



Original Research Article

Global conservation status of marine pufferfishes (Tetraodontiformes: Tetraodontidae)

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ABSTRACT

Puffers are biologically and ecologically fascinating fishes best known for their unique morphology and arsenal of defenses including inflation and bioaccumulation of deadly neurotoxins. These fishes are also commercially, culturally, and ecologically important in many regions. One-hundred-and-fifty-one species of marine puffers were assessed against the International Union for Conservation of Nature (IUCN) Red List Criteria at a 2011 workshop held in Xiamen, China. Here we present the first comprehensive review of puffer geographic and depth distribution, use and trade, and habitats and ecology and a summary of the global conservation status of marine puffers, determined by applying the International Union for Conservation of Nature (IUCN) Red List Criteria. The majority (77%) of puffers were assessed as Least Concern, 15% were Data Deficient, and 8% were threatened (Critically Endangered, Endangered or Vulnerable) or Near Threatened. Of the threatened species, the majority are limited-ranging habitat specialists which are primarily affected by habitat loss due to climate change and coastal development. However, one threatened puffer (*Takifugu chinensis* – CR) and four Near Threatened puffers, also in the genus *Takifugu* (which contains 24 species total), are wide-ranging habitat generalists which are commercially targeted in the international puffer trade. A disproportionate number of species of conservation concern are found along the coast of eastern Asia, from Japan to the South China Sea, with the highest concentration in the East China Sea. Better management of fishing and other conservation efforts are needed for commercially fished *Takifugu* species in this region. Taxonomic issues within the Tetraodontidae confound accurate reporting and produce a lack of resolution in species distributions. Resolution of taxonomy will enable more accurate assessment of the conservation status of many Data Deficient puffers.

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1. Introduction

Fishes of the order Tetraodontiformes (412 extant species in 10 families; Matsuura, 2014) are globally distributed in tropical and temperate seas and freshwaters. Their great diversity of size, structure, and behavior have attracted the attention of ichthyologists and biologists around the world (Matsuura, 2014; Tyler, 1980). The Tetraodontidae, henceforth simply called puffers (Nelson, 2006), are the largest family within the order Tetraodontiformes with 184 recognized species in 27 genera (Matsuura, 2014). They are most diverse in shallow, warm, tropical and temperate seas with some species entering brackish and freshwaters (Alfaro et al., 2007; Matsuura, 2014; Tyler, 1980) and 30 species occurring exclusively in freshwater (K. Matsuura pers. comm. 2015).

Puffers are notable for their arsenal of defenses including inflation and the use of potent toxins to deter predation. Inflation of the body as a form of predator defense is a major functional innovation exhibited by the puffers and their sister family, the Diodontidae (porcupinefishes). Inflation deters predation by making the prey item too large for potential predators to ingest (Wainwright et al., 1995; Wainwright and Turingan, 1997). In addition to inflation, puffers bioaccumulate and deploy potent neurotoxins which are thought to primarily serve as predator deterrents (Kodama et al., 1985; Miyazawa and Noguchi, 2001; Noguchi and Arakawa, 2008; Saito et al., 1985). Tetrodotoxin is the most notorious of puffer neurotoxins, however other neurotoxins such as saxitoxin can co-occur or are sometimes the dominant compound (Landsberg et al., 2006). Tetrodotoxin is highly toxic to humans and can cause rapid fatality preceded by symptoms such as gastrointestinal distress, numbness, paralysis, and respiratory failure (Isbister et al., 2002). Despite their toxicity, and in some cases because of it, puffers have a long and rich culinary history in East Asian cultures including China, Korea, and Japan (Ishige, 2001).

Puffer culinary preparations can range from low-value stews and processed fish products to extravagantly priced luxury commodities (NMFS, 1989). In Japan, two of the most desirable species, the Ocellate Puffer *Takifugu rubripes* and the Chinese Puffer *Takifugu chinensis*, sold for about 8000–15,000¥/kg (\$65–\$123/kg) at Haedomari Fish Market, a specialized puffer market in Shimonoseki City, in the 2010s (K. Matsuura pers. comm. 2015). These highly-desirable species are usually served in expensive restaurants as artfully arranged, thinly-sliced sashimi. Due to the potential to cause human fatality, puffer preparation is regulated through a national chef licensing program in Japan (Ishige, 2001) and is subject to strict import regulations, factors which may contribute to the elevated value of puffer species. However, exaggerated value can also be a result of increasing rarity, which can fuel the disproportionate exploitation of species (Courchamp et al., 2006). While puffer species have been locally harvested for food and/or medicine for centuries in East Asia and elsewhere, modern fishing, aquaculture and transportation technologies have enabled the demand for puffer to be supplied by global trade or supplemented by aquaculture (Kawata, 2003, 2012; NMFS, 1989). The introduction of modern fisheries techniques have depleted many commercial fish stocks worldwide (Hutchings, 2003; Myers and Worms, 2003). Overexploitation has been identified as the primary driver of localized and global extinction in marine populations (Dulvy et al., 2003) and there are indications that some puffer populations have been adversely affected by fishing to supply high demand (Kawata, 2003, 2012). For example, the Tiger Puffer, *Takifugu rubripes*, is the most expensive and preferred among puffers in Japan and experienced drastic localized declines in biomass since the late 1980s due to targeted fishing leading to overexploitation of the resource (Kawata, 2012). As the most highly desirable species have become rare, fishers have switched targets to formerly less desirable species which have been subsequently overexploited (Kawata, 2003).

The global conservation status of puffer populations has not been previously examined. As part of an ongoing initiative to assess the global status of 20,000 key marine species (Dulvy, 2013) for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2012), we assembled the first assessment of the global conservation status of 151 marine puffers, resulting in the first comprehensive review of their geographic and distribution, use and trade, and habitat and ecology and a summary of their global conservation status, determined by applying the International Union for Conservation of Nature (IUCN) Red List Criteria. Research and conservation priorities are then identified based on this work.

2. Methods

2.1. Red List process

The 151 globally recognized marine and estuarine puffers were assessed (the 33 species of freshwater puffers are not included in this analysis) using the IUCN Red List Categories and Criteria (IUCN, 2012). The majority were assessed during a workshop held in Xiamen, China in 2011. The conservation status of Tropical Eastern Pacific endemics was determined in 2008, and three species were assessed using the sampled approach to the Red List Index in 2009. The recently described *Canthigaster criobe* (Williams et al., 2012) and validated *Canthigaster petersii* (Allen and Erdmann, 2012) were assessed via electronic consultation with experts. A pending Red List assessment for the newly-described *Torguigener albomaculosus* (Matsuura, 2015) is not included in these results.

IUCN Red List evaluations are a rigorous process that includes follow-up consultation with experts and several IUCN internal reviews prior to publication on the IUCN Red List of Threatened Species website (<http://www.iucnredlist.org>). This involved process ensures that comprehensive, quantitative measures of extinction risk are applied and that the best available data are used to make these conservation determinations (Mace et al., 2008).

The IUCN Red List is based on the general idea that species with small geographic ranges or those exhibiting rapid population declines are at a higher risk of extinction (Mace et al., 2008; IUCN, 2012). Based on these two paradigms, five

criteria were developed: A) rapid population decline in the past, present or future; B) small geographic range size; C) small, declining population size; D) very small population size; and E) high probability of extinction in the wild based on quantitative analysis (Mace et al., 2008; IUCN, 2012).

Multiple criteria are needed to account for the fact that not all species will exhibit the same characteristics of endangerment (Mace et al., 2008). Thus, the available data for each species are compared against each criterion, and assigned to one of the eight categories: Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), and Data Deficient (DD) (IUCN, 2012). One of the three threatened categories (CR, EN, or VU) is assigned if the specific-specific data meets or exceeds the thresholds for that category in one of the five criteria (see IUCN, 2012 for further details regarding specific thresholds for each criterion). If a species nearly meets the threshold for a VU listing, it is assigned NT; in specific cases, a species can be listed as Near Threatened if the cessation of a conservation or management scheme is likely to lead to population declines in the near future. If there are no known threats or the species is not close to meeting the threshold for a VU listing, it is assigned LC. Finally, a species is listed as Data Deficient if there are insufficient data to make a justifiable application of the Categories and Criteria. For example, taxonomic uncertainty may limit knowledge of the complete geographic distribution or threats are known but associated population declines are poorly quantified (IUCN, 2012).

Specific terminology has been defined to ensure consistent application of the IUCN Red List criteria and does not always follow the biological usage. For example, the term 'population size' (required for criteria A, C and D) refers to mature individuals only, as these are likely to contribute to the next generation, and the term 'generation' or 'generation length' (required for criteria A, C and E) reflects the turnover rate of the mature individuals (IUCN, 2012). Two measures of geographic range size are also defined in the methodology to reflect how characteristics of a species distribution affects its extinction risk. The Extent of Occurrence (EOO) is essentially a minimum bounding geometry around the sites in which the species occurs and reflects the spatial distribution of a species' extinction risk. The Area of Occupancy (AOO) is the area within the EOO that is occupied by the species, measured using a 4 km² grid, and reflects the understanding that there may be substantial unoccupied and/or unsuitable habitat within the EOO (IUCN, 2012). Further details and definitions can be found in IUCN (2012) and IUCN Standards and Petitions Subcommittee (2017).

In preparation for IUCN Red List evaluation, species-specific data were collected on the taxonomy, distribution (including depth distribution), population trends, ecology, utilization, threats, and conservation measures, which are required documentation for all IUCN Red List assessments (IUCN, 2013).

Following data compilation, each species was individually reviewed by regional and international experts in a workshop held in Xiamen, China, in 2011. Following technical and content reviews, the assessments are submitted for a final consistency check by IUCN prior to inclusion on the publicly available IUCN Red List website. All assessments were published by December 2014.

2.2. Spatial analysis

Geographic distribution maps were created for each species in ArcGIS 10.1 based on occurrence records and expert knowledge. For the majority of marine puffers, which occupy shallow, coastal habitats, maps were created using a standard basemap that either follows a maximum depth of 200 m or a 100 km buffer from the coastline, whichever is further from the shore (e.g. Comeros-Raynal et al., 2012, 2016). Although this method provides a consistent representation of the distribution of shallow, coastal species, it does not accurately reflect the distribution of more oceanic species. Therefore, the maps for the four species with known oceanic tendencies (*Lagocephalus lagocephalus*, *Lagocephalus lunaris*, *Lagocephalus sceleratus*, and *Sphoeroides pachygaster*) were digitized by hand, including known and inferred occurrences. Each map was reviewed by taxonomic experts and edited to reflect the best available information on the species' ranges.

To determine biodiversity patterns, each polygon was transformed into the World Cylindrical Area projected coordinate system and converted into a 10 km by 10 km raster grid. A cell was considered occupied if the species' distribution polygon filled more than 50% of the cell area and assigned a value of 1, while all unoccupied cells were assigned a value of 0. Species richness patterns were calculated by summing the number of occupied cells. This was done for all species and subsets of species depending on threat levels and utilization.

Our intent in exploring spatial trends in species richness in this manner is to highlight large geographic regions that may require future research and/or conservation measures. The use of species richness analyses such as those presented here for site-based conservation is not ideal, as other metrics can provide more efficient representation of species (e.g., Prendergast et al., 1993; Csuti et al., 1997; Orme et al., 2005; Albuquerque & Beier, 2015). Furthermore, the generalized distribution maps are relatively broad in scale, and should be supplemented fine-scale surveys at specific localities prior to the identification of site-based conservation priorities (IUCN, 2016).

2.3. Habitat designations

Habitat information was available for 141 species. The following major habitats were assigned to each species based on its occurrence in these environments: coral reef, rocky reefs/rocky bottoms, artificial structures, mangrove, seagrass, tidepools, estuary, sandy bottoms, muddy bottoms, pelagic, deepwater (>200 m), and freshwater (IUCN, 2012; Salafsky et al., 2008). Due to the inconsistent availability of habitat preference information, all occurrences were equally weighted with no consideration given to major habitats and peripheral habitats. Ontogenetic partitioning of habitat was disregarded as detailed information on

habitat use by different life stages was only rarely available. A species was considered a habitat specialist if it was recorded from only one major habitat; if it was recorded from more than one habitat, it was considered a habitat generalist.

3. Results and discussion

3.1. Puffer spatial distribution

Of the 151 primarily marine and estuarine puffers assessed as part of this project, the highest diversity is found in the Indo-West Pacific, from southern Japan to northern Australia and from Indonesia to Papua New Guinea (Fig. 1), with a maximum of 37 species per 100 km² grid cell.

Diversity generally decreases as one moves east to the Pacific Ocean or west to the Indian Ocean from the center of diversity in the Banda Sea. High densities were also recorded around the north coast of Papua New Guinea and the east coast of Australia. The one main exception to this general pattern is an area of high diversity along the east coast of Africa, from Kenya to South Africa, with up to 27 species per 100 km² grid cell. As most puffers are coastal species, the open ocean is relatively depauperate, with only four widely-distributed, pelagic species.

Maximum depth and depth range information was available for 149 species. Of these species, the majority were restricted to maximum depths of less than 50 m. The majority of species (67%) occupied depth ranges (maximum depth – minimum depth) of 50 m or less. Forty-two percent of all puffer species have depth ranges of less than 25 m and 18% have ranges of less than 10 m. Further research may lead to reports of occurrences at increased depths and/or depth ranges in marine puffers.

3.2. Habitat and ecology

Puffers are found worldwide in tropical and sub-tropical waters, are predominantly marine or estuarine, and occupy a variety of habitats. The 141 puffers that could be assigned to at least one habitat type occupied up to seven different habitats, with the modal number of occupied habitats being two. Most tetraodontids (71%) occupied three or fewer habitats. The most frequently recorded habitats of occurrence in descending order are sandy bottoms, estuaries, muddy bottoms, coral reefs, rocky reefs, seagrasses, mangroves, artificial structures, pelagic open water, tidepools, freshwater, and deepwater habitats >200 m. Forty-eight percent of puffers were associated with habitat-forming species (corals, mangroves or seagrasses) which are vulnerable to anthropogenic threats (Carpenter et al., 2008; Polidoro et al., 2010; Short et al., 2011). Twenty-six puffer species (19%) were only recorded in a single habitat, and thus are considered habitat specialists. Many of these habitat specialists are found in habitats which are common and well-connected, such as open-water or sandy substrates. Some are specialists in fragmented or vulnerable habitats, such as forested mangrove creeks or coral reefs. The largest number of habitat specialists occupy coral reef (11 species, 42% of habitat-specialists), although most puffers associated with coral reefs are also found in other habitats.

Diet information, ranging in quality from gut-content analyses (Allen and Randall, 1977; Guzman and Lopez, 1991; Hiatt and Strasburg, 1960; Randall, 1974) to anecdotal observations was available for 74 species (49% of assessed species). Fifty-one species (69%) are primarily carnivorous, 14 (19%) are primarily omnivorous, seven (9%) are primarily herbivorous, and two (3%) are primarily corallivorous. Despite these primary feeding preferences, there is a tendency within the group for generalist feeding behavior: 38% of species qualify as omnivorous based on the presence of both animal and plant matter, regardless of the quantity. Most puffers (93%) are generalists in their feeding preferences, consuming multiple prey items as adults. The most commonly reported prey items are mollusks and crustaceans.

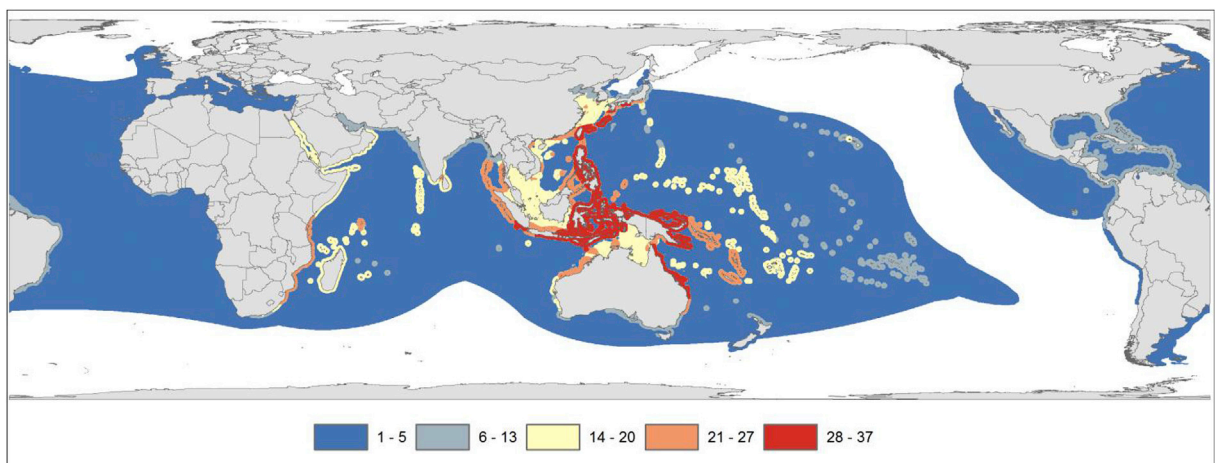


Fig. 1. Species richness of marine and estuarine Tetraodontidae of the world.

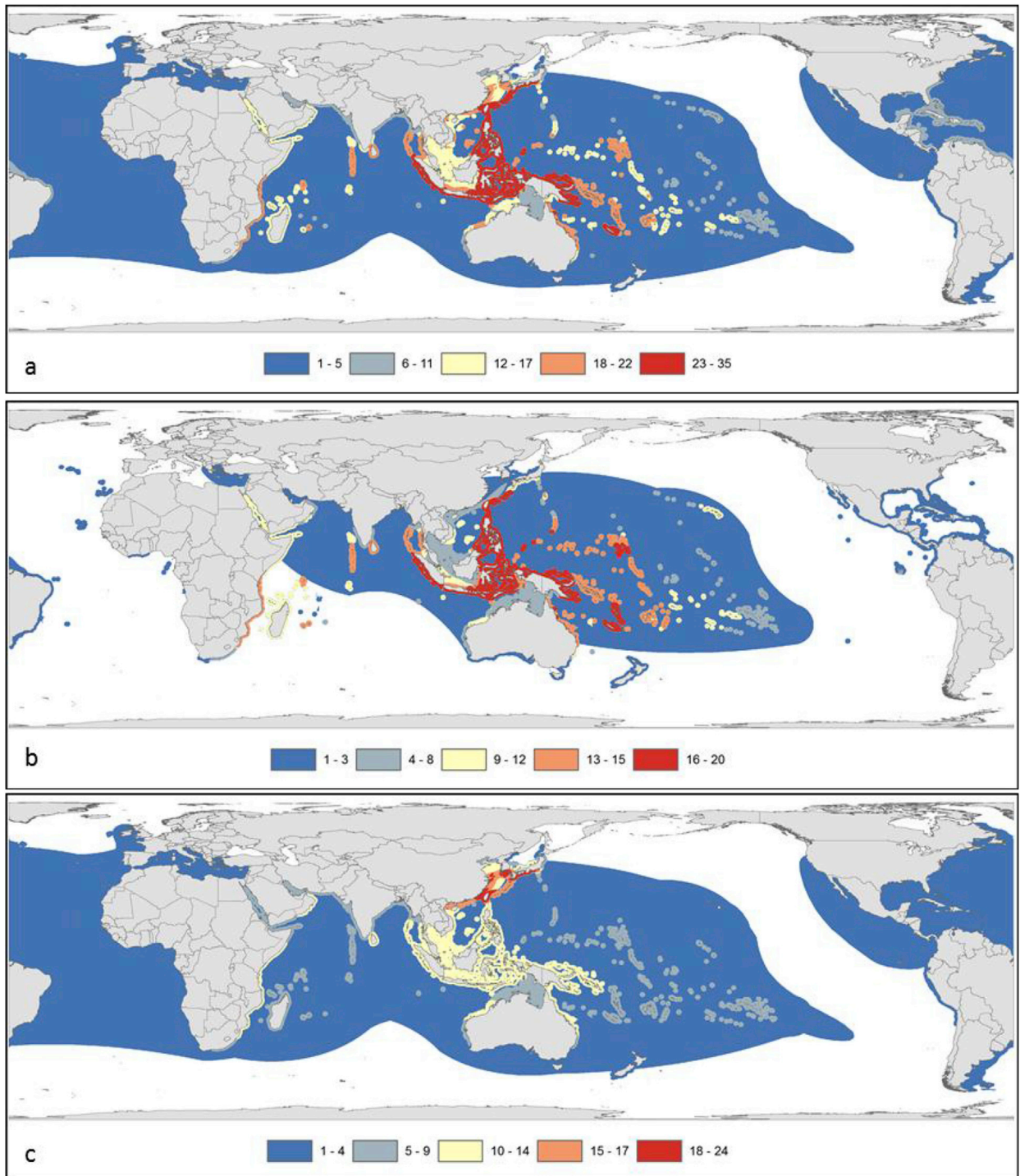


Fig. 2. Species richness of utilized marine and estuarine Tetraodontidae of the world: a) richness of all utilized species, regardless of type of utilization; b) richness of species utilized in the aquarium trade; c) richness of species found in commercial and recreational fisheries. Note that Fig. 2b and c represent subsets of the species presented in Fig. 2a.

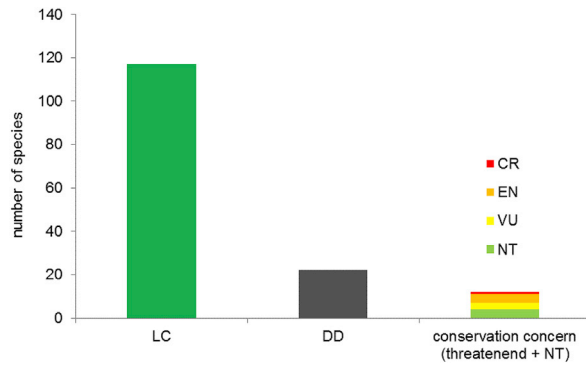


Fig. 3. The proportion of the 151 marine puffers in each IUCN Red List category at the global scale. Threatened Categories include Critically Endangered (CR), Endangered (EN), and Vulnerable (VU). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Among the 48 species recorded in coral reef habitats, diet information was available for 30 species (63%). Of these species, 37% were primary carnivores, 33% were primary omnivores, 23% were primary herbivores, and 7% were primary corallivores. Fifteen of the 30 species found in coral reef habitats (50%) incorporated some coral, typically including skeletal material (Cole et al., 2008), into the diet.

3.3. Use and trade

Eighty-one species of puffer (54%) have at least one recorded use. The most frequently recorded uses are the aquarium trade (44 species, or 29% of all species), followed by food trade (37 species, or 25% of all species). Less frequently recorded uses include research, medicine, the curio trade, poisons, and animal feed (13% of all species). Spatial patterns in the distribution of

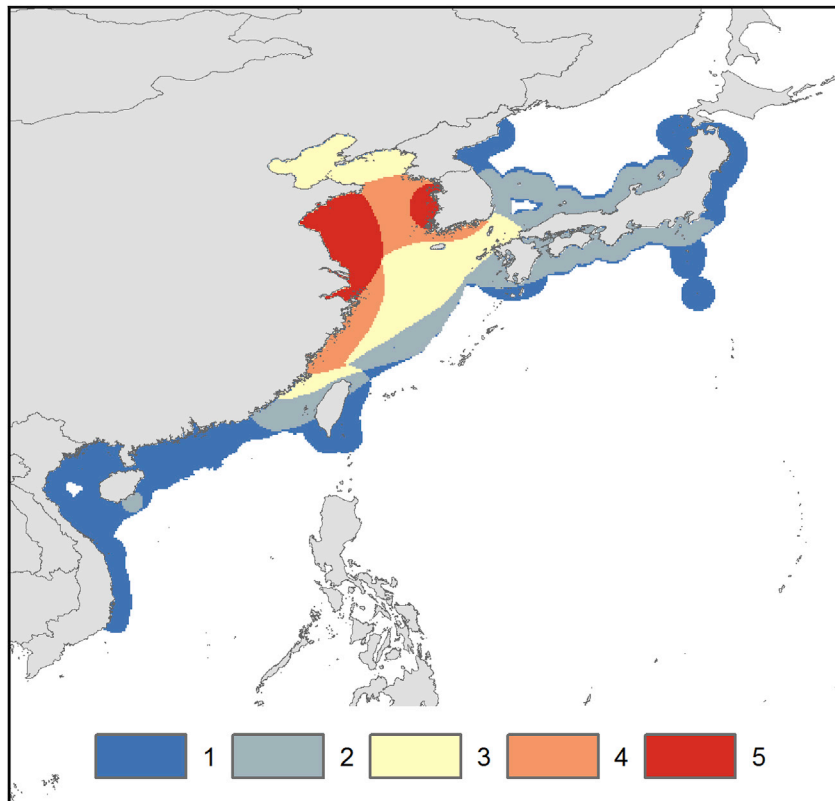


Fig. 4. Species richness of threatened and Near Threatened marine and estuarine Tetraodontidae in the northwestern Pacific Ocean. Additional localities with single threatened or Near Threatened species include the Atlantic islands of Ascension and St. Helena, South Africa, and remote Pacific Islands (e.g., Eastern Island, the Pitcairn Islands and French Polynesia).

Table 1

Threats, estimated single generation length, estimated % decline over 3 generation lengths, and Red List status of species of elevated conservation concern (threatened or Near Threatened) under criterion A.

Species	Threats	Generation length	Decline	RL status and criteria
<i>Takifugu chinensis</i>	overfishing, coastal development, introgression	4 years	>80%	CR (A2bd)
<i>Takifugu flavidus</i>	overfishing, coastal development, introgression	–	unable to quantify across range: highly valued, localized historical declines (>90%), qualitative observations of decline	NT - Conservation Dependence
<i>Takifugu rubripes</i>	overfishing, coastal development, introgression	–	unable to quantify across range: highly valued, localized historical declines (>95%), qualitative observations of decline	NT - Conservation Dependence
<i>Takifugu ocellatus</i>	overfishing, targeted fishing of spawning migrations, coastal development,	–	unable to quantify across range; qualitative observations of decline, highly valued, exhibits predictable mass-spawning migrations	NT - Conservation Dependence
<i>Takifugu vermicularis</i>	overfishing, coastal development, introgression	–	unable to quantify across range; highly valued, decreases in mean size and CPUE in parts of range, localized 75% decrease in mixed landings in parts of range	NT - Conservation Dependence

all utilized species and those found specifically in the aquarium trade generally mirror that of the overall species richness (Fig. 2a and b), with highest diversity occurring the Indo-West Pacific and a secondary center of diversity off east Africa. However, the spatial distribution of fished species (Fig. 2c) presents a different perspective. The highest diversity of fished species occurs from southern Japan to the Yellow and East China seas, despite the lower overall diversity of puffers there. This trend is reflective of the commercial importance of puffers along coastlines of the North-west Pacific.

3.4. Extinction risk of puffers

Of the 151 marine and estuarine puffers for which sufficient data are available, 12 species were of elevated conservation concern - assessed as threatened (Critically Endangered, Endangered or Vulnerable) or Near Threatened. The exact proportion of species of elevated concern is unknown, as the true conservation status of 22 species having insufficient information for evaluation (Data-Deficient species) is undetermined. However, the best estimate is 9%, assuming that the proportion of Data Deficient species which are threatened mirrors the proportion of threatened species in the family for which data were sufficient to assess, and it may range between 8%, assuming no Data Deficient species are of elevated conservation concern and 23%, assuming all Data Deficient species are of elevated conservation concern (Fig. 3; Supplementary Online Material).

These species are primarily found along the coast of East Asia, from Japan to the South China Sea, with the highest concentration in the East China Sea (up to five species per 100 km²) (Fig. 4). Additional localities with single threatened or Near Threatened species include the Atlantic islands of Ascension and St. Helena, South Africa, and three remote Pacific island groups (e.g., Easter Island, the Pitcairn Islands and French Polynesia).

3.5. Puffers of conservation concern— criterion A

Of the 12 species of elevated conservation concern, five were assessed as threatened or Near Threatened under Criterion A. Species which qualify for assessment as threatened or Near Threatened under Criterion A have exhibited an observed,

Table 2

Range, habitat, estimated Area of Occupancy (AOO) and known threats to tetraodonid species assessed as threatened under criteria B2 (restricted AOO). AOO was calculated using ArcGIS based on a bathymetric clip of 1–10 m depth range from the ETOPO global relief model.

Species	Range	Habitat	AOO	Threats	RL status and criteria
<i>Arothron inconstitus</i>	South Africa, Knysa to East London	river mouths, beaches	742 km ²	Habitat loss (coastal development)	VU B2ab(iii)
<i>Canthigaster rapaensis</i>	French Polynesia (Rapa, Tenoko)	coral reef	28 km ²	Habitat loss (coral bleaching)	EN B2ab(iii)
<i>Canthigaster cyanetron</i>	Easter Island (Rapa Nui)	coral reef	27 km ²	Habitat loss (coral bleaching)	EN B2ab(iii)
<i>Canthigaster marquesensis</i>	French Polynesia (Marquesas Islands)	coral reef	511 km ²	Habitat loss (coral bleaching)	VU B1ab(iii)+2 ab(iii)
<i>Canthigaster sanctaehelenae</i>	St. Helena and Ascension	rocky reef	45 km ²	Habitat loss (coastal development)	EN B2ab(iii)
<i>Chelonodon pleurospilus</i>	South Africa, Xora river mouth	sandy or muddy substrate	91 km ²	Habitat loss (coastal development), global warming	EN B2ab(iii)
<i>Takifugu plagiocellatus</i>	Hainan Island, China	seagrass and coral reef	259 km ²	Habitat loss (coastal development)	EN B2ab(iii)

estimated, inferred, or suspected population size reduction over three generation lengths (IUCN, 2012). The primary driver of decline in these species is overexploitation (Table 1).

The commercially important Chinese Puffer (*Takifugu chinensis*) was assessed as Critically Endangered under criterion A2bd based on suspected population declines exceeding 80% over an estimated three-generation lengths, or 12 years. This species is found over sandy and muddy bottoms in the East China and Yellow seas at depths ranging from 5 to 150 m (Nakabo, 2002). It was considered to be among the most valued puffers in Japan (NMFS, 1989) and has exhibited a continuous and precipitous decline in landings since the 1970s (Kawata, 2003). It is now rarely seen in Japanese markets (Yamada et al., 2007). The four species (3%, *Takifugu flavidus*, *T. rubripes*, *T. ocellatus*, *T. vermicularis*) which qualified as Near Threatened are also in the *Takifugu* genus, are habitat generalists, and are components of the East Asian international puffer trade.

The lucrative puffer food trade in East Asia is acknowledged to have been in a state of decline throughout the region due to overfishing, as evidenced by the >90% declines in aggregate puffer landings from the western part of the coast of Japan, the Sea of Japan, Yellow Sea and East China Sea from 1973 to 1999 despite increasing demand (Kawata, 2003). These observations are further supported by the steady decrease in landings declared by Japan and the Republic of Korea (the only nations to declare puffer landings) to the Food and Agriculture Organization (FAO) from 1995, the first year both nations declared landings, to 2011 (Food and Agriculture Organization of the United Nations, 2012). In some cases, declines have been attributed to the use of highly effective fishing gear, including modified long-lines and nets with small mesh sizes, rather than excessive fishing effort (Kawata, 2012). Management of puffer resources in East Asia has been hindered by the practice of switching target species once the status of the present target species has deteriorated, ensuring continuous profits but encouraging overfishing and keeping populations low once they have been overfished (Kawata, 2003). Many *Takifugu* species are dependent on fisheries management, such as off-fishing seasons, restrictions on minimum body size, support for stock enhancement programs, improvements to fishing grounds, and the increasing aquaculture of fish to meet consumer demand which cannot be met by wild stocks alone (Kawata, 2012).

As landings of wild puffer have decreased in East Asia, prices of the most valuable puffers have increased. While bio-economic theory suggests that economic extinction of commercial stocks will occur long before biological extinction (Clark, 1990), this is not always the case for rare, highly valuable species. The anthropogenic Allee effect concept posits that rare species can be disproportionately affected by exploitation if rarity increases their value (Courchamp et al., 2006). The escalating exploitation of rare species can be driven by the desire to showcase wealth and/or social status by consuming rare species as luxury items (Angulo and Courchamp, 2009; Courchamp et al., 2006). Adjusting for inflation, prices for the most expensive puffer species in Japan have nearly doubled from \$44-\$65/kg in 1989 (NMFS, 1989) to \$65-\$123/kg in 2010 (K. Matsuura pers. comm. 2015). Current prices are comparable to those fetched by the Napoleon Wrasse (*Cheilinus undulatus* - EN) in Japan which retailed for \$130/kg in the early 2000s (Sadovy et al., 2003). The Napoleon Wrasse is valued as a luxury item in the live reef fish food trade and is also threatened by overexploitation driven by the anthropogenic Allee effect (Courchamp et al., 2006).

Many *Takifugu* species, including those of elevated conservation concern, are likely to be affected by the range of possible effects of cultured fish on natural populations. Aquaculture of *Takifugu* species has been practiced in East Asia since at least the 1960s (Gao et al., 2014). Data from the Food and Agriculture Organization (FAO) FIGIS Commodities Database indicate that the rate of puffer aquacultural production has increased since the mid-1980s. By the early-2000s, when China first declared this commodity to the FAO, the volume of aquacultured puffer declared exceeded the volume of puffer landings declared. China developed its puffer aquaculture program in the 1990s (Maai et al., 2011) and by the mid-2000s appears to have surpassed Japan as the primary producer of aquacultured puffer (FAO, 2011). Increased intensification and commercialization of aquatic production, which is widespread in East Asia, increases the likelihood of disease outbreaks and transmission to wild populations (Bondad-Reantaso et al., 2005). Additionally, cultured fish are genetically distinct from natural populations, and their intentional or accidental release and interbreeding with wild populations can result in a range of genetic outcomes, from no detectable effect to complete introgression or displacement of wild populations (Hindar et al., 1991). Explosive speciation of *Takifugu* occurred during the Pliocene 1.8–5.3 Ma, and, consequently, species within *Takifugu* are very closely related and more likely to hybridize (Bolnick & Near, 2005; Yamanoue et al., 2008). The Tiger Puffer (*T. rubripes*) is the most economically important aquaculture species in East Asia and has been regularly intentionally hybridized and released into natural waters in large numbers. The questionable genetic integrity of Tiger Puffer of Chinese origin has fueled trade disputes and led to the implementation of export restrictions for Tiger Puffer originating from China (Maai et al., 2011).

3.6. Puffers of conservation concern - criterion B

Of the 12 species of elevated conservation concern, seven qualified as threatened under criterion B2, having a restricted Area of Occupancy (<2000 km²), are known from few threat-based locations, and are inferred to be experiencing a continuing decline in the area, extent, or quality of their respective habitats (IUCN, 2012). The primary threat to these restricted-range species is habitat loss due to climate change and coastal development (Table 2).

In addition to their restricted ranges, *C. cyanetron*, *C. rapaensis*, *C. marquesensis* and *T. plagiocellatus* have varying degrees of association coral reef habitats, however the extent to which they are dependent on live coral cover is unknown. Coral reefs have experienced well-documented declines in abundance, diversity and habitat structure throughout their global ranges due to a combination of overfishing, pollution, disease and coral bleaching caused by climate change (Wilkinson, 2000). Among fishes, coral-dependent fishes are expected experience rapid population declines as live coral

cover is lost (Munday, 2004), which can be attributed to the loss of refuges and recruitment sites (Jones et al., 2004; Feary et al., 2007). Increases in sea-surface temperature are expected to amplify the effects of habitat loss through mechanisms including inducing changes in fish life history, shifts of breeding season, and increased fluctuations in recruitment (Munday, 2004).

Furthermore, *Canthigaster cyanetron*, *C. rapaensis*, *C. marquesensis*, and *Chelonodon pleurospilus* are restricted to single habitats, and thus are likely to be ecologically specialized and reliant on their respective habitats. The ability to utilize multiple habitats influences extinction vulnerability (Dulvy et al., 2003; Roberts and Hawkins, 1999). In the family Tetraodontidae, of the 27 habitat specialists, 15% qualified as threatened or Near Threatened, as compared to only 7% of habitat generalists. Habitat specialization and small population sizes act synergistically to elevate extinction risk above the additive risk of the two factors alone (Brook et al., 2008). Specialization reduces the capacity of a species to adapt to habitat loss by shifting its range or changing its diet (Davies et al., 2004). Additionally, specialist species may have smaller initial population sizes than generalists. Specialists face a dual risk of extinction because their already small populations decline more rapidly than those of generalists (Munday, 2004). In puffers, the species with small ranges also occupied fewer habitats than more widespread species (on average, 1.6 and 2.7 occupied habitats, respectively). For example, *Canthigaster rapaensis* (EN) is found on coral reefs to depths of 30 m and is only known from the remote islands of Rapa and Tenoko in French Polynesia. It has an Area of Occupancy of 28 km² and is threatened by habitat loss due to coral bleaching events, which have been observed in the archipelago in response to warming sea-surface temperatures.

3.7. Uncertainty of threats: the case for Data Deficient puffers

Twenty-two species (15%) were assessed as Data Deficient, most often (17 species, 81%) because of unresolved taxonomic issues or a lack of verified specimens. For example, *Pelagocephalus coheni*, known only from Norfolk Island, was described from a specimen collected by a white tern and dropped under its nest (Tyler and Paxton, 1979), and the only known additional specimen was collected near the island at a depth of 68 m (J. Tyler pers. comm. 2015).

There are many unresolved issues in puffer taxonomy. Puffers possess limited external characters and specimens are often distorted when fixed in formalin and preserved in ethanol, making their identification and description difficult. Genera of concern include *Arothron*, *Chelonodontops*, *Lagocephalus*, *Pau*, *Takifugu*, and *Torquigener* (Matsuura, 2014). The taxonomy of pufferfishes is important not only for the understanding of fish diversity, but also for human welfare (correctly identifying toxic species) and resource management (Matsuura, 2014). Further, such taxonomic issues confound efforts to characterize a species' global Extent of Occurrence and/or Area of Occupancy, which are necessary for evaluation against Criterion B (IUCN, 2012).

Taxa should not be treated as non-threatened when assessed as Data Deficient (IUCN, 2012). Four of the 22 species assessed as Data Deficient are likely to be threatened based on the occurrence of threats, genetic and/or morphological similarity and geographic overlap with threatened species. One of these species of concern is *Takifugu pseudommus*, which is genetically and morphologically similar to the highly-commercial *T. rubripes* (NT) and *T. chinensis* (CR) (Cui et al., 2005; Yamanoue et al., 2008). *Takifugu pseudommus* is directly targeted by the puffer trade and is one of the two most important puffer species cultured in China for export to Japan (Song et al., 2001). It is found in shallow waters to depths of up to 20 m (Nakabo, 2002; Su and Li, 2002) where it is likely to be exposed to coastal fisheries as well as land-based pollution sources. It is inferred that this species, like many other commercially important *Takifugu* species, is threatened by over-exploitation, the loss of genetic integrity, and as habitat deterioration; however, there is little species-specific population information available, preventing application of the IUCN Criteria. Another *Takifugu* species, *T. variomaculatus*, is genetically and morphologically similar to the commercially important *T. ocellatus* (NT), but it is only known from seven type specimens from the mouth of the Pearl River, China (Su and Li, 2002). It is likely that *T. variomaculatus* is being incidentally captured in fisheries targeting *T. ocellatus*; however, the lack of species-specific information prevents application of the IUCN Criteria. Additional DD species of interest include the coral-associated *Arothron carduus* and *Canthigaster criobe*. These species are known from a few specimens, despite being found in shallow water where the likelihood of encountering them is relatively high. *Arothron carduus* was described in 1991 from three specimens, one of which was collected as an inflated specimen in the curio trade (Matsuura and Okuno, 1991). *Canthigaster criobe* was described from a single specimen collected in French Polynesia (Williams et al., 2012). Again, the paucity of species-specific information prevents application of the IUCN Criteria.

3.8. Least Concern puffers

The majority of puffers (77% or 117 species) were listed as Least Concern. These species are generally wide-ranging, occupy a variety of habitats, and are capable of rapid reproductive turnover. The percentage of LC puffers is similar to the estimated 86% of the parrotfishes and surgeonfishes (Comeros-Raynal et al., 2012), but substantially higher than the commercial groupers, where only 44% were considered Least Concern (Sadovy de Mitcheson et al., 2012).

Some puffers are components of commercial, subsistence, or recreational fisheries, are collected for the aquarium trade, or occur in areas experiencing habitat deterioration. However, population trend information, when available, indicates that declines were below the 30% threshold required for placement in a threatened category under criterion A and ranges exceeded the minimum thresholds for placement in a threatened category under criterion B. Some species are experiencing localized population declines; for example, two species, *Takifugu porphyreus* and *T. xanthopterus*, while

abundant in parts of their global ranges, are experiencing localized population declines in East Asia as part of the international puffer trade.

Our review of the ecology of puffers indicates that the majority of marine and estuarine puffers are habitat generalists, and thus are expected to be less susceptible to, or to even benefit from, environmental disturbances (McKinney and Lockwood, 1999). Additionally, the most frequently recorded habitats occupied by puffers are sandy and muddy bottoms, which exist in a nearly continuous band along the continental shelf. Marine fishes with high dispersal ability, living in these and other continuous habitats, such as the pelagic zone, are likely to successfully expand their ranges from tropical to temperate waters in response to global warming (Hiddink and ter Hofstede, 2008). To date, several puffer range expansions have already been recorded (e.g., Corsini et al., 2005; Katsanevakis et al., 2009; Streftaris and Zenetos, 2006). Among these successful range expanders is the Silver-cheeked toadfish, *Lagocephalus sceleratus*, which is considered one of the worst invasive species in the Mediterranean. Because traits which promote adaptation and invasion are often shared among closely related species (McKinney, 1997), it is possible that many puffers will benefit from global warming and other human-induced environmental changes.

4. Conclusion: conservation priorities, current management efforts, and further research

The majority of puffers (77% or 117 species) were assessed as Least Concern; these species exhibit intrinsic characteristics, such as large geographic ranges and generalist habitat and dietary preferences, which generally buffer against heightened extinction risk. Twenty-two species (15%) were assessed as Data Deficient, primarily due to a paucity of known specimens or outstanding taxonomic issues. The assessment of Data Deficient does not imply a lack of threats, however due to a lack of information these species could not be evaluated against the IUCN Criteria. Twelve species (8%) are of conservation concern, having been assessed as threatened (Vulnerable, Endangered, or Critically Endangered) or Near Threatened.

Many puffers of conservation concern and several Data Deficient species are targets or incidental catch in the East Asian international puffer trade, which primarily targets the genus *Takifugu*. Most *Takifugu* species are geographically restricted to the marine waters around Japan, Korea and China, and are often exploited throughout the entirety of their geographic ranges. When possible, population declines were inferred based on declines in landings despite increasing demand and fishing effort over a three-generation time period. The increasing rarity of some species, particularly those valued as luxury items, is likely to fuel, rather than discourage, further exploitation due to increases in perceived value. Furthermore wild stocks of *Takifugu* species appear to be highly susceptible to introgression due to proximity to aquacultured specimens and aquaculture hybrids, as has already occurred with wild *Takifugu rubripes* in China (Maai et al., 2011).

Puffers targeted by the international puffer trade have been the focus of regional fisheries management and conservation efforts in East Asia. Japan announced the Plan for Rebuilding Puffer Resources in April 2005, which set dates for an off-fishing season, restrictions on minimum body size, support for stock-enhancement programs, improvements to fishing grounds, and mandated the release of small fishes. As of 2010, stocks had not fully improved, prompting a re-assessment of the program. Several recommendations have been made to ensure the continuation of puffer fisheries, particularly considering socio-economic constraints which limit the possibility of developing alternative fisheries. Recommendations include gear restrictions and mandating that fishers catch older and heavier fish by postponing the beginning of the fishing season (Kawata, 2012).

In addition to those species threatened by the international puffer trade, several species of conservation concern are restricted-range species with habitat or dietary specializations. These species are threatened by habitat loss due to coral reef degradation and the potential effects of climate change. These factors are more broadly impacting global biodiversity, food security, and other related ecosystem services upon which we rely, the long-term consequences of which are still to be determined.

Our systematic review of the ecology of puffers and our assessment of their extinction risk using the IUCN Red List Categories and Criteria have revealed research and conservation priorities which could improve the status puffers of conservation concern. The paucity of basic ecological knowledge and remaining taxonomic issues within the *Takifugu* genus warrant further research attention, particularly in light of their commercial importance in East Asia. Furthermore, misidentification and aggregation of puffer landing statistics hamper accurate assessments of both stock status and extinction risk in commercially exploited puffers. Population genetic studies focusing on the genus *Takifugu* could provide additional insights on the genetic extent of inbreeding among wild and aquacultured specimens, in addition to informing stock delineation. In addition to being an interesting, albeit understudied, component of marine biodiversity, puffers are of great regional economic importance in East Asia, where they have a rich cultural and culinary heritage worthy of further research and conservation effort.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.gecco.2018.e00388>.

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