again in the moderately sustainable to unsustainable zone. All of the firefishes share very similar productivity and susceptibility traits unique to this group, so it is not wholly unexpected that they would cluster together.

4.2.3. Unsustainable species

Pterapogon kauderni and *Paracanthurus hepatus* comprise the 'unsustainable' cluster (Fig. 2). The GMM grouped these 2 species as a distinct cluster due to their high susceptibility and low productivity scores. The shape of the ellipse should be considered cautionary based on only 2 points. Similarly, the firefishes ellipse is composed of only 2 points since 2 of the 3 data points are identical. This was corrected by using the average standard deviation of the data points contained within the other ellipses to generate additional data points within the unsustainable and firefishes cluster groupings to produce a more accurate ellipse shape.

P. kauderni had the highest vulnerability (v = 1.63) of all MAF evaluated. Additionally, it was used as a benchmark species to test the accuracy of the PSA model, due to its known status of Endangered by the IUCN and threatened on the United States Endangered Species Act. Its high vulnerability score was driven by its very low productivity and high susceptibility. The species' specialized breeding strategy of mouth brooding a small number of eggs that undergo direct development makes replenishing the population challenging; thus, they have low productivity. High susceptibility is the result of its narrow geographic range in the Bangaii archipelago coupled with its high trade volume. Given their high vulnerability and Endangered ICUN status, we recommend it be listed as a Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) Appendix II species. This distinction would require trade restrictions, allowing the wild population to rebound and the local fishery to be rebuilt in a sustainable manner. Until trade is restricted and populations recover, the PSA can be used to recommend that consumers purchase aquacultured *P. kauderni*.

P. hepatus also clustered as unsustainable. This species has recently drawn a considerable amount of concern in the media (King 2016, Militz & Foale 2017) for fear of demand becoming too high for this iconic species to be sustainably fished, although there is no empirical evidence to support this assumption (Veríssimo et al. 2020). The high susceptibility of this species is largely due to its high trade vulnerability score resulting from a fragmented geographic range and large number of fish in the trade. While work on producing this species in aquaculture continues (Dimaggio et al. 2017), it is recommended that the average consumer avoids this species, especially novice hobbyists.

4.3. Country-specific MAF-PSA

For many species, susceptibility can change depending on the location or scope of the PSA. The influence of susceptibility on the vulnerability score marks the importance of calculating it in a way that reflects how these fisheries operate. We re-assessed each MAF species and evaluated their vulnerability based on data from the country of highest export by species (see Supplement 4 for complete details). The sustainability of *Pomacanthus imperator*, a fish that is targeted by both artisanal food fisheries and the MAT, is explained by the MAF-PSA. Our analysis showed that this species has a high productivity, allowing it to sustain its population despite increased mortality due to fishing. When examining susceptibility at the country level, the incidence of cyanide fishing along with a reduced range makes it a more vulnerable species, shifting it from sustainable (v = 0.83) to moderately sustainable (v = 1.18). Although this species is not globally at risk, our analysis indicates that species management, such as trade reduction in countries where they are heavily fished (e.g. Philippines, Indonesia, Sri Lanka) would ensure this species remains sustainable.

When examining firefish at the country level, the PSA showed that as a group their susceptibility score increased by 0.34 but vulnerability only increased by an average of 0.06 (Fig. 5). These trends are explained by looking closely at each species. Only one firefish species, *Nemateleotris magnifica*, experienced an increase in vulnerability, whereas the vulnerability of the other 2 actually decreased. The Philippines is the sole exporter of high volumes of *N. magnifica* (>100 000 fish yr^{-1}), making their trade vulnerability high (s = 3). The other 2 firefish species are exported in much lower volumes across multiple countries, lowering their trade vulnerability score. These examples of the firefish and *P. imperator* highlight how the PSA becomes a much more powerful management tool when applied at the local or national level. Due to the results of the country-specific MAF-PSA, we recommend all future PSA analyses consider local-level assessments to more effectively align the results with management plans.

4.4. Management scenario

Through simulating species management programs in this PSA, the positive effect of such programs can be seen, as there was an overall 8.15% increase in sustainability across all species (see Supplement 3 for full results). Therefore, it is recommended that enhanced monitoring and management programs be developed for MAT fisheries. A well-accepted method of integrating sustainability initiatives, data-driven recommendations, and fishers is through marine tenure (Coulthard et al. 2014, Sethi et al. 2014). Especially in the small fishing villages of the Indo-Pacific and Kenya's coast, where the majority of MAF are caught, employing marine tenure would encourage fishers to preserve their resources and would empower the community to enforce fishing regulations. For instance, local catch limits imposed on unsustainable or moderately sustainable species would aid in population recovery. Another potential management tool is closing a certain location, or species, to fishing for a period of time if locals have seen a significant depletion of a once plentiful fish. A larger monitoring structure needs to be developed in order to document landings and export data in a simplified and accessible manner.

Lastly, species that are ranked as unsustainable or moderately sustainable should be the subjects of aquaculture. Aquaculture should be treated as a sustainability tool, and commercial aquaculture facilities should target vulnerable species for the development of breeding techniques. The supply-side solution of successful aquaculture will fulfil demand from the MAT while allowing wild populations to recover and fisheries to rebuild in a sustainable manner.

4.5. PSA model comparisons

Unlike a traditional arithmetic mean, using an arithmetic mean of logarithms to calculate susceptibility ensures that outlier values will not drastically sway the mean towards an extreme. An example of this can be seen when comparing vulnerability scores of clownfish across studies. In our PSA, *Amphiprion ocellaris* (v = 1.05) and *A. percula* (v = 0.89) appeared in the upper half of the sustainable cluster (Fig. 2). These species have a high productivity score, but also moderately high susceptibility due to high trade flow with a regional distribution, shallow encounterability depth, and because they occupy an important ecological niche (i.e. symbiotic relationship with anemones). Restrictions to scoring higher for productivity are the result of a short larval duration and relatively low fecundity per spawn. *A. clarkii* ranked as sustainable and had a much lower vulnerability score (v = 0.56) because of its decreased susceptibility (s = 1.35). The lower vulnerability estimate for *A. clarkii* can be attributed to its wider geographic distribution, lower trade volume, and greater fecundity than the other 2 species.

In another MAT-centric PSA study (Fujita et al. 2014), *A. ocellaris* and *A. percula* were ranked as the second and third most vulnerable fish in the trade, categorized as 'high vulnerability', which does not align with IUCN rankings or NOAA expert evaluations (Maison

& Graham 2016, Jenkins et al. 2017). Similarly, Dee et al. (2019) overestimated the vulnerability of *A. clarkii* (v = 1.53, Δv = 0.97) and *A. ocellaris* (v = 1.65, Δv = 0.595). These differences in our vulnerability estimations can be attributed to how susceptibility is calculated, as our productivity scores for these species are nearly identical. Therefore, using parameters based on food fish standards for a species with a symbiotic relationship and fragmented distribution has the consequence of overestimating vulnerability (Table S6).

A similar trend of inflated susceptibility score leading to a high vulnerability score can be seen in *Chrysiptera* sp., which are popular aquarium fish that have been harvested for decades. *Chrysiptera* sp. are known to be highly fecund and have a large geographic range. The life history of these fish indicate they are naturally resilient against increased fishing pressure, so a low vulnerability score would be expected. The MAF-PSA outputted low vulnerability scores and they clustered as either sustainable or highly sustainable. In comparison, Dee et al. (2019) saw increased vulnerability scores for these species, most likely due to the differences in factor selection and mean calculation (Δv = 0.595).

The benefit of the modifications made to the current PSA framework can be verified by comparing the results of a multivariate linear regression analysis testing the relationship between productivity, susceptibility, and vulnerability with the results of previous studies (Fujita et al. 2014, Dee et al. 2019). The basic assumption of the PSA vulnerability equation is that as productivity increases and susceptibility decreases, vulnerability will linearly decrease (and vice versa). A linear relationship, seen by an R^2 approximately equal to 1, shows the model is optimally operating. The relationship between all factor scores and vulnerability score was nearly linear (R^2 = 0.98). When examining the relationship between productivity score and productivity factor scores, all models were above 0.95. The difference between models is seen through the linear relationship between susceptibility and susceptibility factor scores. The multivariate linear regression revealed our analysis has the closest to linear relationship (R^2 = 0.97), followed by Dee et al. (2019) (R^2 = 0.86), and lastly Fujita et al. (2014) (R^2 = 0.71). This shows that by streamlining susceptibility factors to include only factors pertinent to a specific fishery, the linear relationship between the 2 improves. The results of the linear regression support that our model has the optimal combination of factors, weightings, and equations to calculate means, as represented in our study. See 'Statistics' in Supplement 1.

5. CONCLUSIONS

Given the success of the MAF-PSA model at predicting the sustainability status of MAF, there are significant implications for how to improve data-limited fisheries assessments, in addition to the more immediate implication of using this data to affect change within the MAT fishery system. For future PSAs aiming to assess any fishery, we suggest customizing productivity and susceptibility factors to align with the dynamics of the targeted species and operational system of the fishery. The improvements to the mathematical framework of the PSA model and its analysis should be implemented, as these mathematical alterations largely eliminated the issue of overestimating species vulnerability. Many of the IUCN assessments align with our sustainability rankings. To further strengthen IUCN evaluations, which largely rely on non-quantitative data and expert opinion and testimony, we recommend that a quantitative index, such as a PSA, be applied to these assessments. This would allow for more frequent re-assessments and increase the overall accuracy of these global assessments, especially for data-deficient species where population data is lacking. We recognize that management will be most effective at the national or local level, and recommend implementing PSAs customized for the country or stock-specific level to attain the most accurate vulnerability estimates. The methodology that has established this PSA can be applied to both global and specific stock assessments for both food and aquarium fisheries. The refined PSA methodology combined with GMM clustering of the output has the ability to provide accurate risk assessments with distinct management implications for fished species with limited catch, population, and life-history data.

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