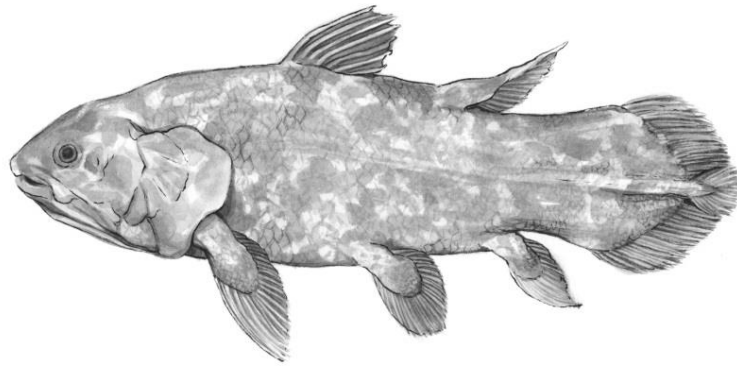


**ENDANGERED SPECIES ACT
STATUS REVIEW REPORT for the COELACANTH**

Latimeria chalumnae



**Kerry Whittaker
OCTOBER 2014**



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INTRODUCTION

Scope and Intent of the Present Document

This status review is in response to a petition¹ to list 81 species as threatened or endangered under the Endangered Species Act (ESA). Under the ESA, if a petition is found to present substantial scientific or commercial information that the petitioned action may be warranted, a status review shall be promptly commenced (16 U.S.C. 1533(b)(3)(A)). The National Marine Fisheries Service (NMFS) decided that the petition had sufficient merit for consideration and that a status review was warranted for 27 of the 81 species (see <http://www.nmfs.noaa.gov/pr/species/petition81.htm> for the Federal Register notices), including the African coelacanth, *Latimeria chalumnae*. The ESA stipulates that listing determinations should be made on the basis of the best scientific and commercial information available. The following status review interprets the best available information available on the species, and is used to evaluate its status in the context of consideration for ESA listing.

Life History and Ecology

Taxonomy and Distinctive Characteristics

Latimeria chalumnae, a fish commonly known as the African coelacanth, belongs to a very old lineage of bony fish, the class Sarcopterygii or lobe-finned fishes, which includes the coelacanths, the lungfish and the very early tetrapods (Table 1). Most species of lobe-finned fish are extinct. Among the lobe-finned fishes, *Latimeria chalumnae* is one of only two living species belonging to the order Coelacanthiformes. The two living coelacanth species have long been considered “living fossils”, with the living species bearing strong morphological resemblance to fossils that date back over 400 million years. The most closely related species in the fossil record is *Macropoma lewesiensis*, a sister species to *Latimeria chalumnae*, which was thought to have become extinct over 65 million years ago.

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Sarcopterygii
Subclass:	Actinistia
Order:	Coelacanthiformes
Family:	Coelacanthidae
Genus:	<i>Latimeria</i> J.L.B. Smith, 1931
Species	
<i>L. chalumnae</i> <i>L. menadoensis</i>	

Table 1. Scientific classification of *L. chalumnae*

¹ (1) WildEarth Guardians submitted to U.S. Secretary of Commerce, Acting through the National Marine Fisheries Service, July 15, 2013, “Petition to list eighty-one marine species under the Endangered Species Act.”

The belief that the ‘coelacanth’ had gone extinct over 65 million years ago made the discovery of a living specimen off the coast of South Africa in 1938 particularly sensational (McAllister, 1971). The coelacanth’s taxonomic position as an ancient lobe-finned fish stirred much debate surrounding their potential role as the sister group of modern tetrapods, forming the ‘missing link’ between aquatic and terrestrial vertebrates (Meyer, 1995; Zardoya et al., 1998; Takezaki et al., 2004). While molecular evidence suggests that the lungfish is more likely the closest living relative to modern tetrapods (Takezaki et al., 2004), recent genomic sequencing of living coelacanths has provided insight into the evolutionary transformation from aquatic to terrestrial life (Amemiya et al., 2013) (Figure 1).

Although *Latimeria chalumnae* and its living sister species *Latimeria menadoensis*, commonly known as the Indonesian coelacanth, are genetically and geographically distinct, their ancestor is hypothesized to have been continuously distributed in deep water along the coasts of Africa, Madagascar and Eurasia (Springer, 1999). Today, *Latimeria chalumnae* inhabits coasts along the western Indian Ocean, while its living sister species, *Latimeria menadoensis*, commonly known as the Indonesian coelacanth, appears to be restricted to Indonesian and probably western Pacific waters (Erdmann et al., 1998; Erdmann, 1999; Fricke et al., 2000b, Hissman pers. com.). *Latimeria menadoensis* was observed for the first time in 1997 (Erdmann et al., 1998). The Indonesian and Western Indian Ocean populations are regarded as distinct evolutionary lineages (Fricke et al., 2000b). One geologic explanation for their species-level divergence points to the formation of the Himalayan Mountains 50 million years ago, and the subsequent development of rivers which contributed to broad siltation along the Indian coast;

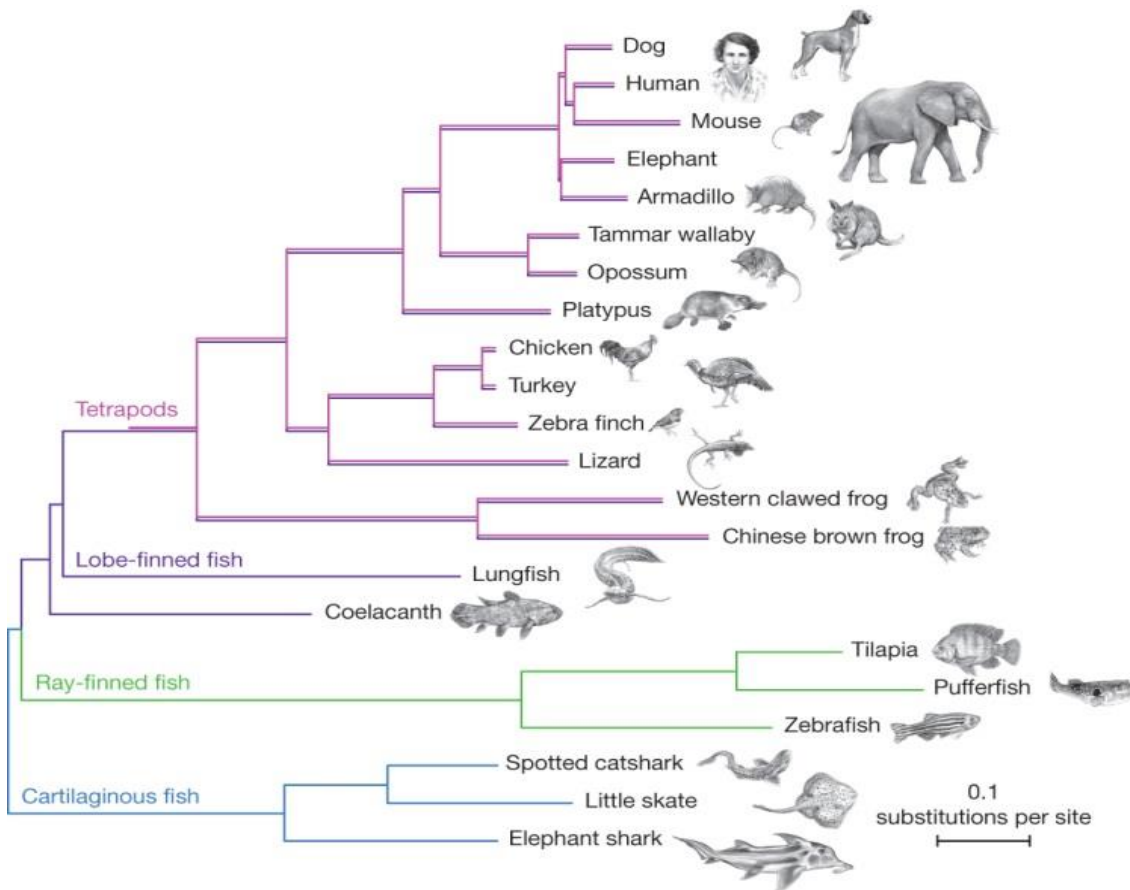


Figure 1. Phylogenetic tree demonstrates the coelacanth’s position as an ‘aunt’ to modern-day tetrapods. C.T. Amemiya *et al.* 2013.

widespread siltation is thought to have limited coelacanth habitat, and led to the isolation of coelacanth populations to the east and west of India, resulting in their eventual speciation (Springer, 1999). The divergence between *L. chalumnae* and *L. menadoensis* during the Eocene or mid-Miocene, 15-50 MYA is supported by molecular clock estimates based upon the slow evolutionary rates of shark mtDNA sequences (Holder et al., 1999; Inoue et al., 2005). Based on analysis of full mitochondrial genomes, the overall nucleotide difference between the two species is 4.28%, indicating substantial species-level divergence (Inoue, 2005). Thus, *Latimeria chalumnae* species classification, and its distinction from *Latimeria menadoensis*, is supported by molecular and biogeographical evidence (Holder et al., 1999).

The coelacanth has a number of unique morphological features. Most obvious are its stalked dorsal, pelvic, anal, and caudal fins (Figure 2). The body of the fish appears iridescent dark blue in film or video footage, but under natural light the color is light brown with white blotches throughout that have been used for individual identification in the field. When individuals die, their color shifts from blue to brown. The name *coelacanth* comes from the Greek words for 'hollow' and 'spine,' referring to the fish's hollow oil-filled notochord, which supports the dorsal and ventral caudal fin rays (Balon et al., 1988). This notochord is composed of collagen which is stiffened under fluid pressure (Balon, 1988). Coelacanths have a unique intracranial joint allowing them to simultaneously open the lower and upper jaws, possibly an adaptation for feeding (Balon et al., 1988). The coelacanths undergo osmoregulation via retention of urea (Griffith, 1991). Their swim bladder is filled with wax-esters used to passively regulate buoyancy, allowing the fish to reach depths of 700 meters during nightly feeding excursions (Hissmann et al., 2000). Males and females exhibit apparent sexual dimorphism in size, where the standard length of females is greater than that of males (160 vs. 130 cm) (Bruton et al., 1991b).

While the African and Indonesian coelacanth species are clearly genetically differentiated, their morphological differences are more difficult to discern. Originally, Pouyaud et al. (1999) described the Indonesian coelacanth as a new species based on nine morphological and meristic differences. This conclusion was based on a single specimen of the Indonesian coelacanth as compared with several specimens of the African species. Erdmann (1999) later contested this conclusion based on comparison of external morphological measurements from a greater number of specimens, concluding that the Indonesian coelacanth is morphologically extremely similar to its African sister species. An additional survey of the literature compiled by Holder et al. (1999) demonstrated that 4 of the characters used to distinguish the Indonesian from African species exhibit clear overlaps between the two species. Thus, while genetically distinct, the Indonesian and African coelacanth species exhibit overlapping morphological traits, challenging their differentiation based on morphology alone.

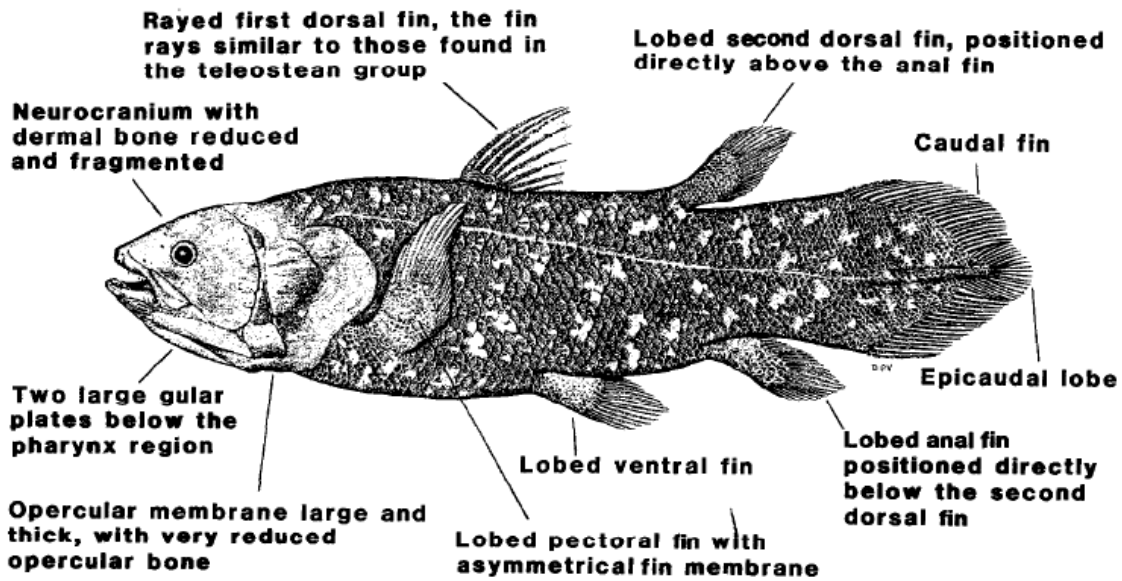
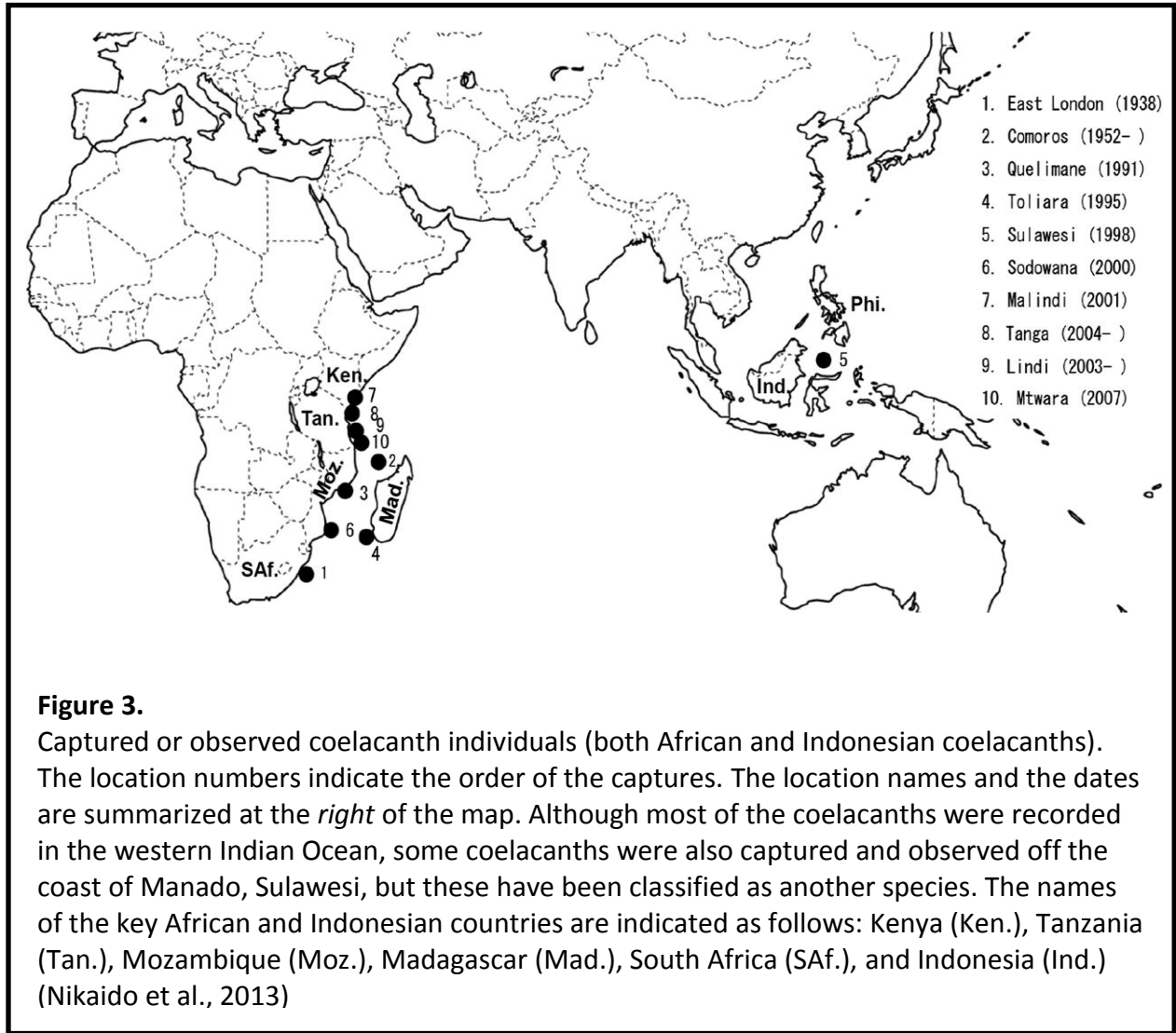


Figure 2. Description of coelacanth fin morphology, from Balon (Balon et al., 1988).

Range and Habitat Use

The natural range of *Latimeria chalumnae* was once thought to be restricted to the Comoro Island Archipelago, located in the Western Indian Ocean (WIO) between Madagascar and Mozambique. For many years, specimens caught off of South Africa, Mozambique, and Madagascar were thought to be strays from the Comoro population (Schliewen et al., 1993; Hissmann et al., 1998). However, between 1995 and 2001, catches and observations of coelacanths from the coasts of Kenya (De Vos et al., 2002), Tanzania (Benno et al., 2006), South Africa (Hissmann et al., 2006), and Madagascar (Heemstra et al., 1996) suggested that the species was more widespread than previously thought, occupying deep water coastal habitat in several locations throughout the WIO. The range extent of the coelacanth remains unclear, as direct observations of established populations rely on dedicated deep water canyon surveys, or bycatch observations from gillnets and artisanal handlines (Hissmann et al., 2006). Bycatch events have been carefully inventoried, and provide valuable insight into the fish's distribution (Figure 3).



Historically, the highest number of coelacanths has been observed off Grand Comoro Island via targeted deep-water surveys, or as bycatch to the artisanal oilfish fishery that targets fish using deep handlines. Grand Comoro Island is part of the volcanic Comoro Island archipelago comprised of three additional islands, Anjouan, Moheli, and Mayonette. The youngest island (Grand Comoro) formed about 1 to 1.3 million years ago and oldest island (Mayonette) formed 7 to 12 million years ago (Stobbs et al., 1991). Grand Comoro's underwater profile is characterized by steep slopes, exceeding 45 degrees, which descend rapidly to 3000-3500m depth (Fricke et al., 1988). The Comoro islands are affected by monsoons, tropical cyclones, and frequent tropical thunderstorms (Bruton et al., 1991c). In the Comoro islands, coelacanths have primarily been caught on the southwest and west coast of Grand Comoro, with fewer catches along the northern, western shores of Anjouan, and no fish caught off of Moheli or Mayonette, despite the occurrence of nearshore handline fishing off many other coasts of those islands (Stobbs et al., 1991).

To date, the best data addressing coelacanth habitat use come from *in situ* observations of the fish off the coast of Grand Comoro. The coelacanth is known to inhabit waters deeper than 100m, making surveys difficult and reliant upon sophisticated technology including submersibles and remotely operated vehicles (ROVs), or highly-trained divers using special gas mixtures. Two decades of coelacanth observation off the steep volcanic coasts of Grand Comoro (9 submersible expeditions) demonstrate that the coelacanth inhabits deep submarine caves and canyons which are thought to provide shelter from predation and ocean currents (Fricke et al., 2011). The fish aggregate in these caves in groups of up to 16 individuals (Hissman et al., 2006) (Figure 4). Retreat into these caves after nightly feeding activity is most likely a key factor for coelacanth survival, allowing the fish to rest and conserve energy in a deep-water, low-prey environment (Fricke et al., 1991a). Coelacanth settlement is thought to depend upon the high structural complexity of these deep shelf features (Fricke et al., 2011). At night, coelacanths occupy deeper waters to actively feed, spending the majority of their time between 200 and 300m (Fricke et al., 1994; Hissmann et al., 2000). Larger individuals are known to excursion below 400m, with the deepest observation at 698m (Hissmann et al., 2000). Coelacanth tracking experiments have shown that the fish spend 75% of their time at a temperature range of 15-19°C, and the rest of their time in colder water foraging (Hissmann et



Figure 4. Aggregation of seven African coelacanths beside a submarine cave in Jesser Canyon, South Africa, at a depth of 111m. (from Hissman *et al.* 2006).
al., 2000).

South African coelacanth habitat has also been studied, although to a lesser extent than in the Comoro Islands (Venter et al., 2000; Hissmann et al., 2006; Roberts et al., 2006). Specifically, three coelacanth surveys have been conducted in deep-water canyons off of Sodwana Bay, South Africa (Hissmann et al., 2006). Out of twelve canyons surveyed between 2002 and 2004, coelacanths were only observed on Jesser, Wright, and Chaka canyons (Hissmann et al., 2006). Like coelacanths in the Comoros, those in South Africa use highly complex deep-water cave and canyon habitat, which provides suitable shelter from the strong Aguelhas current that runs close to shore (Hissmann et al., 2006). In the Sodwana canyons, suitable caves are found at depths of 100–130 m, whereas at Grand Comoro Island, most caves are in depths of 180–230 m (Heemstra et al., 2006). However, a shallow coelacanth observation occurred at 53m in a deep reef complex on the South African shelf, suggesting that habitats with conducive temperature, shelter, and current conditions may support coelacanth activity (Hissmann et al., 2006). In general, it is thought that the deep overhangs and caves found off the shelf of South Africa provide suitable shelter and refuge for coelacanths, and although these caves occur at shallower depths than those in the Comoros, the temperature range at which the coelacanth occurs in these two regions is very similar (between ~15 and 20°C) (Roberts et al., 2006).

Habitat off of Tanzania consists of rocky terraces occurring between 70-140m depth; the water temperature at coelacanth catch depths is around 20°C (Nyandwi, 2009). A large number (n=19) of Tanzanian coelacanths have been caught in the outer reefs near the village of Tanga; some of these catches were reported at depths of 40-60m, but these reports may be unreliable (Benno et al., 2006; Nyandwi, 2009). These incidents may indicate a shallower depth preference for Tanzanian coelacanths than that exhibited by Comoran coelacanths; however, more surveys are needed to better understand coelacanth habitat use in this region (Benno et al., 2006). The benthic substrate off the coast of Tanzania is sedimentary limestone rather than the volcanic rock of the Comoros. In this habitat coelacanths are thought to use submarine cavities and shelves that have eroded out of the limestone composite for shelter.

Coelacanths demonstrate strong site fidelity with relatively large overlapping home ranges, greater than 8km, as demonstrated at Comoro and South African sites where expeditions have tracked individual movements using ultrasonic transmitters (Fricke et al., 1994; Heemstra et al., 2006). Surveys off Grand Comoro over 21 years demonstrate that individual coelacanths may inhabit the same network of caves for decades; for example, 17 individuals originally identified in 1989 were re-sighted in 2008 in the same survey area (Fricke et al., 2011). Typically, coelacanths migrate 3-4km per night, and individuals have not been observed more than 35km from their home caves (Fricke et al., 1994; Hissmann et al., 2006). Coelacanths have been observed to return to caves at night, presumably to rest, but appear to use a series of caves within a broad home range, and may occupy caves outside of their home ranges for certain periods of time (Fricke et al., 2011). Their mode of navigation and homing is not fully understood; it is thought that magnetic anomalies and magnetic orientation may help them to return to the same caves after relatively long excursions (Fricke et al., 1994). Alternatively, their site fidelity may be related to traditional use and understanding of the cave topography and surroundings (Fricke et al., 1994).

Temperature use for the Comoran coelacanth, based on survey observations, was found to be between 16.5 and 22.8°C (Fricke et al., 1991b). Surveys of South African coelacanth habitat off of Sodwana Bay confirm this temperature use across a broad portion of its range (Hissmann et al., 2006). This corresponds to estimates of thermal requirements based on the temperature-dependent oxygen saturation of their blood, with an optimum at 15 °C and an upper threshold at 22-23°C (Hughes et al., 1972). Thus, the coelacanth is dependent upon cooler waters to help maintain its oxygen demands. Most likely, the depth distribution of coelacanth depends partly on this temperature requirement. The coelacanth's ecological niche is likely shaped by this narrow temperature requirement, prey abundance, and the need for shelter and oxygen.

It is thought that sedimentation and siltation act as a negative influence on coelacanth distribution. This is supported by a hypothesis surrounding the split between the two living coelacanth species estimated to have occurred 40-30 Mya, corresponding with the collision between India and Eurasia (50 Mya) (Inoue et al., 2005) discussed above. This hypothesis has been supported by some surveys off of Sodwana Bay where it was observed that some canyons, despite offering suitable habitat requirements, were not occupied by coelacanths; it was concluded that the turbidity of the water in these caves discouraged coelacanth habitation, as nearby canyons not affected by turbidity were occupied by coelacanths (Hissmann et al., 2006; Roberts et al., 2006).

Reproduction, Feeding and Growth

Coelacanths are ovoviviparous, meaning their embryos are provided with a yolk within the adult female until they are delivered as live births. Eggs remain in gestation for three years; this period of embryogenesis has been determined by scale rings of embryo and newborn coelacanth specimens (Froese et al., 2000). The coelacanth gestation period is considered the longest of any vertebrate (Froese et al., 2000). Within the coelacanth literature, the fish's life span has been estimated several times. The earliest life span estimate of 11 years was based on the scale rings of a single 180cm female specimen (Hureau et al., 1977). Later, another large specimen was used to estimate a 7-8 year life span (Uyeno, 1984). These two earlier estimates were based on the assumption that the fish lays down two scale rings per year at a linear rate throughout its lifetime (Hureau et al., 1977; Uyeno, 1984). These estimates are considered low according to Balon et al. (Balon et al., 1988), who suggested that only one ring would be laid down each year with an annual circadian rhythm as is observed in other tropical fishes. Bruton and Armstrong suggested that the coelacanth may live longer than 20 years, and possibly 40 or 50 years (Bruton et al., 1991a). Based on coelacanth observations in the Comoros, it has been suggested that the fish may live as long as 100 years (Fricke et al., 2011). Using previously published data from 87 specimens containing length and weight estimates, Froese and Palomares estimated population structure, demographic factors, and von Bertalanffy growth function parameters of the coelacanth; these data suggested an average life span of 48 years, agreeing with Bruton and Armstrong's estimate (Bruton et al., 1991c; Froese et al., 2000).

Coelacanth generation times are long. In fact, they are expected to reach reproductive maturity between 16 and 19 years of age (Froese et al., 2000). Coelacanth fecundity is not well known; 26 embryos were found within one female caught in 2001 from off of Mozambique, and other known fecundities are 5, 19, and 23 pups (Fricke et al., 1992a).

Coelacanths are extremely slow drift-hunters. They descend at least 50 to 100m below their daytime habitat to feed at night on the bottom or near-bottom, and are thought to consume benthic or epibenthic prey (Uyeno et al., 1991; Fricke et al., 1994). Stomach content analysis has revealed a variety of prey items (table 2) from cephalopods to eels, cuttlefish, and deepwater fishes (Uyeno et al., 1991). Feeding behavior, as determined from photographic evidence, may involve drifting in a headstand position just above the ocean floor, sometimes at depths greater than 600m (Fricke et al., 1992b); the low-energy drift feeding behavior is thought to conserve energy and oxygen for the fish. The diurnal movement of the coelacanth is dependent on prey availability. In fact, in the Comoro Islands, coelacanths perform a vertical movement to depth to feed, which is opposite of many other fish or zooplankton species that travel to the surface to feed at night (Hissmann et al., 2000). In Sodwana Bay, a single coelacanth was tracked and exhibited nocturnal movement to shallower water, and receded to deeper cave systems at night, an opposite diel movement pattern to what is observed in the Comoro Islands; this evidence suggests that coelacanth movement may be partially driven by prey availability, either above or below cave depth (Benno et al., 2006).

Metabolic demands have been studied in the coelacanth, and demonstrate that they have one of the lowest resting metabolisms of all vertebrates (Hughes et al., 1972; Fricke et al., 2000a). Based on studies of prey availability, activity pattern, feeding behavior, and hunting success, Fricke and Hissman (2000a) estimated the metabolic rates and food requirements of male and female coelacanths off the Comoros (Fricke et al., 2000a). They estimated that females require 60g of prey per day, and males (which are smaller) require 33g of prey per day; metabolic rates for females and males were estimated at $3.7 \text{ ml O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ and $4.5 \text{ ml O}_2 \text{ kg}^{-1} \text{ h}^{-1}$, respectively.

CCC no.	Prey items	Prey size, depth of natural occurrence and notes	Reference and older specimen identification
?	<i>Diaphus metopoclampus</i> lanternfish	TL 20 cm whole; 375–850 m daytime; 90–850 m at night	Millot & Anthony (1958, p. 2592)
2	Scales and eyeballs	in intestine	Smith (1953, p. 101); RUSI 614
57	<i>Polymixia nobilis</i> stout beardfish	SL 17–18 cm (gill arches, hyoid, dentary, cleithrum, several vertebrae); near bottom dweller, 183–640 m	McCosker (1979, p. 20); USNM 20587
69	<i>Coranthus polyacanthus</i> (two) deepwater cardinal fish	SL 12–14 cm, partly digested; 150 m	McCosker (1979; p. 21); CAS 24862
73	Entire cuttlefish		McAllister (1971, p. 17)
88	Scales and otoliths	in intestine	McCosker (1979, p. 21); SIO 75-347
90	<i>Symphysanadon</i> sp. (two) deepwater snappers	SL 7–8 cm, intact and partially digested; some species 119–500 m on or near bottom	McCosker (1979, p. 20); CAS 33111
123	Cephalopod beak		Uyeno & Tsutsumi (this paper); JASEC no. 1
135	<i>Ilyophis bruneus</i> deepsea witcheel	TL 4.9 cm, whole, partially digested; 600–2668 m	Suyehiro et al. (1984, p. 12, Uyeno 1989, p. 20); JASEC no. 3
136	<i>Cephaloscyllium sufflans</i> swell shark	TL 48 cm, whole, partially digested; 40–440 m	Uyeno (1990, p. 20); JASEC no. 2
149	<i>Beryx decadactylus</i>	SL 34.5 cm, slightly digested; 200–600 m	Uyeno (1990, p. 21); JASEC no. 6

Table 2. Prey items found in the stomach and intestine of the coelacanth. The ‘CCC no.’ refers to the Coelacanth Conservation Council inventory number given by Bruton and Coutovidis, 1991. Table from Uyeno (1991).

The coelacanth’s gill surface area is much smaller than other fishes of their size; this morphological feature is a factor thought to heavily limit their growth rate and productivity due to its control over oxygen utilization (Froese et al., 2000). Studies of the fish’s blood physiology have demonstrated that the oxygen dissociation curve is temperature dependent, and shows an affinity for oxygen at lower temperatures (15°C). Small gill surface area and blood physiology are thought to influence the coelacanth’s restriction to cold deep water habitat, and may correlate with their low metabolic rates, meager food consumption and generally slow growth and maturation (Froese et al., 2000). The link between gill surface area and cold-water dependence was corroborated by an observation by Uyeno (1991), wherein a live coelacanth specimen was released and observed to demonstrate increased activity in deeper, cooler water. It has been hypothesized that cooler deep water temperature and respiratory demands prevent the coelacanth from occupying shallower warmer water (Fricke et al., 1988).

Population structure

Genetic data on coelacanth population structure are limited and known distribution of coelacanth populations is potentially biased by targeted survey efforts and fishery catch data. However, recent whole-genome sequencing and genetic data available for multiple coelacanth specimens can be used to cautiously infer some patterns of population structure

and connectivity across the coelacanth's known range (Nikaido et al., 2011; Lampert et al., 2012; Nikaido et al., 2013). Currently, whole-genome sequences exist for multiple individuals from Tanzania, the Comoros, and from the Indonesian coelacanth *L. menadoensis*.

Significant genetic divergence at the species level has been demonstrated to exist between *L. chalumnae* and *L. menadoensis* (Inoue et al., 2005) as described above.

Intraspecific population structure has been examined using *L. chalumnae* specimens from Tanzania, the Comoros, and southern Africa (Nikaido et al., 2011; Lampert et al., 2012; Nikaido et al., 2013). These studies suggest that *L. chalumnae* is comprised of multiple independent populations distributed across the WIO. However, based on limited samples, the geographic patterns and relatedness among coelacanth populations are little understood. Using mitochondrial DNA analyses, Nikaido et al. (2011) demonstrated that individuals from northern Tanzania differ from those from southern Tanzania and the Comoros. In fact, this study estimated that a northern Tanzanian population diverged from the rest of the species an estimated 200,000 years ago. Nikaido et al. (2011) hypothesized that differentiation of individuals from northern Tanzania may relate to divergence of currents in this region, where hydrography limits gene flow and reduces the potential for drifting migrants. More recent data reflecting a greater number of samples and higher-resolution population analyses do not support a genetic break between individuals from north and south Tanzania. Instead, this more robust population-genetics approach reveals significant divergence among individuals from South Africa, Tanzania, and two sympatric populations within the Comoros; the mechanism of divergence between the two sympatric populations of the Comoros remains unclear (Lampert et al., 2012). All studies are consistent in that they demonstrate low absolute divergence among populations, which either relates to extremely low evolutionary rates in *L. chalumnae*, or recent divergence of populations after going through a bottleneck (such as a founding effect) (Lampert et al., 2012). Mitochondrial DNA haplotype frequency data support the Comoros as an ancestral population to other populations distributed throughout the WIO, because this population appears to have a greater number of ancestral haplotypes (Nikaido, 2011).

All coelacanth populations demonstrate the common characteristic of low diversity, but the Comoros population is the least diverse (Nikaido, 2011, Nikaido, 2013). Genetic evidence for inbreeding has been observed in investigations of coelacanth mitochondrial DNA and DNA fingerprinting, where high band-sharing coefficients showed significant inbreeding effects (Schartl et al., 2005). The species *L. chalumnae* exhibits significantly lower levels of genetic divergence than its sister species *L. menadoensis* (Nikaido 2013). Because rates of molecular substitution and evolution are thought to be similar for these two species, the significantly lower diversity measures for *L. chalumnae* points to small populations (as compared to *L. menadoensis*) or the occurrence of repeated genetic bottlenecks rather than slow evolution rate alone (Nikaido 2013). Low diversity within populations and evidence for inbreeding suggest that populations are independent and small.

While population structure is not clearly resolved across the region, available genetic data suggest the following: 1) Oceanographic and environmental conditions may cause uneven gene

flow among coelacanth populations across the region; 2) populations across the WIO are independent, and do not represent strays from the Comoros, or a panmictic population; 3) Evolutionary rates of coelacanths are extremely slow, and lower diversity in *L. chalumnae* as compared with *L. menadoensis* points to small population sizes and/or genetic bottleneck effects.

DISTRIBUTION AND ABUNDANCE

It was once thought that coelacanths were restricted to the Comoro Island Archipelago, and that individuals caught in other locations in the Western Indian Ocean were strays or drifters. However, growing evidence suggests that *L. chalumnae* consists of several established populations throughout the WIO (Schartl et al., 2005). Two resident and scientifically surveyed coelacanth populations exist in waters off of South Africa and the Comoro Islands (Hissmann et al., 2006; Fricke et al., 2011). Increases in coelacanth catch off the coast of Tanzania during the last decade and genetic analysis of individuals caught there demonstrated that an established population exists there as well, as confirmed by the observance of 9 coelacanth individuals during a 2007 survey off the Tanzanian coast (as cited in (Nikaido et al., 2011)). Additional coelacanth catches have been recorded off of Madagascar, Mozambique, and Kenya, but these regions have not yet been surveyed (Nulens et al., 2011) so their status is unclear. What is known of the coelacanth's distribution is largely based on bycatch data. Thus, the true number of established coelacanth populations, and the extent of the species' range across the WIO remain uncertain.

Insufficient data exist to quantitatively estimate coelacanth population abundance or trends over time for the majority of its range. Population abundance estimates are greatly challenged by sampling and survey conditions wherein deep technical scuba or submersibles are necessary to reach and document the coelacanth in its natural habitat.

Quantitative estimates of coelacanth abundance have only been made for the Comoro Islands. Coelacanth population abundance estimates for the western coastline of Grand Comoro were initially made in the late 1980's by Fricke et al (1991a) and updated to include survey data from 1991 (Fricke et al., 1994). These estimates showed a relatively stable population ranging between 230-650 individuals (Fricke et al., 1994). The range of this estimate was attributed to observational errors, as it is likely that some caves within the survey area containing resident coelacanths remained undiscovered. Researchers considered the population along the west coast of Grand Comoro to be stable, suggesting that artisanal bycatch had little impact on population size (Fricke et al., 1994).

Surveys conducted in 1994 across the southwestern coast of Grand Comoro (the same sample area as earlier surveys) revealed a 68% decrease in cave inhabitants and a 32% decrease in the total number of coelacanths encountered as compared to a 1991 survey which covered the same area at the same time of year (Hissmann et al., 1998). As before, the survey area covered 9% of the projected coelacanth habitat along the western coast of Grand Comoro (Hissmann et

al., 1998). The reduction in coelacanth abundance observed during the 1994 survey was originally attributed to increases in artisanal fishing that occurred in the mid 1990's, as described by Plante et al. (1998). However, other causes could not be eliminated. For instance, individuals may have moved out of the survey area, as coelacanths are known to shift their preference for certain caves over time (Fricke et al., 1994). The 1994 survey occurred 20 days later [in the year] than the 1991 survey, and thus the water temperature of caves surveyed was 3°C higher; given the tight relationship between temperature and oxygen saturation for the species, this increase in temperature may relate to a movement of individuals to cooler areas and explain the reduction in coelacanth encounter rate during the 1994 survey. In fact, the water temperature of caves surveyed in 1994 was the highest recorded by researchers (25.1°C as compared to 21.1°C in 1991). It is now thought that high temperature is the best explanation for low cave occupation rates during this 1994 survey (Fricke et al., 2011).

Three additional surveys of the western coast of Grand Comoro occurred in the 2000's, and are summarized in Fricke *et al.* (2011). These survey methods and area were consistent with earlier surveys occurring in the late 1980's and 1990s. During surveys between 2000 and 2009, several marked individuals not sighted in 1994 re-appeared, and cave occupancy rates in these later surveys were similar to surveys of the early 1990's (Fricke et al., 2011). In total, nine dedicated coelacanth surveys have occurred in this area since 1986 (Fricke et al., 2011). Estimates of population abundance along the western coast of Grand Comoro, based on repeated surveys over almost 2 decades, are between 300 and 400 individuals, with 145 individuals identifiable via unique markings (Fricke et al., 2011). The 1994 survey showing population declines is thought to be an anomaly driven by higher water temperature, as later surveys demonstrate that the local population of western Grand Comoro has remained stable since the 1980's (Fricke et al., 2011). Some local Comoran fishermen have suggested that seasonal abundance patterns may exist for the coelacanth as they do for the locally-targeted oilfish, but there are insufficient data to address this phenomenon (Stobbs et al., 1991).

Juveniles (<100cm) are largely absent from survey and catch data, suggesting that earlier life stages may exhibit differences in distribution and habitat use (Fricke et al., 2011). Length at birth is assumed to be 40 cm (Bruton et al., 1991a). Size classes between 40 and 100 cm are largely absent from surveys of the Comoros, South Africa, and Tanzania; these smaller sizes are also absent from shallower water, suggesting that they inhabit deeper water than older individuals (Fricke et al., 2011). Only eight total specimens between 42.5 and 85 cm have been caught since 1938 (Bruton et al., 1991b; Nulens et al., 2011). In general, the distribution and relative abundance of juveniles across the coelacanth's range remains unknown.

Population estimates have not been conducted in other parts of the coelacanth's range, and it is possible that undiscovered populations exist across the WIO because coelacanths have been caught (in low numbers) off the coast of Madagascar, Kenya and Mozambique. Based on current understanding, coelacanth habitat and distribution is determined by the species' need for cool water and structurally complex caves and shelf overhangs for refuge. Using these requirements, Green *et al.* (2009) conducted a bathymetric survey using data coverage of the Western Indian Ocean in order to identify potential habitat for coelacanth populations, beyond

occupied habitat already identified. The authors identified several locations off of Mozambique and South Africa that met characteristics of coelacanth habitat. Lack of adequate data coverage for Tanzania and Madagascar precluded thorough analyses of these regions, so the authors did not rule out these locations as suitable coelacanth habitat. Although this bathymetric study did not lead to any additional surveys to groundtruth its findings, the analysis demonstrates the presence of suitable habitat throughout the Western Indian Ocean, and thus the potential for yet-undiscovered coelacanth populations. Based on the data presented, populations that have been surveyed appear to be stable with unknown abundance and trends elsewhere.

ANALYSIS OF THE ESA SECTION 4(a)(1) FACTORS

Destruction, modification, or curtailment of habitat or range

There is no evidence curtailment of the historical range of *L. chalumnae* has occurred throughout its evolutionary history, either due to human interactions or natural forces. No fossils within the genus *Latimeria* have ever been discovered. The most closely related species in the fossil record is *Macropoma lewesiensis*, a sister species to *Latimeria chalumnae*, which is thought to have become extinct over 65 million years ago. Genetic data and geological history suggest that the split between *Latimeria chalumnae* and its Indonesian sister species *Latimeria mendosis* occurred 40-30 Mya, and that the genus was previously distributed throughout the coasts of Africa and Eurasia (Springer, 1999; Inoue et al., 2005). However, no data are available to inform an understanding of historical changes in the range of the species *Latimeria chalumnae*. Although it was previously thought to be restricted to the Comoros, accumulating evidence suggests that the species is comprised of several independent populations distributed throughout the coastal Western Indian Ocean (Fricke et al., 1990; Fricke et al., 2011). In addition, surveys and models of possible coelacanth habitat suggest that yet undiscovered populations exist throughout the Western Indian Ocean (Green et al., 2009; Owens et al., 2012). Although the order Coelacanthiformes was deemed to have become extinct 65 million years before the 1938 discovery in South Africa, this surprising encounter cannot be used as evidence for a curtailment of the species' range from historical levels given lack of any historical data on the species prior to its discovery. The species is naturally hidden from human observation, and therefore, highly technical diving, deep water survey equipment, or unique fishing techniques (such as hand lines) are required to reach the fish's cavernous, structurally complex, and deep habitat; thus, the contemporary and historical extent of its range remains unclear.

Due to its occurrence in deep water (>100 meters), the coelacanth may be particularly buffered from human disturbance (Heemstra et al., 2006). Nonetheless, increases in human population and development along the coastline of the Western Indian Ocean could impart long-term effects on the fish throughout its range. World human population forecasts predict that the largest percentage increase by 2050 will be in Africa, where the population is expected to at

least double to 2.1 billion (Kincaid, 2010). The result of increased population density on coastal ecosystems of East Africa may include increased pollution and siltation, which may impact the coelacanth despite its use of a deep and relatively stable environment.

Human population growth will likely lead to increases in agricultural production, industrial development, and water use along the coast of the Western Indian Ocean; these land use changes may increase near shore sedimentation, possibly affecting coelacanth habitat. As described earlier, sedimentation is theorized to negatively impact coelacanth distribution (Springer, 1999). The coelacanth has been shown to avoid caves with turbid water, even if other preferred conditions of shelter and food are present (Hissmann et al., 2006). Many East African countries are still developing, and the population is growing. Increased food demand may lead to changes in land and water use, and an increase in agriculture and thus run-off and siltation to the coast. It is possible that, if increases in siltation occur, coelacanth habitat may be affected, and range reduced. However, the nature of these economic and land use changes, as well as their direct effect on sedimentation and subsequent impact on coelacanth habitat, remain highly uncertain.

Pollution of coastal African waters does not currently pose a direct threat to the coelacanth. A review of heavy metals in aquatic ecosystems of Africa showed generally low concentrations, close to background levels, and much reduced from more industrial regions of the world (Biney et al., 1994). Yet, surprisingly, a toxicological study of two coelacanth specimens detected lipophilic organochlorine pollutants such as PCB and DDT (Hale et al., 1991). Levels ranged from 89 to 510 pg kg^{-1} for PCB and 210 to 840 pg kg^{-1} for Σ DDT, and were highest in lipid-rich tissues such as the swim bladder and liver (Hale et al., 1991). The coelacanth has high lipid content, and its trophic position may increase the probability of toxic bioaccumulation. Insufficient data are available to determine the impact of these toxins on coelacanth health and productivity.

Direct habitat destruction may impact coelacanths off the coast of Tanga, Tanzania. Plans are in place to build a new deep-sea port in Mwambani Bay, 8km south of the original Tanga Port. The construction of the Mwambani port is part of a large project to develop an alternative sea route for Uganda and other land-locked countries that have been depending on the port of Mombasa. Development of the port would include submarine blasting and channel dredging and destruction of known coelacanth habitat in the vicinity of Yambe and Karange islands - the site of several of the Tanzanian coelacanth catches (Hamlin, 2014). The new port is scheduled to be built in the middle of a newly-implemented Tanga Coelacanth Marine Park. The plans for Mwambani Bay's deep-sea port construction appear to be ongoing, despite conservation concerns. If built, the port may disrupt coelacanth habitat by direct elimination of deep-water shelters, or by a large influx of siltation that would likely result in coelacanth displacement.

Habitat destruction in the form of nearshore dynamite fishing on coral reefs may indirectly impact the coelacanth due to a reduction in prey availability, but these impacts are highly uncertain. As a restricted shallow-water activity, this destructive fishing would not impact the coelacanth's deep (+100 m) habitat directly. However, coral reefs in this region provide

essential fish nursery habitat and are hot spots for biodiversity (Salm, 1983). Loss of nearshore coral habitat may negatively impact pelagic fish species due to loss of nursery habitat; it is highly uncertain how these impacts may affect the prey availability for the coelacanth. Dynamite fishing in the Comoros was observed recently by researchers (Fricke et al., 2011). While this method is not widespread throughout the Comoros, reduction in the sustainability of nearshore or pelagic fish populations may encourage fishermen to increase use of these new methods. Dynamite fishing in Tanzania is widespread, and has led to destruction of nearshore coral reefs and disruption of essential fish habitat (Wells, 2009). Destructive fishing practices occur throughout coral reefs along the coast of the Western Indian Ocean (Salm, 1983). The true extent to which the destruction of near shore coral habitat may affect the coelacanth remains uncertain, especially as the fish is thought to consume primarily deep-water prey (Uyeno, 1991; Uyeno et al., 1991).

Method of Capture	Date	Number of Specimens
Handlining (Comoros)	1952-2011	215
Shark gillnets (Tanzania, Madagascar)	1995-2011	76
Demersal Trawling (South Africa, Mozambique, Kenya)	1938-2011	3

Table 3. Method of capture, date, and number of coelacanth specimens caught between 1938 and 2011. From Nulens et al., 2011.

Overutilization for commercial, recreational, scientific, or educational purposes

Bycatch

Since its discovery in 1938, all known coelacanth catches are considered to have been the result of bycatch. Particularly in the Comoro Islands, where the highest number of coelacanth catches has occurred, researchers have found no evidence of a targeted coelacanth fishery given that methods do not exist to directly catch the deep-dwelling fish (Bruton et al., 1991c). The coelacanth meat is undesirable, and thus the fish is not consumed by humans (Fricke, 1998).

Out of 294 coelacanth catches since its 1939 discovery, the majority of catches (n =215 as of 2011) have been a result of bycatch in the oilfish, or *Revetus*, artisanal fishery occurring only in the Comoro Island archipelago (Stobbs et al., 1991; Nulens et al., 2011) (Table 3). The Comoros oilfish fishery uses unmotorized outrigger canoes (locally called *galawas*). The fish are caught using handlines and hooks close to shore at depths as great as 800m (Stobbs et al., 1991). This traditional fishery is known locally as *mazé* fishing, and coelacanth catches have only occurred on Grand Comoro and Anjouan Islands (Stobbs et al., 1991). Oilfish are traditionally caught at night, an act considered locally to be very dangerous (Stobbs et al., 1991). Often, this artisanal fishing is performed only on dark moonless calm nights. In general, subsistence fishing in the region is limited by weather conditions, and often disrupted by monsoon or tropical storms. This fishery is also limited by a tradition of social pressure which restricts fishing to offshore waters adjacent to each fisherman’s village (Stobbs et al., 1991).

The oilfish occurs in similar habitat to the coelacanth. While this fishery has led to far greater coelacanth catches in the Comoros than elsewhere, reviews of coelacanth bycatch in the Comoros demonstrate there has been no measurable increase in catch rate for coelacanths since its 1938 discovery (Stobbs et al., 1991). In fact, authors note a shift in fishing effort from artisanal near shore benthic fishing to offshore trolling for pelagic species (associated with a low probability of coelacanth bycatch) (Stobbs et al., 1991). Deep-water hand lines remain the only method for coelacanth bycatch in this region, and have experienced no major technological advances (Stobbs et al., 1991). It is thought that the shift from artisanal fishing methods to the deployment of more modern motorized boats and pelagic fish aggregation devices decreases the risk of coelacanth catches (Bruton et al., 1991c).

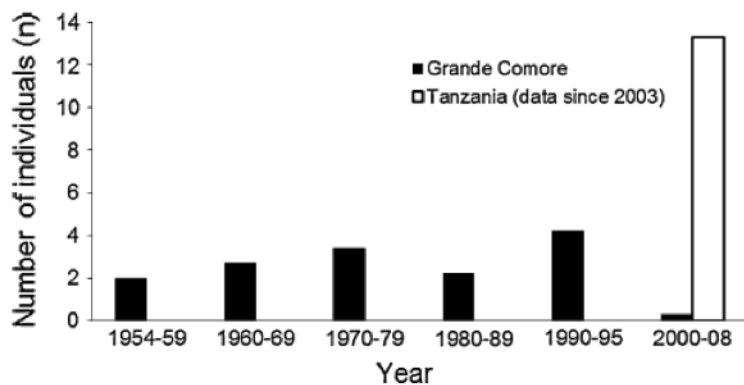


Figure 6. The annual catch rate of coelacanths at Grand Comore since their discovery in 1954 (black bars) in comparison with the annual catch rate of Tanzania (open bar). From Fricke et al. 2011.

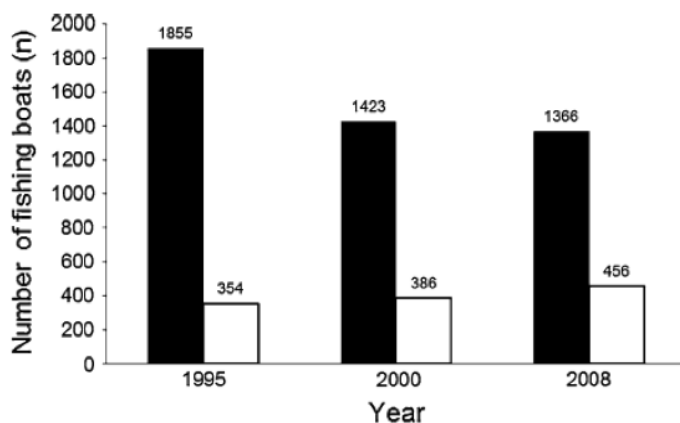


Figure 5. The development of motorized (open bars) and unmotorized (galawas, black bars) fishery at Grand Comore from 1995 to 2008. From Fricke et al. 2011.

Fishing catch per unit effort (CPUE) and total catch is not geographically consistent throughout the Comoro Islands. The majority of coelacanths are caught along the west coast of Grand Comoro. Fricke et al. (1988) explain this phenomenon as related to the difference in habitat, the west being associated with steeper and more structured rock than the older more heavily eroded east coast, less suitable for coelacanth habitation (Plante et al., 1998). Along the west coast of Grand Comoro, Plante et al (1998) calculated fishing effort, and its variation from north to south. They separated the west coast into 5 fishing sectors running from north to south, with 1 being the farthest north, and 5 the farthest south (Plante et al., 1998). The authors found that the greatest number of catches (38 fish between 1954 and 1995) occurred in sector 4, which also experienced the highest CPUE, at 3.1 per 100 galawas.

While coelacanth catch rate in the Comoros shows no significant trend

over time, it has fluctuated historically with changes in fishing technology and shifts in the ratio between artisanal and more modern pelagic fishing methods (Stobbs et al., 1991; Plante et al., 1998). Since its discovery in the Comoros (in 1938), coelacanth catch rate has been low, between 2-4 individuals year⁻¹. In the 1950's, rates were 1.9 individuals year⁻¹. Between 1954 and 1970 coelacanth catch rates increased in the Comoros, possibly due to an increase in human population and nearshore artisanal fishing pressure (Plante et al., 1998). In later decades, the catch rate stabilized at a higher rate (4.9 in the 1960's, 4.8 in the 1970's, and 4.0 in the 1980's) (Bruton et al., 1991a). The increase in catch was interrupted by a campaign in the 1980's to introduce motorized boats and offshore fishing to the Comoran Islands. At this time, motors were provided for local fishermen, and Fish Aggregation Devices (FADs) were moored in deep pelagic waters. These FADs are comprised of an array of buoys and ribbons to attract pelagic fish, facilitating their catch, and diverting fishing pressure away from the near shore deep water habitat of the coelacanth. Coelacanth bycatch rates decreased between 1986 and 1991 as a result of this campaign. Motors could not be repaired on the island due to lack of workshops or replacement parts, and thus their use declined in the early to mid 1990's. Plante et al (1998) measured changes in the ratio of motorized boats to outrigger canoe fishing effort between 1991 and 1995 at 9 fishing villages on the west coast. In 1991, the number of motorized versus unmotorized canoes was 181 and 465 respectively; this changed to 153 and 550, respectively, in 1995 (Plante et al., 1998). The authors correlated this shift back to artisanal fishing to an increase in coelacanth bycatch over that short time frame. From a broader temporal perspective, there was an increasing but insignificant change in coelacanth catch from the Comoros from 1954 to 1995 (Plante et al., 1998). Between 1995 to 2008, the number of galawas in the Comoros has declined steadily, corresponding with a steady increase in motorized boats (Fricke et al., 2011) (Figure 5). The most recent update of coelacanth catch inventory indicates that catch rates in the Comoro archipelago have declined and stabilized over the past decade (Nulens et al., 2011). In fact, between 2000 and 2008, catch rates were the lowest ever observed, likely due to the increase in motorized boats and decreased artisanal handline fishing over the past decade (Fricke et al., 2011).

In 1991, Stobbs et al. reviewed anecdotes from fishermen, catch data, and data from fishing effort to understand the effect local Comoran fishing may have on the coelacanth: 1) They found no evidence that the coelacanth could be directly targeted, as they have only been caught as infrequent bycatch of the traditional handline fishery for oilfish, and demonstrate no preferences for gear or bait. 2) There has been a directed shift in effort toward the pelagic fishery, which uses more efficient technology such as motorized vessels, nets, and Fish Aggregation Devices, and avoids the dangers of *mazé* night fishing. 3) Provided that modern motorized net fishing does not move inshore and to deeper waters (which is unlikely because rocky steep-sloped coelacanth habitat is unfriendly to trawl nets), they did not expect increases in coelacanth catch rates and in fact expected a decrease in future catch effort (Stobbs et al., 1991). This prediction has held to be true, as the number of galawas have steadily decreased in recent years, (Fricke et al., 2011) (Figures 5 and 6). Today, *mazé* fishing is generally considered dangerous, is performed by older experienced fishermen, and is going out of favor in the Comoros (Plante et al., 1998; Fricke et al., 2011); this trend is expected to continue into the future, and releases fishing pressure on the coelacanth in this region, most likely explaining the

reduction in coelacanth catch over the past decade (Stobbs et al., 1991; Plante et al., 1998; Fricke et al., 2011; Nulens et al., 2011).

For the Comoro Islands, Bruton *et al.* (1991a) estimated total mortality rate based on demographic factors derived by measurements of length, weight, sex, and age distribution of all coelacanths caught since the 1950's. They estimated that natural mortality rate ranged between 0.166 and 0.198 (or 85 to 82% annual survival). Based on an estimated population size of 500 catchable individuals (<100 cm) throughout the Comoro archipelago, Bruton showed that a sustainable population could be maintained at a fishing mortality rate of 0.4% of the population within that size range. Bruton further determined that the natural mortality, most likely due to shark predation, was higher than mortality due to fishing pressure (Bruton, 1991). Recently, Fricke *et al.* (2011) performed an analysis of local mortality rate of the coelacanth based on 21 years of survey data. They estimated that the local death rate (in the 8-km survey area) was 1-3.3 individuals per year and that the number of recruits per year was 1.8-2.2. They concluded that the population is near equilibrium and limited by recruitment (Fricke et al., 2011). This recent work estimated an even lower natural mortality rate of 0.044 (0.039-0.048), and fishing mortality was determined to be negligible in the Comoros population (Fricke et al., 2011).

Outside of the Comoros, coelacanths have been caught in Tanzania, Madagascar, Mozambique, Kenya, and South Africa (Nulens et al., 2011). Historically, far fewer coelacanth catches have occurred outside of the Comoros Islands. However, over the past decade, the trend in coelacanth catches shows a drastic increase in catch rate off of Tanzania via shark gillnets (Fricke et al., 2011; Nulens et al., 2011). Hand line *mazé* fisheries are absent outside of the Comoros, thus catches across the rest of the Western Indian Ocean have occurred using different gear - deep-set shark gillnets and trawls. Trawls have been the mechanism for only 3 total coelacanth catches; minimal catch through trawling is thought to relate to the coelacanth's preferred rocky steep cavernous habitat, substrate not suitable for trawling activity (Benno et al., 2006). The first confirmed coelacanth catches using shark gillnets occurred in Madagascar in 1995 and in Tanzania in 2003, although a few earlier unconfirmed catches in these locations may have occurred as early as 1953 (Benno et al., 2006). The first Tanzanian catch in 2003 followed the introduction of shark gillnets in the region in 2001 (Benno et al., 2006). As of September 2003, the capture of coelacanths has been dominated by those caught in Tanzania (Nulens et al., 2011). Since the first 2003 catch in Tanzania, over 60 catches via deep water gillnets have been reported, with over 12 fish caught/year between 2003 and 2008 (Benno et al., 2006; Nulens et al., 2011). These shark gillnets are set at depths between 50 and 150m, and it is thought that accidental coelacanth catches in Tanzania occur when coelacanths leave their caves for nighttime hunting (Nyandwi, 2009).

Expansion of the shark gillnet fishery across the Western Indian Ocean may result in increased bycatch of the coelacanth, as has been observed off the coast of Tanzania, however the potential for such an increase is uncertain. Available information suggests that shark fishing effort has been increasing off the coast of east Africa, including the coelacanth range countries of Mozambique, Madagascar, Kenya, and South Africa (Smale, 2008). Techniques for catching

sharks in this region include deep-set shark gillnets, such as those responsible for the commencement of coelacanth bycatch in Tanzania, which began in 2003 (Nulins et al., 2011). Shark gillnet fishing is used in other East African countries, such as Mozambique, where these fisheries are highly profitable, and are driven by the demand for fin exports, with evidence for frequent illegal export occurring (Pierce et al., 2008). Despite the use of gillnet fishing practices elsewhere in East Africa, other areas have not shown a similar spike in coelacanth bycatch as has been observed in Tanzania. Enumeration of effort from the shark gill net fishery in South Africa has been challenging due to high levels of illegal or unreported fishing occurring; for example, as little as 21% of the actual catch for shark gillnet and seine fisheries may be reported in South Africa (Hutchings et al., 2002). Nonetheless, shark fisheries in this region are thought to be overexploited, which may lead to an increase in future effort due to sustained global demand (Hutchings et al., 2002, Kiska, 2012 SWIOFP). It is reasonable to conclude that the use of shark gillnets will continue or increase in Tanzania and will continue to expand throughout the Western Indian Ocean; however, whether this trend will result in an increased threat of coelacanth bycatch is uncertain, especially given the uncertainty over the fish's range and habitat use throughout the coast of East Africa.

Commercial interest

The coelacanth is not desirable commercially as a traditional food source or for artisanal handicrafts. In fact, the local name 'gombessa' means 'taboo' or 'strictly forbidden' in Swahili. This name is thought to be derived from the oily flesh of the coelacanth, suspected to be used locally as a medicinal laxative, but not desirable as food (Stobbs, 1989). Targeted methods of fishing the coelacanth have never been developed, and local cultures do not value the coelacanth commercially or for subsistence purposes (Fricke, 1998).

Since its discovery in 1938, the coelacanth has inspired global artwork and poetry, and has been incorporated into handicrafts, works of fiction, cartoons, and stories due to its sensational story as a living species once thought to be extinct. Fricke (1998) provides a review of the local and global cultural importance of the coelacanth, and its development over the past few decades (Fricke, 1998). In the Comoros, the coelacanth has become a source of pride and national heritage (Fricke, 1998). The cultural interest in the coelacanth does not put the fish at risk, and on the contrary, may encourage its conservation. Commercial interest through tourism to the coelacanth's habitat is not a realistic threat either, as the deepwater habitat is largely inaccessible.

In the 1980's there was a rumor that Japanese scientists were attempting to develop a new anti-aging serum using the coelacanth notochord oil. Although these claims made international headlines, the rumor has since been rejected. As Fricke pointed out (Fricke, 1998), the unsubstantiated rumor of the 'fountain of youth' serum had an unexpected result of stirring publicity and conservation interest in the fish. Interest in the coelacanth notochord oil for medicinal purposes does not pose a threat to the species, as claims of its life extending properties are unsubstantiated.

Interest in coelacanth specimens on the black market is a possible threat to the species. The concern mostly surrounds a curio trade rather than a potential aquarium trade. Because the fish is deep-water dependent, it survives for only a short period of time at the surface, and thus, thus far, is not maintained in aquariums. Several attempts have been made to keep the coelacanth alive in captivity, but have demonstrated that the deep water fish is fragile, and has been shown to survive at the surface for less than 10 hours (Hughes et al., 1972); the cause of death is thought to be a combination of capture stress and overheating resulting in asphyxiation. Comment threads found in the popular website Monster Fish Keepers, a forum for private aquarium and fish hobbyists, reveal widespread knowledge of the coelacanth's fragility; these hobbyists express general understanding that the coelacanth's life can be sustained at surface depth no longer than a few hours (Hamlin, 1992; Monsterfish, 2007). Thus, black market trade of the coelacanth for private aquaria is not a realistic threat. However, the black-market curio trade may be a source of exploitation. The same fish hobbyist forums reveal general interest in the fish as a curio specimen, and willingness to pay more than \$4500 for a dead specimen (Monsterfish, 2009). This sum is equivalent to over 20 years income for a local Comoran worker. Thus, black market curio trade may provide an economic incentive for capture of the fish. However, I was unable to find data suggesting that a black market curio trade is currently active.

Scientific interest

Since its early discovery, international scientists and researchers have cherished the coelacanth as the only representative of an important evolutionary branch in the tree of life. The coelacanth was originally thought to be the 'missing link' between aquatic organisms and modern tetrapods, sparking much interest from a variety of disciplines including evolutionary biology and paleontology. Current understanding places lungfish as the sister group to tetrapods, and the coelacanth is considered now to be an evolutionary 'aunt' to the tetrapods. Nonetheless, the coelacanth continues to provide valuable insight into the history of evolution on earth as the oldest living lineage of Sarcopterygii, more closely related to reptiles and mammals than they are to ray-finned fishes.

Scientific interest in the coelacanth has persisted throughout the international research community since the 1938 discovery. This has led to a long history of surveys to better understand the fish's ecology, habitat, distribution, and evolution (Table 3). A tissue library from bycaught specimens is maintained at the Max Planck Institute Germany, which provides the opportunity for scientific use of samples derived from these accidental coelacanth catches (Fricke, 1998). Coelacanth specimens have been used by more than 30 laboratories. In earlier years of coelacanth research, a reward of US\$300-400 was offered to fishermen for each coelacanth caught (Fricke, 1998). However, those rewards have not been offered for decades. Prior to strict regulations on coelacanth trade, the global museum trade offered between US\$400 and US\$2000 for each specimen caught. Today, unauthorized trade of the coelacanth is forbidden by the Convention on International Trade in Endangered Species (CITES), but some transfer of specimens for scientific study is permitted. The coelacanth is listed as an Appendix I species, which prohibits international commercial trade. I was unable to find any evidence that

targeted coelacanth catch for scientific purposes is occurring. Thus, the demand for specimens for scientific research is not considered a threat.

In the future, scientific interest and study may be used as a basis for the public display of the coelacanth. The public display of the fish would be of high commercial value, and efforts to keep the coelacanth in captivity have already been made. In the late 1980's and early 1990's, American and Japanese aquariums attempted to directly capture and bring the coelacanth into captivity (Suzuki et al., 1985; Hamlin, 1992). These attempts were not successful; it was determined that coelacanth cannot be directly caught, and that they only survive for a few hours outside of their deep water environments (Hamlin, 1992). In the future, larger aquariums may pursue the use of pressurized tanks to keep the coelacanth alive in captivity, but their success is uncertain given the challenge in transporting a fish from its native habitat, and then maintaining it in an aquarium environment.

Table 4. List of scientific endeavors and expeditions to study, observe, and collect the African coelacanth.

Year	Country	Institution	Aim	Source
1954	France	Jacques Cousteau Museum of Natural History	Survey, filming	Smith (1956)
1954	Italy	Spedizione Zoologica Italianae	Filming	Smith (1956)
1963	France	Jacques Cousteau Museum of Nat. Historie	Filming	Bureau Cousteau, Paris
1964	USA	University of Southern California	Survey	
1969	England	Royal Society	Survey	Forster et al. (1970)
1972	England, France, USA	Royal Society	Survey, general biology, collection	Thompson (1973)
1975	USA	California Academy of Science	General biology, filming	McCosker & Lagios (1979)
1979	England	BBC	Filming	Thompson (1991)
1981	Belgium	Royal Museum	Survey	Thys van den Andenaerde 1984)
1981	Japan	JASEC	Survey, ecology	Suzuki et al. (1985)

1983	Belgium	Royal Museum	Survey	Thys van den Andenaerde (1984)
1983	Japan	JASEC	Survey, ecology	Suzuki et al. (1985)
1986	Japan	JASEC	Survey, filming	Suzuki (pers. Com)
1986	S. Africa	JLB Smith Institute	Survey, conservation	Bruton & Stobbs (1991)
1986/7	Germany	Max Planck Institute	Survey, ecology	Fricke et al. (1987)
1987	S. Africa	JLB Smith Institute	Survey, conservation	Bruton & Stobbs (1991)
1987	Germany	Max Planck Institute	Ecology, Filming	Fricke et al (1987)
1987	S. Africa	JLB Smith Institute	Conservation	Bruton & Stobbs (1991)
1987/88	USA	Explorer Club and New York Aquarium	Collecting	Hamelin (1992)
1989	Japan, Germany	TOBA Aquarium	Collecting	Musick et al (1991)
1989	Germany	Max Planck Institute	Ecology, filming	Fricke et al. (1991)
1990	S. Africa	JLB Smith Institute	Conservation	Bruton and Stobbs (1991)
1991	Germany	Max Planck Institute	Ecology, conservation	Fricke and Hissman (1994)
1994	Germany	Max Planck Institute	Ecology, conservation	Hissmann et al. (1998)
1995	Germany, France	Max Planck Institute and Foundation N. Hulot	Conservation, filming	Plante et al , Hissamann et al. (1998)
2000	France	Trimex, Andromede Oceanology, France	Exploratory dive	Venter et al. (2000)
2000	Germany	Max Planck Institute	Survey, ecology	Hissman et al. (2000)
2007	Japan	Japan Aquamarine	Filming, Survey	
2008	Germany	Max Planck Institute	Survey, ecology	Fricke (2011)
2009	Germany	Max Planck	Survey, ecology	Fricke (2011)

Disease or Predation

Although no direct evidence of predation has been observed, it is thought that sharks pose a predatory risk to the coelacanth. During surveys off the Comoros Islands, large sharks, including the sand tiger shark, *Odontaspis ferox*, have been observed (Fricke et al., 2000a). It is thought that other deep sea sharks such as *Hexanchus griseus*, and other pelagic sharks occurring in the Comoros and throughout the Western Indian Ocean, may eat the coelacanth. Some coelacanths surveyed demonstrate fin damage and deformities, which may relate to shark encounters (Hissmann et al., 2006). The predation rate is not known, though it has been suggested that natural predation may contribute substantially to the coelacanth natural mortality (Fricke et al., 2011).

In general, coelacanth specimens appear to have very few parasites. Two individuals captured off the Comoros were cited to have low-abundance anisakine (having a life cycle that involves fish and marine mammal hosts) nematode parasites identified as either the genus *Terranova* or *Pulchrascaris* (Thoney et al., 1991). Other specimens have been associated with low levels of isopods, cestodes, and parasite larvae of a gnathiid isopod (KAME, 1971; Thoney et al., 1991). Due to the generally low abundance of parasites observed on coelacanth specimens, I do not consider parasitism to pose a threat to the fish.

Other natural or human factors affecting continued existence

Climate change

Coelacanth habitat preference and distribution is dictated by specialized requirements for appropriate shelter (caves, caverns, and shelves), prey availability, and a combination of depth and temperature that meets the fish's need for oxygen (relating to their optimal blood saturation at 15°C) (Hughes, 1972). Evidence from coelacanth habitation in South Africa is particularly useful in demonstrating the trade-offs among these important characteristics: here, coelacanths occupy depths of 100-140m. The optimal temperature for the uptake of oxygen (15°C) occurs at lower depths of 200m where fewer caves exist. It is thought that the occupation of shallower depths is a trade-off between the need for shelter and optimal oxygen uptake; increases in oceanic temperature may disrupt the tight balance between their metabolic needs and the need for refuge (Roberts et al., 2006).

Across the globe, ocean temperature is increasing at an accelerated rate (IPCC, 2013). The extent of this warming is reaching deeper and deeper waters (Abraham et al., 2013). Increase of global mean surface temperatures for 2081–2100 relative to 1986–2005 is projected to likely be in the ranges derived from the concentration-driven CMIP5 model simulations by IPCC, that

is, 0.3°C to 1.7°C (RCP2.6), 1.1°C to 2.6°C (RCP4.5), 1.4°C to 3.1°C (RCP6.0), or 2.6°C to 4.8°C (RCP8.5) (IPCC, 2013). While these predictions relate to surface ocean temperatures, evidence from deep-water ocean measurements and models suggest that heat flux to the deep ocean has accelerated over the last decade (Abraham et al., 2013). If deep-water warming continues to keep pace with (or exceed the pace of) surface warming, even the most conservative IPCC scenarios may mean a warming of current coelacanth habitat.

The coelacanth is typically observed at 15-20°C, with upper thermal limits of 22-23°C (Hughes et al., 1972). The effect of these thermal limits on the coelacanth's distribution has been demonstrated by a 1994 survey of the Comoro Islands, which revealed a 68% decrease in cave inhabitants and a 32% decrease in the total number of coelacanths encountered as compared to a 1991 survey (Hissmann et al., 1998). Temperature is thought to have directly led to this decline in coelacanth observations; in 1994, temperature of the survey region was 25.1°C, the warmest ever recorded by researchers there (Hissmann et al., 1998). However, it's important to note that coelacanths had returned to their previous habitat in subsequent surveys (Fricke et al. 2011); this suggests that the warm conditions in 1994 led to a displacement of coelacanth habitat, but did not lead to extirpation of that population, or a reduction in the population. This information suggests that warming may impact coelacanth distribution, but there may be suitable habitat to accommodate a displacement of populations, where warming may not lead to decreases in population sizes or extirpation of populations. Despite deep water warming that has occurred over the last decade, the surveyed coelacanth population in the Comoros is described as stable, and not declining (Fricke et al. 2011).

Based on the majority of climate model predictions, it is likely that current coelacanth habitat will reach temperatures exceeding the fish's thermal limits by 2100 (IPCC, 2013). It is unlikely that the low-diversity fish with long generation times will physiologically adapt to withstand the metabolic stress of a warming ocean. However, the fish may be able to move to suitable habitat outside of its current range, thus adapting its range to avoid the warming deep water conditions. If the fish is displaced based on its need for cooler waters, but complex cave shelters are not available, local extirpation or range restriction may occur. However, currently, these impacts and responses are highly uncertain. Thus, it is reasonable to conclude that a warming ocean may impact the fish's distribution, but the impact of warming on the future viability of the species is uncertain. Due to the coelacanth's temperature-dependent oxygen demand, coupled with a highly specific need for deep structurally complex cave shelter, warming oceanic waters may pose a threat to the coelacanth and displacement of populations, but the impact of this threat on the future viability of the species is highly uncertain, and climate change threats have not been clearly or mechanistically linked to any decline in coelacanth populations.

Inadequacy of regulatory mechanisms

CITES Appendix I regulates trade in species in order to reduce the threat international trade poses to those species. The coelacanth is included in CITES-Appendix I. Appendix I addresses those species deemed threatened with extinction by international trade. CITES prohibits international trade in specimens of these species except when the purpose of the import is not commercial, meets criteria for other types of permits, and can otherwise be legally done

without affecting the sustainability of the population, for instance for scientific research. In these exceptional cases, trade may take place provided it is authorized by the granting of both an import permit and an export permit (or re-export certificate). There is no evidence of illegal trade of the coelacanth. Trade is limited to transfer of specimens for scientific purposes. There is no evidence that CITES regulations are inadequate to address known threats such that it is contributing to the extinction risk of the species.

The coelacanth is also listed as Critically Endangered on the International Union for the Conservation of Nature's (IUCN) Red List. The IUCN is not a regulatory body, and thus the critically endangered listing does not impart any regulatory authority to conserve the species.

The threat to the coelacanth stemming from anthropogenic climate change includes elevated ocean temperature reaching its deep-water habitat and resulting in decreased fitness or relocation of populations based on elimination of suitable habitat, which may become restricted due to the tight interaction between the coelacanth's thermal requirements and need for highly complex cave shelter and prey. Impacts of climate change on the marine environment are already being observed in the Indian Ocean and elsewhere (Hoerling et al., 2004; Melillo et al., 2014) and the most recent United Nations Intergovernmental Panel on Climate Change (IPCC) assessment provides a high degree of certainty that human sources of greenhouse gases are contributing to global climate change (IPCC, 2013). Countries have responded to climate change through various international and national mechanisms, including the Kyoto Protocol of 2007. Because climate change-related threats have not been clearly or mechanistically linked to decline of coelacanths, the adequacy of existing or developing measures to control climate change threats is not possible to fully assess, nor are sufficient data available to determine what regulatory measures would be needed to adequately protect this species from climate change. While it is not possible to conclude that the current efforts have been inadequate such that they have contributed to the decline of this species, we consider it likely that coelacanth will be negatively impacted by climate change given the predictions of widespread ocean warming (IPCC, 2013).

ASSESSMENT OF EXTINCTION RISK

I assessed the extinction risk for the coelacanth by considering two types of information: (1) demographic viability characteristics (*e.g.* abundance, growth rate/productivity, spatial structure/connectivity, and diversity) reflecting the past and present conditions; and (2) threats faced by the species (*e.g.*, curio trade, bycatch, etc.) as described in terms of the ESA 4(a)(1) factors.

Demographic characteristics of, and threats to, the coelacanth, now and in the foreseeable future, were used to estimate the overall risk of extinction. I analyzed the contribution of each factor to the risk of extinction separately and considered the synergistic effect of all factors. Specifically, I accounted for demographic information including abundance, growth rate/productivity, spatial structure/connectivity, and diversity of the species as described in Wainwright and Kope (1999), and McElhany (2000); these factors are thought to be good

indicators of extinction risk when considered alongside threats to the species, and are firmly founded in conservation biology. I assessed the ways in which these demographic characteristics contribute to the species' vulnerability to extinction given the current threats, and those in the foreseeable future. This approach has been applied in assessing extinction risk for a number of species listed under the ESA. The demographic risk criteria were evaluated based on the present species' status in the context of historical information, if available, and threats that might alter the determination of the species' overall level of extinction risk. These characteristics are critical considerations in evaluating a species' extinction risk and were analyzed using the standard of best available science required by the ESA.

I rated all demographic factors and threats as very low, low, moderate, or high based on their likelihood to contribute to the risk of extinction; the determination of risk relied upon the most current literature and best scientific understanding of the species' status and threat impact. Each demographic factor and threat was first considered separately. However, evaluating demographic factors and threats separately may underestimate the synergy and interaction among them. Therefore, demographic factors and threats were evaluated holistically to determine the overall likelihood of extinction now and in the foreseeable future. The definitions of each risk rating are as follows:

- (1) **Very low** - it is very unlikely that the particular factor contributes significantly to the risk of extinction;
- (2) **Low** - it is unlikely that the particular factor contributes significantly to the risk of extinction;
- (3) **Moderate** - it is likely that the particular factor contributes significantly to the risk of extinction; and,
- (4) **High** - it is highly likely that the particular factor contributes significantly to the risk of extinction.

(Note: I use the term "significantly" here as it is generally defined – i.e., in a sufficiently great or important way as to be worthy of attention.)

Qualitative Assessment of Demographic Risks

Abundance

Coelacanth abundance across its entire range is not well understood. While abundance off the Comoros is expected to be low (<400 individuals), insufficient data are available to assess the true number of populations across the Western Indian Ocean, or the size of these populations. The coelacanth has very restricted and specific habitat requirements and low growth rates. Based on these data, I conclude that it is likely that population sizes across the Western Indian Ocean are small for reasons further discussed below. However, based on coastal surveys, it has been suggested that suitable coelacanth habitat exists throughout the region in locations where populations have not yet been discovered (Green et al., 2009). Low levels of genetic diversity have been observed in specimens sampled across its range which may relate to slow rates of evolution, small population sizes, or genetic bottleneck effects and inbreeding (Nikaido, 2013). *Latimeria chalumnae* exhibits significantly lower levels of diversity than *L. menadoensis*. These

two species are thought to have similar rates of evolution. Thus, it is likely that the lower extent of diversity in *L. chalumnae* is related to smaller population sizes or a strong genetic bottleneck or inbreeding effect, rather than low evolutionary rates alone. Long generation times and restricted habitat suggest that coelacanth populations are small throughout its range (Hissmann et al., 2006; Fricke et al., 2011). Abundance trends are not available across the range of the species, but in the Comoros there is no evidence of a decline. However, the likelihood of low abundance makes coelacanth populations more vulnerable to extinction by elevating the impact of stochastic events or chronic threats resulting in coelacanth mortality. Thus, I classify the risk of low abundance as moderate.

Growth rate/productivity

The coelacanth has one of the slowest metabolisms of any vertebrate. Their productivity is limited by this slow metabolism, and relates to their meager demand for food, slow swim speed and passive foraging, need for refuge to rest, and small gill surface area which limits their absorption of oxygen. In addition, their gestation period is longer than any vertebrate (3 years), although their fecundity is moderate. They are long-lived species, with long generation times. The extremely long gestation period and late maturity makes the coelacanth particularly vulnerable to external threats such as bycatch, possibly impeding recovery from mortality events (Froese et al., 2000). Because of this, I classify the risk of slow growth rate of the coelacanth as high.

Spatial structure/connectivity

Genetic data suggest that the coelacanth is comprised of independent and isolated populations, originating in the Comoros, but fully established along the Western Indian Ocean. Currently only three populations have been confirmed using dedicated deep-water surveys: Tanzania, South Africa, and the Comoros. The isolated nature of populations across the region may lower the potential for their replacement and recovery from external threats. Fast-moving currents along the Eastern coast of Africa are thought to prevent connectivity among populations in the region (Nikaido et al., 2011). This may be particularly true for Tanzania. While the biogeographic pattern of coelacanth populations remains unresolved, clear evidence points to significant population structure across the species' range (Schartl et al., 2005). Divergence among populations is low, but this is thought to reflect the low evolutionary rate of the species (Lampert et al., 2012). In addition, the highly specific habitat needs of the coelacanth may lead to this patchy distribution of populations, and limit their exchange. I consider current evidence for coelacanth population structure across the Western Indian Ocean to contribute to a moderate risk of extinction, as it may increase vulnerability of isolated populations by preventing their replacement and recovery from external threats and mortality events, and increase the potential for local extirpations.

Diversity

Although the coelacanth is considered to be a 'living fossil,' more careful phylogenetic and morphological inference suggests that the fish most likely has been evolving continuously for the past 65 million years (Casane et al., 2013). In fact, the continued evolution of the coelacanth is supported by evidence for population structure, suggesting that divergence within

the species is ongoing (Lampert et al., 2012). Thus, the term ‘living fossil’ may not accurately reflect the evolutionary state of the coelacanth. However, genomic analyses have revealed that divergence and diversity within and among populations is very low (Nikaido 2013). Low levels of diversity may relate to low molecular substitution rates, or small population sizes and elevated levels of inbreeding (Nikaido 2013). However, because diversity in *L. chalumnae* is significantly lower than its sister species *L. menadoensis*, small populations and genetic bottlenecks are the more likely source of low diversity. In fact, coelacanth populations exhibit molecular evidence of inbreeding on the level of inbred laboratory fish (Schartl et al., 2005). Low levels of diversity reflect low adaptive and evolutionary potential, making the coelacanth particularly vulnerable to environmental change and episodic events. These events may reduce diversity further, and result in a significant change or loss of variation in life history characteristics (such as reproductive fitness and fecundity), morphology, behavior, or other adaptive characteristics. Due to their low diversity, coelacanth populations may be at an increased risk of random genetic drift and could experience the fixing of recessive detrimental genes that could further contribute to the species’ extinction risk (Musick 2011). I classify the risk of the consistently low diversity across coelacanth populations to be high.

Threats Assessment

Regarding habitat threats to the coelacanth, loss and degradation of coelacanth habitat can take the form of pollution, dynamite fishing, sedimentation, and direct loss through development. Future human population growth and land use changes off the coast of East Africa may increase these threats to the coelacanth, but their trends and impacts are highly uncertain. In general, the coelacanth is largely buffered from habitat impacts due to its occurrence in deep water. Nonetheless, the occurrence of dynamite fishing throughout the Western Indian Ocean eliminates coral nursery habitat, but the effect of this impact on the coelacanth is highly uncertain; given the low metabolism of the fish, it is unlikely that it is under threat of limited prey availability. Pollution discharge from the East African coast is generally low (Biney, et al. 1994). However, pollutants thought to be globally-distributed have been observed in coelacanth fatty tissues; the lipid-rich tissues of the fish may facilitate bioaccumulation of global toxins. A rapidly growing human population may lead to land-use changes along the coast of East Africa that could increase siltation to the coelacanth’s habitat in the foreseeable future but, again, the extent and impact of this threat remains uncertain. The direct loss of coelacanth habitat may occur if the deep port of Mwambami Bay is developed. However, whether plans to build this port will come to fruition remains uncertain, and the effects will impact a small portion of the coelacanth’s range. The threat of port development does not represent a widespread threat to the species, and port of Mwambami Bay is the only large coastal development project (that I could find) that would directly impact the fish. I classify the risk of habitat loss or degradation as very low.

As for impacts from overutilization, bycatch has historically been thought to pose the greatest threat to the coelacanth, but survey data show there is no observed link between coelacanth bycatch and population decline. A decade ago, the Comoros oilfish fishery was responsible for the highest rate of coelacanth bycatch. Historically, the Comoran fishery was responsible for catch rates of about 3 fish year⁻¹, and is not thought to have contributed to declines in

population abundance. While the Comoran oilfish fishery has seen recent declines in effort and has never contributed to population decline of the coelacanth, a greater threat of bycatch has emerged in Tanzania over the last decade. As evidenced by high rates of coelacanth bycatch via the shark gillnet fishery, which began in 2001 in Tanzania, this fishing method has the potential to impact the coelacanth. Since 2003 in Tanzania, coelacanth catch rates have been more than 3 times greater than ever observed in the Comoros, at over 10 fish per year. It is unclear whether this catch rate is unsustainable due to limited information on trends and abundance of the Tanzanian population. While traditional Comoran handline fishing is no longer the most pressing bycatch threat to the fish, data suggest that the expansion of a shark gill net fishery throughout the Western Indian Ocean could result in additional coelacanth bycatch. The reduction of sustainable fisheries throughout the east African and South African coastline may encourage shifts to alternative fishing methods, such as gillnets, or trawling closer to shore, both of which could increase the probability of coelacanth bycatch. Bycatch in Tanzania is an ongoing threat, and potential for additional coelacanth bycatch across the fish’s range poses a potential but uncertain threat to the fish’s persistence into the foreseeable future. Coelacanth population abundance in Tanzania, and whether or not current bycatch rates are unsustainable, is unknown. Thus, I classify the threat of bycatch throughout the coelacanth’s range as low.

The overutilization of the coelacanth for scientific purposes or capture is not a current threat. However, in the future, scientific interest and study may be used as a basis for the public display of the coelacanth. Attempts have been made to capture the fish for large aquaria, but have not been successful. Yet, the capture of the coelacanth for public display remains a potential future, yet uncertain, threat. The development of custom pressurized aquaria or instruments to sustain the coelacanth at the surface may spur further attempts to collect the fish. The public display of the coelacanth would be of high commercial value, and thus may be economically incentivized. However, there is no real indication that overutilization for scientific purposes or public display is occurring. I consider the threat of overutilization for scientific purposes or capture for public display as low.

ESA Factor	Threat	Risk Likelihood
Habitat	<i>Loss, degradation</i>	Very Low
Overutilization	<i>Bycatch</i>	Low
	<i>Curio Trade</i>	Low
	<i>Scientific Interest</i>	Low
Disease/Predation	<i>Parasites</i>	Very Low
	<i>Shark Predation</i>	Very Low
Inadequacy of regulatory mechanisms	<i>Lack of enforcement, implementation, or effectiveness</i>	Low
Other	<i>Climate Change</i>	Low

The willingness of private individuals to pay upwards of \$4500 for a single coelacanth specimen makes trade and capture for curio purposes a potential threat. Because CITES trade protections are in place, curio trade would have to occur on the black market. I was unable to find

evidence that this black market trade is currently occurring. But, the economic incentive for such a trade may fuel a future market. Thus, I classify the curio trade of the coelacanth as a low risk.

With respect to disease and predation, parasites and shark mortality contribute a low risk of extinction to the coelacanth. Shark mortality likely contributes to the natural mortality rate of the species, but direct evidence for shark predation has not been observed. Coelacanths are generally associated with very low levels of parasites, which are unlikely to impact the future survival of the species. I classify the risk of disease and predation as very low.

Regulatory mechanisms addressing the coelacanth are sparse, but evidence suggests that threats are low throughout the coelacanth's range. I consider the threat of inadequate regulatory mechanisms as low.

Regarding other natural or manmade factors, the threat of climate change via ocean warming may work synergistically to enhance all other threats to the coelacanth across its range, but the nature of these impacts is highly uncertain. The coelacanth habitat and survival is restricted by its need for oxygen, a narrow temperature requirement, and highly complex deep-water cave systems. Accelerated warming of the global ocean may impact the coelacanth by further narrowing suitable habitat leading to range loss, displacement, and increasing metabolic and physiological stress on the fish. Increased stress and reduction of habitat associated with future ocean warming may make the fish less resilient to mortality events, disease, bycatch, and catastrophic events. While the IPCC predicts that several degrees of surface ocean warming is likely by 2100, the extension of this warming to deep-water habitat (100+ meters) is not well known, and predictions are unavailable (IPCC 2013). However, recent work has demonstrated a multidecadal increase in heat content in deep ocean waters, and an accelerated heat flux from the surface to deep water (Abraham et al., 2013). Thus, continued warming of deeper and deeper waters is likely to occur. Ocean warming may lead to coelacanth displacement due to the species' temperature-restricted habitat requirements, possibly resulting in range loss where other specific features such as prey availability and complex cave structures are not available. However, the extent of this impact on the coelacanth remains uncertain, and there has been no clear or mechanistic link between climate change or temperature warming and coelacanth population declines. Thus, I classify the risk of climate change as low.

Overall Extinction Risk: Synthesis and Finding

In determining the overall extinction risk of the coelacanth, I first analyzed the demographic risks to the species. Following this analysis, I assessed the threats to the species to determine if these threats are appreciably reducing the fitness of the species. In sum, based on the life history characteristics of the coelacanth, which indicate high vulnerability to demographic risks (due to low production, growth, and productivity, fragmented spatial structure and connectivity, and low diversity), coupled with ongoing and projected threats of habitat degradation, overutilization by bycatch, and the threat of future utilization through public

display and the curio trade, as well as other natural or manmade factors such as climate change, I found that demographic risks and threats to the species may impact the overall vulnerability and resiliency of the species. Although abundance trends are not available to assess the direct impact of bycatch throughout the Western Indian Ocean, the fish's demographic characteristics may make it particularly vulnerable to elevated catch rates. Yet, whether or not current bycatch rates in Tanzania are sustainable is not clear. For example, the coelacanth exhibits low fecundity, long generation times, and one of the slowest growth rates of all vertebrates. These factors impede rapid recovery and regeneration from mortality events. Additionally, the coelacanth is likely comprised of isolated populations distributed throughout the Western Indian Ocean. Only three of these populations have been confirmed via dedicated surveys (South Africa, the Comoros, and Tanzania), though others may remain undiscovered and unexplored. The pattern of isolated populations experiencing low connectivity may pose a demographic threat to the coelacanth, increasing the vulnerability of each population to bycatch by reducing the potential for replacement and recovery, and increasing the probability of local extirpations. Whether these demographic factors have resulted in decreased fitness and population declines in Tanzania as a result of increases in bycatch occurring over the last decade is uncertain. The threat of coelacanth bycatch due to shark gillnet fisheries may expand to other regions of the Western Indian Ocean in the foreseeable future as a result of the global demand and market for sharks, but the probability of this threat is uncertain, especially since a growing number of shark species are regulated under CITES. Also, whether or not additional isolated populations exist throughout the East African coast remains unclear. The fish's demographic characteristics may make the coelacanth vulnerable to loss through habitat destruction, reduced prey abundance, scientific or curio trade, or increased stress and habitat restriction via climate change; however, these threats appear to be low. Current regulatory mechanisms do not necessarily appear to be inadequate as threats to the species are low, and data do not support declines in coelacanth populations. With regard to climate change, future ocean warming is likely and can be reliably predicted up to 2100 (IUCN 2014); heat flux to the deep ocean appears to be accelerating (Abraham et al., 2013). Ocean warming may lead to coelacanth displacement because of the species' temperature-restricted habitat requirements, possibly resulting in range loss where other specific features such as prey availability and complex cave structures are not available; however, these climate change impacts have not been mechanistically linked to a reduction of population stability. The coelacanth's extremely low diversity not only indicates the likelihood of small population sizes, but also a reduced adaptive capacity, but low and isolated population may be a normal characteristic of this rare fish. Based on the best available information, coelacanth populations appear to be stable in surveyed regions, and in un-surveyed regions, threats appear to be low.

Overall, the fish's demographic factors make it particularly vulnerable to ongoing and future threats, but existing threats pose a generally low risk. Thus, I find that the coelacanth is at a low risk of extinction due to current and projected threats to the species.

Conservation Efforts

Since its discovery, much debate has surrounded the need to conserve the coelacanth, as an evolutionary relic and for its value to science. The long history of this debate was summarized by Bruton (1991). The international organization, the Coelacanth Conservation Council (CCC), has been the primary body advocating for coelacanth conservation over the years since 1987. The CCC has its headquarters in Moroni, Comoros and the Secretariat is currently in Grahamstown, South Africa with agencies in Canada, the United Kingdom, the U.S.A., Germany and Japan. The CCC has set forth general objectives of promoting coelacanth research and conservation, along with establishing an international registry of coelacanth researchers and the compilation of a coelacanth inventory and bibliography which were published for the first time in 1991, and recently updated in 2011 (Bruton et al., 1991b; Nulens et al., 2011).

Several conservation initiatives were implemented in the Comoros in the 1990's to reduce coelacanth bycatch. For instance, FADs were installed to encourage pelagic fishing and reduce pressure on the coelacanth from nearshore handline fishing. During this time, the use of motorized boats was encouraged for the same purpose, in order to direct fishing off-shore and reduce the use of artisanal handlines. Initially, there were some challenges, including lack of infrastructure preventing the repair of motors. However, the fishing trend today in the Comoros shows a clear shift to motorized pelagic fishing, and reduced interest in traditional handline fishing; this trend is occurring due to a natural shift in social perspectives and local economic trends, without the encouragement of coelacanth conservation groups.

A supporter of coelacanth conservation and member of the US Explorer Club, Jerome Hamlin, author and curator of the website DINO FISH.com, has encouraged the use of a 'Deep Release Kit' for coelacanth conservation when bycaught. The Deep Release Kit was created in response to the 'Save the Coelacanth Contest' sponsored by DINO FISH.com (Hamlin, 2014). The kit consists of a barbless hook attached to a sack. The fisherman puts some of his sinker stones in the sack, places the hook in the lower jaw of the fish he has just caught with the shank pointing down to the sack, and releases the fish to the bottom where it frees itself. The purpose of the Deep Release procedure is to get the fish quickly to the cold bottom water with no further exertion on its part. A surface release (in theory) leaves the fish without the strength to get back down to depth. Hundreds of these devices have been distributed in the Comoros and Tanzania. These kits are some of the only direct coelacanth conservation measures in the Comoros or Tanzania. Yet, it is unclear whether these have been used at sea, their success is unproven, and whether the method has been adopted by local fishermen is unknown.

Ongoing scientific research on the coelacanth may play a role in coelacanth conservation, as management of the species can improve with a more complete understanding of its biology and natural history. In 2002, South Africa instituted its African Coelacanth Ecosystem Programme, which has coordinated an extensive array of research including bathymetric surveys, taxonomic studies, and observational expeditions. This program is funded by the Global Environment Facility of the World Bank and it is on its third phase, taking an ecosystem-based approach to understand coelacanth distribution and habitat utilization across the Western Indian Ocean, and providing deep-water research tools and resources for this research.

A new marine park in Tanga, Tanzania has been put in place, and was initiated by increases in coelacanth catch in the region. The Tanga Coelacanth Marine Park is located on the northern coastline of Tanzania, extending north of the Pangani River estuary 100 km along the coastline towards Mafuriko village just north of Tanga city (Figure 8). The park covers an area of 552km² of which 85km² are terrestrial and 467 km² are marine. The plans for the park were announced in 2009, and a general management plan published in 2011 (Parks; MPRU, 2011). The goal of the Tanga Coelacanth Marine Park is to conserve marine biodiversity, resource abundance, and ecosystem functions of the Park, including the coelacanth and its habitat; and enable sustainable livelihoods and full participation of local community users and other key stakeholders. The plans for the park, specific to the coelacanth, are to restrict fishing within its boundaries, including fishing with deep-set shark gillnets, the primary source of coelacanth bycatch in the area. Additional restrictions against destructive fishing and development practices have been set forth in the park's 2011 general management plan (MPRU, 2011). Partnership and guidance from the IUCN has encouraged plans for community-based and adaptive park management (Harrison, 2010). However, the implementation and enforcement of the park's regulations and goals are unclear and untested. There are several reasons to believe that infrastructure, funding, and park management may not be adequate to fully prevent coelacanth bycatch within the park's boundaries. For one, illegal fishing off the coast of Tanzania is high (Tobey et al., 2006; Hempson, 2008; Wells, 2009). Widespread poverty and other regional socio-economic challenges in the region have reduced the effectiveness and implementation of other east African marine parks, and it is likely that the Tanga Coelacanth Marine Park will face similar challenges (Toby, 2006; Wells, 2012). Although recommendations and goals are set in place to increase tourism to the Park as an economic offset for stricter fishing regulations, the economic infrastructure and incentives needed for this shift are not in place or have not yet been proven. Next, there are plans to build a new deep-sea port in Mwambani Bay, just 8km south of the original old Tanga Port, which would include submarine blasting and channel dredging and destruction of known coelacanth habitat in the vicinity of Yambe and Karange islands - the site of several of the Tanzanian coelacanth catches. The new port is scheduled to be built in the middle of the Tanga Coelacanth Marine Park. The construction of Mwambani port is part of a large project to develop an alternative sea route for Uganda and other land-locked countries which have been depending on the port of Mombasa. The plans for Mwambani Bay's deep-sea port construction appear to be ongoing, despite conservation concerns. It is unclear whether this port will be built, but its presence would negate many of the benefits (even now, unproven) of the Park. The general management plan for the park will be fully evaluated every 10 years, with a mid-term review every 5 years. The effectiveness of Tanga Coelacanth Marine Park is not yet known.

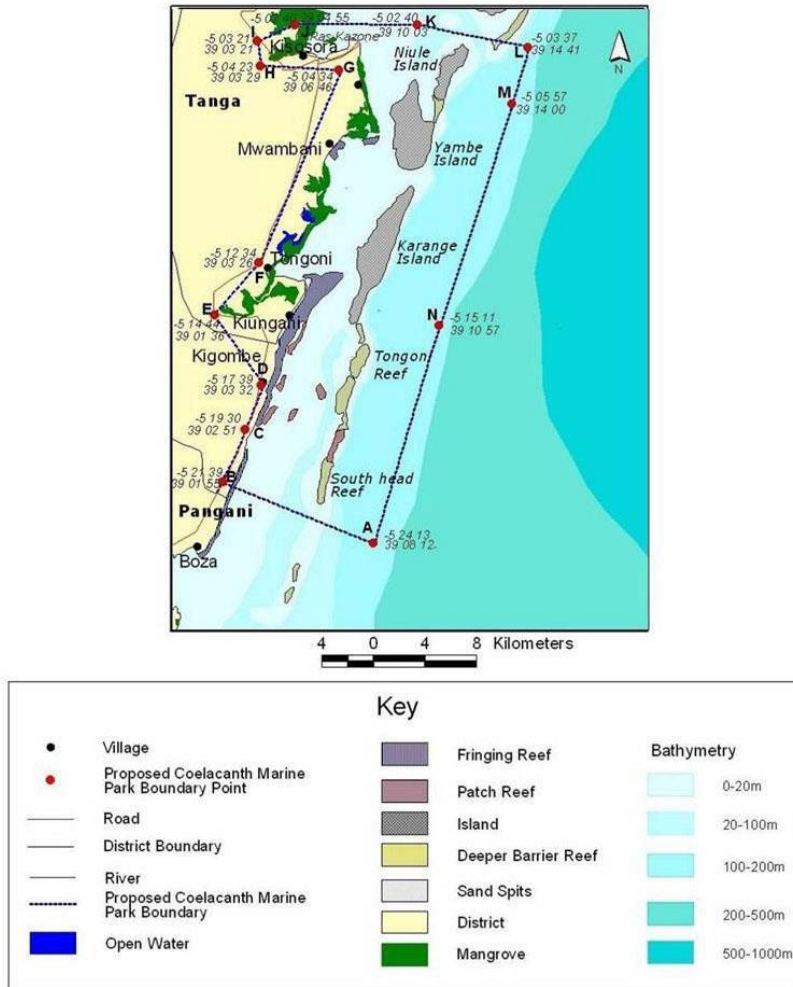


Figure 8. Tanga Coelacanth Marine Park, Gazetted in 2009.

Local efforts for marine conservation exist in the Comoros. For example, the Mohéli Marine Park takes a co-management approach to stop some destructive fishing and marine habitat conservation using a series of no-take reserves (Figure 7). The park encompasses 212km², and was set up during a 5-year biodiversity conservation project which began in 1998, funded by the World Bank's Global Environment Facility; the goals of the project were to address the loss of biodiversity in Comoros and develop local capacity for natural resource management (Granek et al., 2005). However, no alternative revenue generating activities have been provided, making life difficult for some fishermen. The World Bank's Global Environment Facility biodiversity management project in the Park ended in 2003, and there has been no source of additional financing to continue the resource co-management. The Moheli Park has brought together some key institutions (DGE and CNDRS; and NGOs, AIDE and Ulanga) to encourage sustainable management and monitoring of marine habitat of the Comoros; however, specific laws have not been enacted, and existing legislation has not been enforced (Ahamada et al., 2002). No coelacanths have ever been caught off the island of Moheli, so the park's impact on bycatch of the species is not applicable.

Other conservation efforts in the form of Marine Parks distributed throughout the Western Indian Ocean may benefit the coelacanth by reducing habitat destruction and improving prey availability; however, the direct impacts of these conservation efforts on the species is difficult to evaluate. Efforts to improve marine resource management and conservation in developing nations of east Africa have increased in the past decade. Today, 8.7% of the continental shelf in Kenya, 8.1% in Tanzania, and 4.0% in Mozambique have been designated as marine protected areas (Wells et al., 2007) (Figure 9). Many of these parks intersect with known coelacanth habitat, or are in range countries where coelacanths have been caught and potential populations exist. However, in many areas, ongoing socioeconomic challenges have precluded effective management of these regions (Francis et al., 2002). Analysis of east African MPA management has demonstrated that socio-economic barriers make it more difficult to reach conservation goals (Tobey et al., 2006). Because of this, much effort has gone into creating community-based conservation planning in recent years (e.g., Harrison (2010)). Management constraints still remain. First, there are large gaps in ecosystem knowledge surrounding these marine parks; for instance, many vital habitats and species are not yet fully represented by MPA's in place today (Wells et al., 2007). Next, monitoring is not widely implemented and data are not available to determine whether biodiversity or socio-economic goals are being met (Wells et al., 2007).

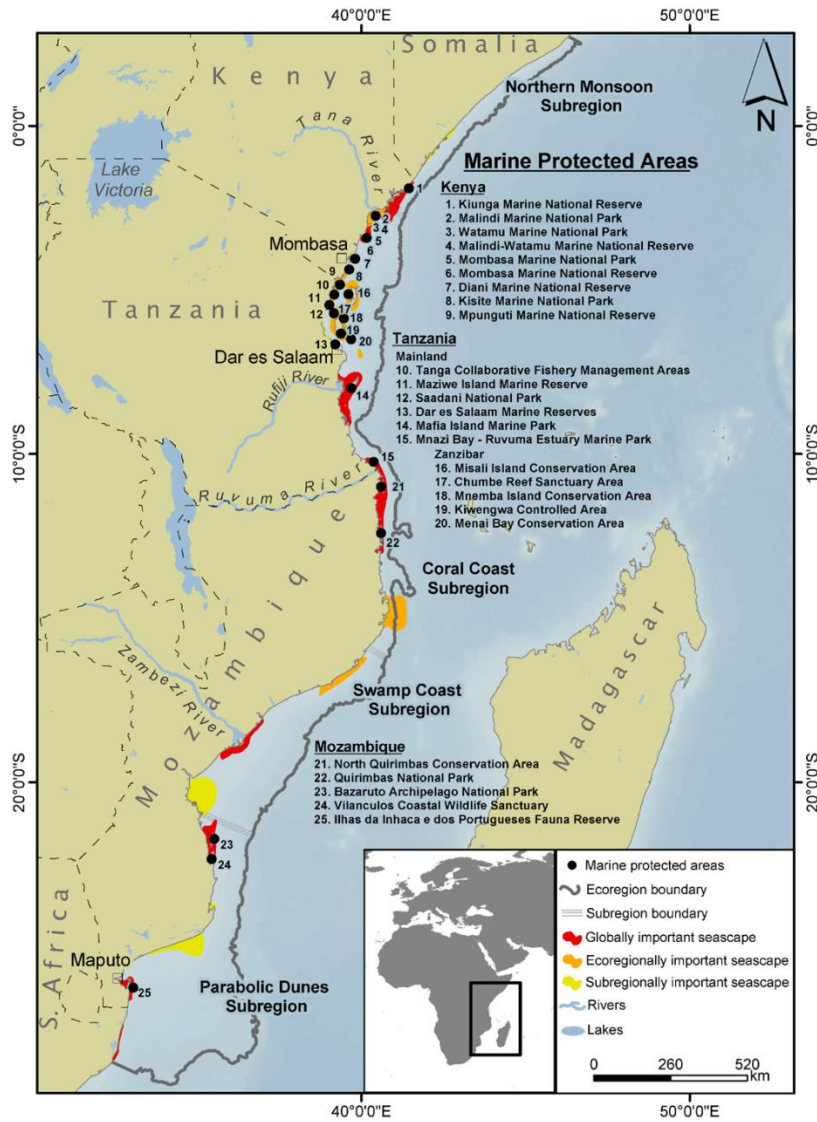


Figure 9. Distribution of marine protected areas along the coast of east African countries. From Wells, 2007.

Significant Portion of its Range Analysis

Because we find that the species is at a low risk of extinction throughout its range, we must also consider whether it may have a higher risk of extinction in a significant portion of its range per the Significant Portion of its Range Policy (79 FR 37577; July 1, 2014). After a review of the best available information, we identified the Tanzanian population of the African coelacanth as a population facing concentrated threats because of increased catch rates in this region since 2003, and the threat of a deep-water port directly impacting coelacanth habitat in this region. If we believe this population also constitutes a significant portion of the range of the African coelacanth, then we would evaluate the extinction risk of this population to determine whether it is threatened or endangered in that portion.

We proceeded to evaluate whether this population represents a significant portion of the range of the African coelacanth. The Tanzanian population is one of only three confirmed populations of the African coelacanth, all considered to be small and isolated. Because all three populations are isolated, the loss of one would not directly impact the other remaining populations. However, loss of any one of the three known coelacanth populations could significantly increase the extinction risk of the species as a whole, as only two small populations would remain, making them more vulnerable to catastrophic events. While the Tanzanian and Comoran populations are only a few hundred miles apart, ocean currents are thought to have led to their divergence over 200,000 years ago, and connectivity between them is not thought to be maintained (Nikiado et al., 2011). The South African population is separated from the Comoran and Tanzanian populations by thousands of miles. The Tanzanian population exhibits the greatest genetic divergence, suggesting that it may be the most reproductively isolated among them (Lampert et al., 2012). Potential catastrophic events such as storms or significant temperature changes may affect the Comoran and Tanzanian populations simultaneously, due to their closer geographic proximity. The South African population, while not as genetically isolated, may experience isolated catastrophic events due to its geographic isolation. Loss of any single coelacanth population would put the species at greater risk of loss from catastrophic events as storms, disease, or temperature anomalies. This reasoning supports our conclusion that the Tanzanian population comprises a significant portion of the range of the species because this portion's contribution to the viability of the African coelacanth is so important that, without the members in that portion, the African coelacanth would be likely to become in danger of extinction in the foreseeable future, throughout all of its range.

Because the Tanzanian population of the coelacanth was determined to represent a significant portion of the range of the species, we performed an extinction risk assessment on the Tanzanian population by evaluating how the demographic factors (abundance, productivity/growth rate, spatial structure/connectivity, and diversity) of the species would be impacted by the ESA section 4(a)(1) factors, considering only those factors affecting the Tanzanian population.

Coelacanth abundance across its entire range is not well understood, and no abundance estimates exist for the Tanzanian population. Based on general knowledge of the African coelacanth, the Tanzanian population is likely associated with very restricted and specific habitat requirements and low growth rates. We conclude that it is likely that the population size of the Tanzanian population is small for the same reasons described above for the species as a whole: they exhibit low levels of diversity (Nikaido et al., 2013), long generation times, and restricted habitat

(Hissmann *et al.*, 2006; Fricke *et al.*, 2011). The likelihood of low abundance makes the Tanzanian population more vulnerable to extinction by elevating the impact of stochastic events or chronic threats resulting in coelacanth mortality.

Growth rate and productivity for the Tanzanian population is thought to exhibit similar characteristics to other populations of the species. The species as a whole has one of the slowest metabolisms of any vertebrate. The extremely long gestation period and late maturity makes the Tanzanian population particularly vulnerable to external threats such as bycatch, possibly impeding recovery from mortality events (Froese *et al.*, 2000).

The Tanzanian population is thought to represent a single isolated population of the species. It has been estimated that this population diverged from the rest of the species 200,000 years ago (Nikaïdo *et al.*, 2011). Differentiation of individuals from the Tanzanian population may relate to divergence of currents in this region, where hydrography limits gene flow and reduces the potential for drifting migrants. The isolated nature of the Tanzanian population lowers the potential for its recovery from external threats; the population is not thought to maintain connectivity with other populations, and thus has no source for replacement of individuals lost outside of its own reproductive processes. Fast-moving currents along the Eastern coast of Africa are thought to prevent connectivity among populations in the region (Nikaïdo *et al.*, 2011). This may be particularly true for Tanzania. We consider current evidence for the Tanzanian population's high isolation and low (or no) connectivity with the rest of the species to contribute to a moderate risk of extinction, as it may increase vulnerability of this population by preventing its replacement and recovery from external threats and mortality events, and increase the potential for extinction.

Genomic analyses of individuals from the Tanzanian population and other representatives of the species reveal that divergence and diversity within and among populations is very low (Nikaïdo *et al.*, 2013). Low levels of diversity reflect low adaptive and evolutionary potential, making the Tanzanian population particularly vulnerable to environmental change and episodic events. These events may reduce diversity further, and result in a significant change or loss of variation in life history characteristics (such as reproductive fitness and fecundity), morphology, behavior, or other adaptive characteristics. Due to the Tanzanian population's low diversity, this population may be at an increased risk of random genetic drift and could experience the fixing of recessive detrimental genes that could further contribute to the species' extinction risk (Musick, 2011).

Regarding habitat threats to the Tanzanian population, loss and degradation of coelacanth habitat can take the form of pollution, dynamite fishing, sedimentation, and direct loss through development. Future human population growth and land use changes off the coast of Tanzania increase these threats to the Tanzanian population, but their trends and impacts are highly uncertain. In general, the coelacanth is largely buffered from habitat impacts due to its occurrence in deep water, and general effects of pollution and development are similar to those described for the rest of the species. However, specifically related to the Tanzanian population, direct loss of habitat may occur if the deep port of Mwambami Bay is developed. The port is planned to be built just 8 km south of the original old Tanga Port, and this would include submarine blasting and channel dredging and destruction of known coelacanth habitat in the

vicinity of Yambe and Karange islands - the site of several of the Tanzanian coelacanth catches. The new port is scheduled to be built in the middle of the Tanga Coelacanth Marine Park. The construction of Mwambani port is part of a large project to develop an alternative sea route for Uganda and other land-locked countries that have been depending on the port of Mombasa. The plans for Mwambani Bay's deep-sea port construction appear to be ongoing, despite conservation concerns. Whether plans to build this port will come to fruition remains uncertain, but if built, the deep port would be devastating to the Tanzanian population by destroying habitat directly. For the Tanzanian population, the construction of this deep-water port could be catastrophic, and it is clear that the boundaries of the new Tanga Marine Park are insufficient in halting plans for the port's development.

As for impacts from overutilization, bycatch has historically been thought to pose the greatest threat to the coelacanth. While survey data from the Comoros show there is no observed link between coelacanth bycatch and population decline, since 2003 in Tanzania, coelacanth catch rates have been more than 3 times greater than ever observed in the Comoros, at over 10 fish per year. It is unclear whether this catch rate is sustainable due to limited information on trends and abundance of the Tanzanian population. The further expansion of a shark gill net fishery in Tanzania, as has been observed over the last decade, could result in additional coelacanth bycatch. Bycatch in Tanzania is an ongoing threat. While direct data assessing Tanzanian coelacanth population decline are not available, the relatively high and persistent catch rate in this region has the potential to deplete this small and isolated population, which has life history characteristics that greatly impede its recovery and resiliency to mortality.

We consider the threat of overutilization for scientific purposes, public display, or for the curio trade as low for reasons described above, as they apply to the rest of the species.

We consider the threat of inadequate regulatory mechanisms as low for the Tanzanian population for the same reasons described above for the rest of the species. Additionally, we classify the risk of climate change as low for the Tanzanian population for the same reasons described above for the rest of the species.

Overall, the Tanzanian population's demographic factors make it particularly vulnerable to ongoing and future threats, which pose a moderate risk to the species. Based on the best available information, threats of bycatch to the Tanzanian population appear to be persistent, and the potential development of a deep port within this population's habitat could be catastrophic to the population in the foreseeable future. Thus, we find that the Tanzanian population is at a moderate risk of extinction due to current and projected threats.

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