A Petition to List Chambered Nautilus (*Nautilus pompilius*) as Endangered or Threatened Species Under the Endangered Species Act

Photo: Gregory J. Barord

Submitted to the U.S. Secretary of Commerce acting through the National Oceanic and Atmospheric Administration and the National Marine Fisheries Service

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Pursuant to Section 4(b) of the Endangered Species Act ("ESA"), 16 U.S.C. § 1533(b), Section 553(e) of the Administrative Procedure Act, 5 U.S.C. § 533(e), and 50 C.F.R. § 424.14(a), the Center for Biological Diversity ("the petitioner") hereby petitions the Secretary of Commerce and the National Oceanic and Atmospheric Administration ("NOAA"), through the National Marine Fisheries Service ("NMFS" or "NOAA Fisheries"), to list the chambered nautilus (*Nautilus pompilius*) as a threatened or endangered species.

The Center for Biological Diversity ("the Center") is a non-profit, public interest environmental organization dedicated to the protection of native species and their habitats through science, policy, and environmental law. The Center has more than one million members and online activists. The Center and its members are concerned with the conservation of endangered species and the effective implementation of the ESA.

NMFS has jurisdiction over this petition. This petition sets in motion a specific process, placing definite response requirements on NMFS. Specifically, NMFS must issue an initial finding as to whether the petition "presents substantial scientific or commercial information indicating that the petitioned action may be warranted." 16 U.S.C. § 1533(b)(3)(A). NMFS must make this initial finding "[t]o the maximum extent practicable, within 90 days after receiving the petition." *Id*. § 1533 (b)(3)(A). The petitioner does not need to demonstrate that the petitioned action is warranted, rather, the petitioner must only present information demonstrating that such action may be warranted. While the petitioner believes that the best available science demonstrates that listing the chambered nautilus as threatened or endangered is in fact warranted, there can be no reasonable dispute that the available information indicates that listing this species as either threatened or endangered may be warranted. As such, NMFS must promptly make a positive initial finding on the petition and commence a status review as required by the ESA.

TABLE OF CONTENTS

1. Introduction

The chambered nautilus or pearly nautilus (*Nautilus pompilius*) is a charismatic cephalopod species known for its exceptional spiraling chambered shell. Chambered nautiluses belong to a family that has barely changed since its apparition in the fossil records around 500 million years ago, leading scientist to describe it as a “living fossil”.

Today, however, populations of the chambered nautilus are at risk of extinction due to overfishing to satisfy the international shell trade market. Targeted for its large chambered shells, evidence shows that unique nautilus populations have been unsustainably harvested in some areas of the Philippines, local extirpations have already occurred, and other fished nautilus populations are believed to be declining. Unique life history characteristic such as slow growth rates, low fecundity, long generation and gestation times, also make chambered nautilus particularly vulnerable to even light levels of fishing intensities. In this sense, the species is more similar to oceanic sharks than their cousin squids and octopi. Additionally, chambered nautiluses have very restricted capacity to rebound since migration and population distribution is rather limited, resulting in especially isolated populations with poor or not connectivity. Therefore, the loss of isolated populations represents a loss in genetic biodiversity and potential loss of unique subspecies.

The Center formally requests that the Secretary of Commerce, acting through the National Marine Fisheries Service (“NMFS”), list the chambered nautilus (*Nautilus pompilius*) as an “endangered” or alternatively as a “threatened” species under the Endangered Species Act (“ESA”)[1]. The greatest threat to the chambered nautilus’ continued survival is overfishing for the international shell trade that has led to significant population declines and extirpations in some regions of the Indo-Pacific. In recognition of other ongoing and growing threats to the species including habitat degradation, climate change, and intrinsically vulnerable life history strategies, listing the chambered nautilus as endangered or threatened is clearly warranted under the ESA.

2. Governing Provisions of the Endangered Species Act

The ESA was enacted in 1973 “to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, and to provide a program for the conservation of such endangered species and threatened species.” 16 U.S.C. § 1531(b). Protection under the ESA only applies to species that have been listed as endangered or threatened according to the provisions of the statute. Thus listing species that need ESA protection is vital to their conservation.

Specifically, once listed as an “endangered” species, the ESA prohibits the “take” or the killing, capture, or harassment of individual animals, as well as the sale, export, or import of such species. *Id.* §§ 1538(a); 1532(19) (defining “take”). Alternatively, if a species is listed as “threatened”, NMFS “shall issue such regulations as [it] deems necessary and advisable for the conservation of” the species including potentially the same bans applicable to endangered species. Additionally, whenever a U.S. federal agency takes any action that “may affect” a

[1] 16 U.S.C. § 1531-44

threatened or endangered species, that agency "shall" consult with NMFS or the Fish and Wildlife Service (FWS) regarding those impacts, and the consulting agencies may establish mitigation measures for the project. *Id.* § 1536(a).

While the chambered nautilus does occur in the United States, particularly in American Samoa, ESA protections can also assist in the conservation of foreign chambered nautilus populations. Specifically, the ESA generally bans the import of any endangered species into the United States, as well as the interstate sale of foreign chambered nautiluses on the U.S. market; and as discussed below, the United States is a major destination for chambered nautiluses in the international shell trade. Additionally, listing a foreign species can raise the profile of the species and its threats and prompt other range countries to adopt similar protections. ESA listing of chambered nautilus may also prompt protection of the species under the Convention on International Trade in Endangered Species ("CITES"), which would regulate the worldwide chambered nautilus trade. Recently, the U.S. and other range States submitted a proposal[2] to include the entire Family Nautilidae in Appendix II of CITES. The CITES parties will decide on the proposal at the Seventeenth meeting of the Conference of the Parties (CoP17) that will be held in Johannesburg, South Africa in the Fall of 2016.

2.1. Species Definition under the ESA

The term "species" is broadly defined under the ESA to include "any subspecies of fish, or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." 16 U.S.C. § 1532 (16). Accordingly, any species or subspecies of chambered nautiluses may be listed, although the distinct population segment ("DPS") language does not apply to invertebrate species such as the chambered nautilus.

2.2. Significant Portion of the Species' Range

The ESA defines an "endangered species" as any species that is "in danger of extinction throughout all or a significant portion of its range," 16 U.S.C. § 1532(6), and a "threatened species" as one that "is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." *Id*. § 1532(20). NMFS interprets a portion of the range of a species to be significant if "the species is not currently endangered or threatened throughout all of its range, but the portion's contribution to the viability of the species is so important that, without the members in that portion, the species would be in danger of extinction, or likely to become so in the foreseeable future, throughout all of its range."[3] This policy allows ESA protection for a species that are regionally in trouble but are not currently imperiled throughout all of its range. Thus, the Center requests that NMFS analyze whether the chambered nautilus is endangered or threatened throughout all or any significant portion of its range. If the analysis of the significant portion of its range reveals that the species is either threatened or endangered throughout a significant portion of its range, then the entire species would be listed

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[2] Proposal: Inclusion of the Family Nautilidae (Blainville, 1825) in Appendix II in accordance with Article II paragraph 2 (a) of the Convention and satisfying Criterion B in Annex 2a of Resolution Conf. 9.24 (Rev. CoP16). http://www.fws.gov/international/cites/cop17/ussubmissions/chambered_nautilus_appendixII.pdf

[3] Final Policy on Interpretation of the Phrase "Significant Portion of its range" in the Endangered Species Act's Definitions of "Endangered Species" and "Threatened Species" 79 Fed. Reg. 37,578 (July 1, 2014).

as threatened or endangered, and ESA protection must be apply to all populations where the species is found.

The current interpretation of the significant portion of the species' range emphasizes its biological importance in terms of an increase in the risk of extinction[4]. Under this policy, NMFS should ask whether the species would be in danger of extinction or likely to become so in the foreseeable future without that specific portion. As such the significant portion of the species' range is a portion of the current extant range of the species (e.g., population(s)) that if completely extirpated would lead to the imminent or foreseeable extinction of the species[4]. For example, without the population in the significant portion of the range, the remainder populations throughout the species' range might not be large enough to be resilient to wide environmental fluctuations, human impacts, or environmental catastrophes. Moreover, based on NMFS's interpretation, the viability of the entire species or subspecies will depend on the productivity of the population in the significant portion of the range. As such, without the population in the significant portion of the range, the remainder population in the range might not be able to maintain an adequate growth rate to face ongoing threats. In addition, a population in the significant portion of the range could contain high genetic diversity such as that without this population, the remaining populations may not be genetically diverse enough to maintain viability and adaptation to changing conditions. Thus, a significant portion of the species' range with high genetic diversity will function as a buffer against environmental fluctuations and provides evolutionary resilience[4].

2.3. Listing Factors

Under the ESA, NMFS must make a determination whether a species is endangered or threatened based on the best readily available scientific or commercial information on the following five listing factors, 16 U.S.C. §1533(a)(1):

A. The present or threatened destruction, modification, or curtailment of its habitat or range;
B. Overutilization for commercial, recreational, scientific, or education purposes;
C. Disease or predation;
D. The inadequacy of exiting regulatory mechanism; and
E. Other natural or manmade factors affecting its continue existence.

For a species to be listed under the ESA it needs to only face a substantial threat under one of the above mentioned factors. In addition, any combination of threats that can be considered cumulatively under multiple factors would also support ESA listing. The chambered nautilus faces threats from several of the ESA listing factors in at least a significant portion of their range.

2.4. 90-Day and 12-Month Findings

NMFS is required to determine "to the maximum extent practicable … whether [a] petition presents substantial scientific or commercial information indication that the petitioned action may be warranted" within 90 days of receiving a petition to list a species. *Id.* § 1533(b)(3)(A).

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[4] Final Policy on Interpretation of the Phrase "Significant Portion of its range" in the Endangered Species Act's Definitions of "Endangered Species" and "Threatened Species" 79 Fed. Reg. 37,578 (July 1, 2014).

This is also known as the “90-day finding”. A “negative” 90-day finding will end the listing process. *Id.* § 1533(b)(3)(C)(ii). A “positive” 90-day finding will lead to a more comprehensive “status review” and to a “12-month finding” that determines, based on the best available scientific and commercial information, whether listing the species as endangered or threatened is warranted, not warranted, or warranted but precluded by other pending listing proposals for higher priority species. *Id.* § 1533(b)(3)(B). Negative outcomes like a negative 90-day finding, a not warranted finding, or a warranted but precluded 12-month finding are subject to judicial review. *Id.* § 1533(b)(3)(C)(ii).

For the purposes of the 90-day finding, “substantial information” is defined as “the amount of information that would lead a reasonable person to believe that the measure proposed in the petition may be warranted” 50 C.F.R. § 424.14(b)(1). Under NMFS’s regulations a petition presents “substantial information” if it:

i. Clearly indicates the administrative measure recommended and gives the scientific and any common name of the species involved;
ii. Contains detailed narrative justification for the recommended measure; describing, based on available information, past and present numbers and distribution of the species involved and any threats faced by the species;
iii. Provides information regarding the status of the species over all or a significant portion of its range; and
iv. Is accompanied by appropriate supporting documentation in the form of bibliographic references, reprints of pertinent publications, copies of reports or letters from authorities, and maps.

50 C.F.R. §§ 424.14(b)(2)(i)–(iv).

2.5. Reasonable Person Standards

During the initial petition review to make a 90-day finding the ESA does not require “conclusive evidence of a high probability of species extinction” to support a positive outcome. 50 C.F.R. § 424.14(b)(1). Instead, during the initial 90-day review process, NMFS must consider whether a reasonable person could determine that the petition contains substantial information that may warrant a more in-depth status review of the petitioned species. Thus this initial review should be characterized as a “threshold determination.” Accordingly, a petition does not need to demonstrate a high likelihood that a species is endangered or threatened during the 90-day finding process, but just that it warrants further comprehensive and in detail review.

2.6. Best Available Scientific and Commercial Data

NMFS is required to make an ESA listing determination for the chambered nautilus considering the five listing factors based on the best available scientific and commercial data. 16 U.S.C § 1533(b)(1)(A). NMFS cannot deny a listing for which little information is available if the best available information indicates that the species is endangered or threatened throughout all, or a significant portion of its range.

3. Species Description

3.1. Common Names

In this petition we will refer to *Nautilus pompilius* by the common name of “chambered nautilus” or “nautilus”. However, the general name of “chambered nautiluses” will be used when referring to the entire family Nautilidae that include at least seven recognized species. Other common names for the chambered nautilus include: pearly nautilus and pearly chambered nautilus. Local names in areas of the Philippines are “bubo panglagang” or “lagang” (Green 2004, del Norte-Campos 2005).

3.2. Taxonomy

The taxonomy of the nautiloids has been controversial for decades. Currently, only two genera of nautiloids exist, *Nautilus* (Linnaeus, 1758) and *Allonautilus* (Ward and Saunders 1997), with six or seven possible species (Saunders 2010). These possible species have been recognized as *Nautilus pompilius* (Linnaeus, 1758), *N. stenomphalus* (Sowerby, 1849), *N. belauensis* (Saunders, 1981), *N. repertus* (Iredale, 1944), *N. macromphalus* (Sowerby, 1849), *Allonautilus scrobiculatus* (Lightfoot, 1786), and *A. perforatus* (Conrad, 1949). However, new genetic analysis suggests that only two species within the genus *Nautilus* are valid, *N. pompilius* and *N. macromphalus* (Ward et al. 2016). Detailed phylogenetic analysis suggests that only two well discrete species may exist today, *N. macromphalus* and *A. scrobiculatus* (Bonacum et al. 2011). New analysis combining genetics and morphological results call for invalidating former possible species such as *N. stenomphalus*, *N. repertus*, and *N. belauensis* since they are more parsimoniously placed within *N. pompilius* (Ward et al. 2016). Genetic analysis suggests that isolated archipelagos, islands, and continental regions separated by extended deep water expands may be inhabited by genetically distinct subspecies or clades within species (Woodruff et al. 2010, Bonacum et al. 2011, Williams et al. 2015, Ward et al. 2016) *(see below for details).*

Among all potential species within the Nautilidae family, the chambered nautilus, *N. pompilius*, is the most common and possibly the most studied. In this petition, the taxonomy of *N. pompilius* was based on the Integrated Taxonomic Information System (“ITIS”),[5] and is as follows:

Kingdom Animalia
Phylum Mollusca
Class Cephalopoda Cuvier, 1797
Subclass Nautiloidea Agassiz, 1847
Order Nautilida Agassiz, 1847
Family Nautilidae Blainville, 1825
Genus *Nautilus* Linnaeus, 1758
Species *Nautilus pompilius* Linnaeus, 1758
Subspecies *Nautilus pompilius pompilius* Linnaeaus, 1758
Nautilus pompilius suluensis Have & Okutani, 1988

[5] Integrated Taxonomic Information System: *Nautilus pompilius* Linnaeaus, 1758. Taxonomic Serial No.: 557222 http://www.itis.gov/servlet/SingleRpt/SingleRpt?search_topic=TSN&search_value=557222

3.1. Synonyms

Several synonyms exist for *N. pompilius* and although they may not be taxonomically valid or recognized subspecies, these are related names under which specimens can be found in international trade. Several species reported in U.S. trade data may be synonyms of other species.[6] For example, *A. perforatus* which is native to Indonesia may be synonym of *A. scrobiculatus* which is endemic of Papua New Guinea and the Solomon Islands; and *N. repertus* (native of Western Australia) may be synonym of *N. pompilius*. The following is list of synonyms based on IT IS:

Nautilus alumnus (Iredale, 1944)
Nautilus ambiguus (Sowerby, 1849)
Nautilus pompilius pompilius (Linnaeus, 1758)
Nautilus pompilius suluensis (Habe & Okutani, 1988)
Nautilus pompilius var. *caudatus* (Lister, 1685)
Nautilus pompilius var. *marginalis* (Willey, 1896)
Nautilus pompilius var. *moretoni* (Willey, 1896)
Nautilus pompilius var. *perforatus* (Wille , 1896)
Nautilus pompilius var. *pompilia* (Shimansky, 1948)
Nautilus pompilius var. *rumphii* (Shimansky, 1948)
Nautilus repertus (Iredale, 1944)
Nautilus stenomphalus (see Ward et al. 2016)

3.2. Evolutionary Origin

Chambered nautiluses are modern survivors of a previously abundant externally-shelled group of cephalopods that appeared at least 450 million years ago (Boyle and Rodhouse 2008, Woodruff et al. 2010). They are often called “living fossils” (Ward 1984, 2008, Woodruff et al. 2010) because they have persisted almost unchanged through five major mass-extinction events (Strugnell and Lindgren 2007). Nautiloidea is the oldest group (subclass) within the cephalopods, substantially differing in morphology from all other more recent species in the class, the coeloids (octopus, squid, and cuttlefish). Nautiloidea represents a monophyletic group which contains the only extant cephalopods with an external shell (Bonnaud et al. 2004).

The evolutionary origin of the most abundant genus (*Nautilus*) is surprisingly obscured due to the poor recent fossil record, morphological conservatism, and uncertainties about the taxonomy of extant species (Teichert and Matsumoto 2010, Woodruff et al. 2010, Ward et al. 2016). The genus and thus the several species may have descended from a once dominant similar group that arose over 500 million years ago after the Cambrian explosion (Strugnell and Lindgren 2007, Woodruff et al. 2010, Kröger et al. 2011). More precise estimates based on molecular biology suggests that cephalopods diverged into nautiloids and coleoids (i.e., cuttlefish, squids, and octopods) during the mid-Palaeozoic approximately 416 million years ago (Kröger et al. 2011). Ward et al. (2016) have found specimens that can be placed in the genus *Nautilus* from the Early

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Cretaceous of Australia, the Late Cretaceous of California and British Columbia, the Paleocene of Australia, and the Ecocene of Great Britain, widely ranging from 145 to 66 million years ago. Others studies track the origin to the late Eocene ~37 million years ago (Squires 1988, Teichert and Matsumoto 2010). Interestingly, based on the fossil record Cretaceous and Paleocene nautilids mostly inhabited shallower waters not associated with fore reefs but the taxon may had been driven to deeper habitats due to the expansion of shell breaking teleost predators (Ward et al. 2016). Current nautilus species, however, may have originated as late as five to one million years ago (Woodruff et al. 2010).

Accordingly, genetic work suggests that nautiluses have been undergoing a rapid adaptive radiation since the Pliocene (5.33 to 2.58 million years ago) with the Coral Triangle being the origin of modern radiation (Sinclair et al. 2011, Bonacum et al. 2011, Ward et al. 2016). Thus the number of unrecognized subspecies or species that are endemic to isolated islands, sea mounts, and land masses might be higher than currently identified, since it is possible that genetically distinct chambered nautilus populations from isolated areas are at least distinct subspecies (Sinclair et al. 2011, Bonacum et al. 2011, Ward et al. 2016). This implies that the loss of any population around isolated islands or geographically isolated areas represent a significant loss in genetic biodiversity and potential loss of unrecognized subspecies.

3.3. Morphological Characteristics

Chambered nautiluses are substantially different from the other species of cephalopods (Fig. 1). A bulky brown and white external and spiral shell that aids in buoyancy and provides protection, pinhole camera eyes, and up to 47 pairs of arm-like appendices around the mouth are perhaps the most prominent characteristics that distinguish nautiloids from the rest of cephalopods (Fig. 1). Other diagnostic features include two pairs of gills, a lack of suckers and hooks on the appendices, a lack of chromatophores and ink sac, and a funnel formed by two lobes which fold together to form a tube-like structure (Fig. 1). The general anatomy of chambered nautiluses has been extensively described before (Jereb 2005, Jereb and Roper 2005, Sasaki et al. 2010). Below is a brief description of the most important features that distinguish the group.

Nautiluses are the only extant cephalopod with an external coiled calcium carbonate shell that is divided into several compartments, called chambers (Fig. 1). The shell is compressed and involutes to umbilicate where in some cases a perforation or an umbilical callus is present. The shell has irregular red to yellow-brown stripes on the dorsal and lateral sides radiating from the umbilicus that fade out towards the ventral side and the aperture in adults (Fig. 1). Sculptures of sinuous growth lines and fine ridges are present. The shell is broader and larger in mature males than in mature females. The interior wall of the shell can be covered by a nacreous luster layer or by bands or bright colors. Shell diameter in *N. pompilius* varies among regions typically smaller (170-180 mm in diameter) around Fiji and the Philippines and larger (up to 222 mm and mean weight of 1,675 g) in the Western Australian population (Tanabe et al. 1990, Tanabe and Tsukahara 2010, Barord et al. 2014).

The shell provides buoyancy and protection to the animal through the series of interconnected chambers (28 or more in mature individuals) filled with gas and fluid (Ward 1987, Arnold 2010, Shapiro and Saunders 2010, Dunstan et al. 2011b). Buoyancy regulation occurs by changing the amount of gas and fluid in each chamber through a fleshy tube structure called siphuncle

(Denton and Gilpin-Brown 1966, Greenwald and Ward 2010). As the animal growths the outer shell also growths, the body moves forward, more chambers are consecutively added by producing inter chamber walls called septum that seals off the older chambers, (Saunders 1983, Collins and Ward 2010, Landman and Cochran 2010). The animal lives and is protected in the anterior and largest chamber, into which it can completely withdraw by closing the opening with a leathery hood structure (Jereb 2005, Jereb and Roper 2005) (Fig. 1). Morphological studies suggest that renal appendages may be used to store calcium phosphate used in shell production (Cochran et al. 1981, Ward 1987, Landman and Cochran 2010, Ward et al. 2014). In general, mature individuals present a black band on the edge of shell and a black layer on the shell above the head contains thickened layers and conspicuous growth lines (Ward et al. 2016).

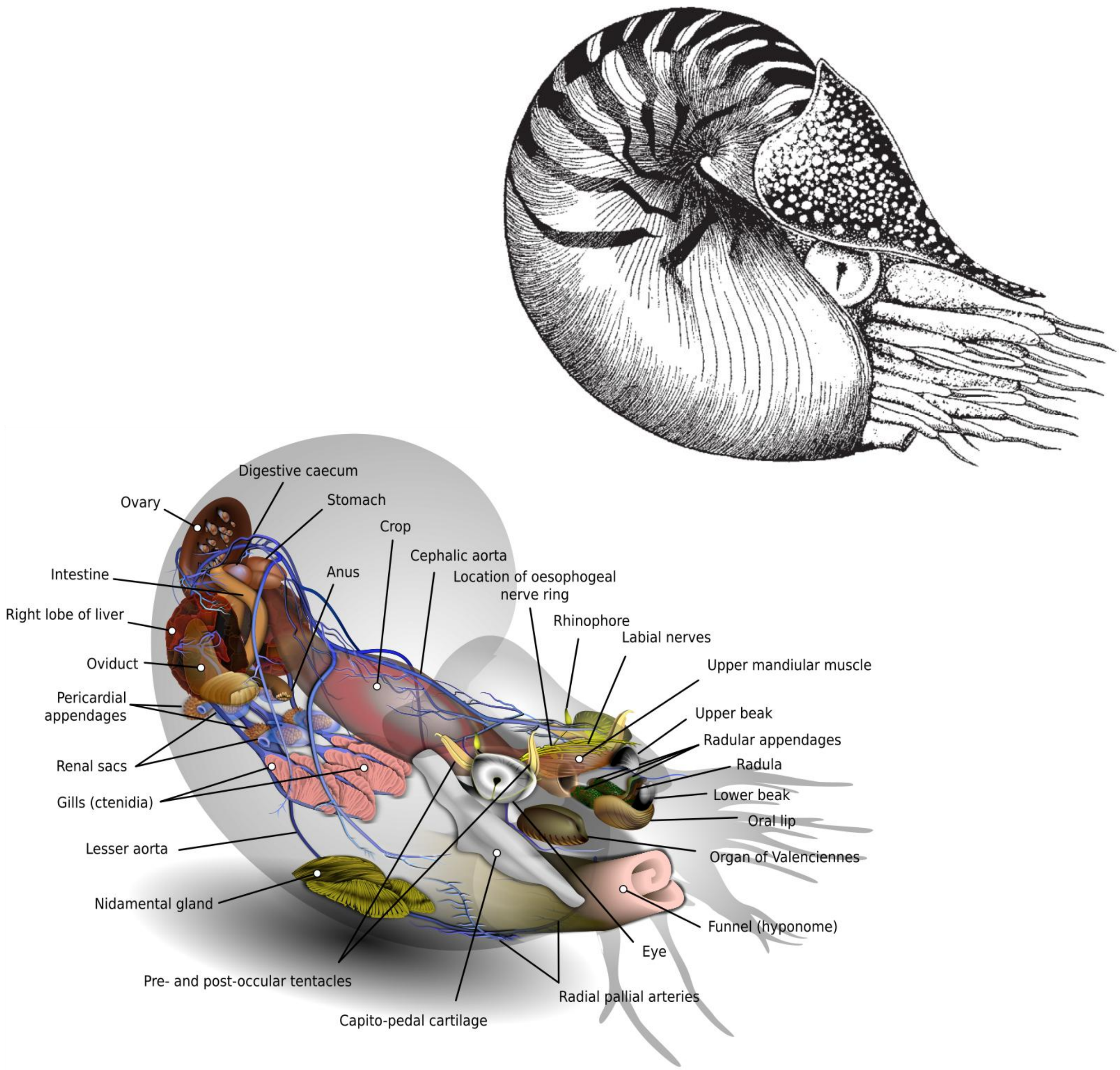


Figure 1. External morphology (upper panel) and schematic cross-section with labels (lower panel) of the chambered nautilus (*Nautilius pompilius*). *Drawing after Jereb (2005). Diagram of the anatomical structures and internal organs of a female N. pompilius by K.D. Schroeder*

The 'head' of chambered nautiluses is profoundly different from the rest of coeloid cephalopods (octopus, squids, and cuttlefish). Chambered nautiluses have up to 90 oral tentacles (pairs of over 47 arm-like appendices) that can be extended and retracted into buccal sheaths (Fig. 1) (Jereb and Roper 2005, Fukuda 2010 p. 201, Kier 2010). Although chambered nautiluses lack suckers or hooks on the tentacles they have adhesive structures on the oral side of the digital tentacles that produce "glue" aiding in prey capture and handling (Fukuda 2010, von Byern et al. 2012). Jaws have calcite denticulation and in contrast to coleoids cephalopods, the radula has 13 elements with two lateral teeth and two inner marginal support plates (Jereb 2005). Chambered nautiluses also lack complex lensed eyes found in coeleoid cephalopod, but exhibit a relatively large pinhole camera-type eye that is advantageous for dark environments (Fig. 1). Unlike coeleoid cephalopods, nautiluses lack chromatophores and retain many primitive anatomical features (Sasaki et al. 2010). As other cephalopods, nautiluses use jet propulsion to swim.

The nautilus's brain is also different from the brain of other cephalopods and neural structures that support learning and memory present in octopus and cuttlefish are absent (Crook and Basil 2013). Although nautiloids have a simpler, ring shape brain with few differentiated lobes, the brain is larger than non-cephalopod mollusk brains. However, chambered nautiluses are capable of both spatial learning and navigational strategy (Crook et al. 2009, Crook and Basil 2013). Although they live mostly in complete darkness, laboratory experiments have demonstrated that chambered nautilus can rely on proximate and distant visual cues for orientation (Crook and Basil 2013).

Small morphological differences associated with mature shell length, color patterns, tentacle sheath form, and radula structure are observed among geographic-isolated populations (Tanabe et al. 1990, Swan and Saunders 2010, Tanabe and Tsukahara 2010). Several processes tend to increase morphological differences among populations including: different selection pressure in different environments (e.g., resource availability, habitat characteristics, environmental fluctuations), genetic isolation due to geographical and behavioral factors, isolation time, and random genetic drift (Swan and Saunders 2010).

3.4. Geographic Distribution

Specific areas of known chambered nautilus (*N. pompilius*) populations include American Samoa (USA), Australia, Fiji, India, Indonesia, Malaysia, New Caledonia, Papua New Guinea, the Philippines, Solomon Islands, and Vanuatu (Fig. 2), based on studies of population biology (Haven 1977, Saunders and Spinosa 1978, Ward and Martin 1980, Saunders 1990, Tanabe et al. 1990, del Norte-Campos 2005, Jereb and Roper 2005, Sinclair et al. 2007, Hayasaka et al. 2010, House 2010, Saunders and Ward 2010, Swan and Saunders 2010, Dunstan et al. 2010, 2011b). The species may be also native to China, Myanmar, Thailand, Viet Nam, and Western Samoa.[7] Although most chambered nautilus species are endemic to specific islands, countries, or subregions, *N. pompilius* is the most wide-ranging recognized species and occupies all countries previously listed. Within this range, *N. pompilius* populations seem to be distributed erratically in

[7]Proposal: Inclusion of the Family Nautilidae (Blainville, 1825) in Appendix II in accordance with Article II paragraph 2 (a) of the Convention and satisfying Criterion B in Annex 2a of Resolution Conf. 9.24 (Rev. CoP16). http://www.fws.gov/international/cites/cop17/ussubmissions/chambered_nautilus_appendixII.pdf

association with deep fore-reefs, but suitable habitat does not necessarily indicate the species presence (Jereb and Roper 2005, House 2010, Saunders and Ward 2010, Dunstan et al. 2011b). Physiological constrains in chambered nautiluses substantially limit their vertical and horizontal distribution to geographically isolated areas with suitable habitat (Ward and Martin 1980, Saunders 1984, Jereb and Roper 2005, Saunders and Ward 2010, Dunstan et al. 2010, 2011a, 2011b, 2011c, Barord et al. 2014, Williams et al. 2015).

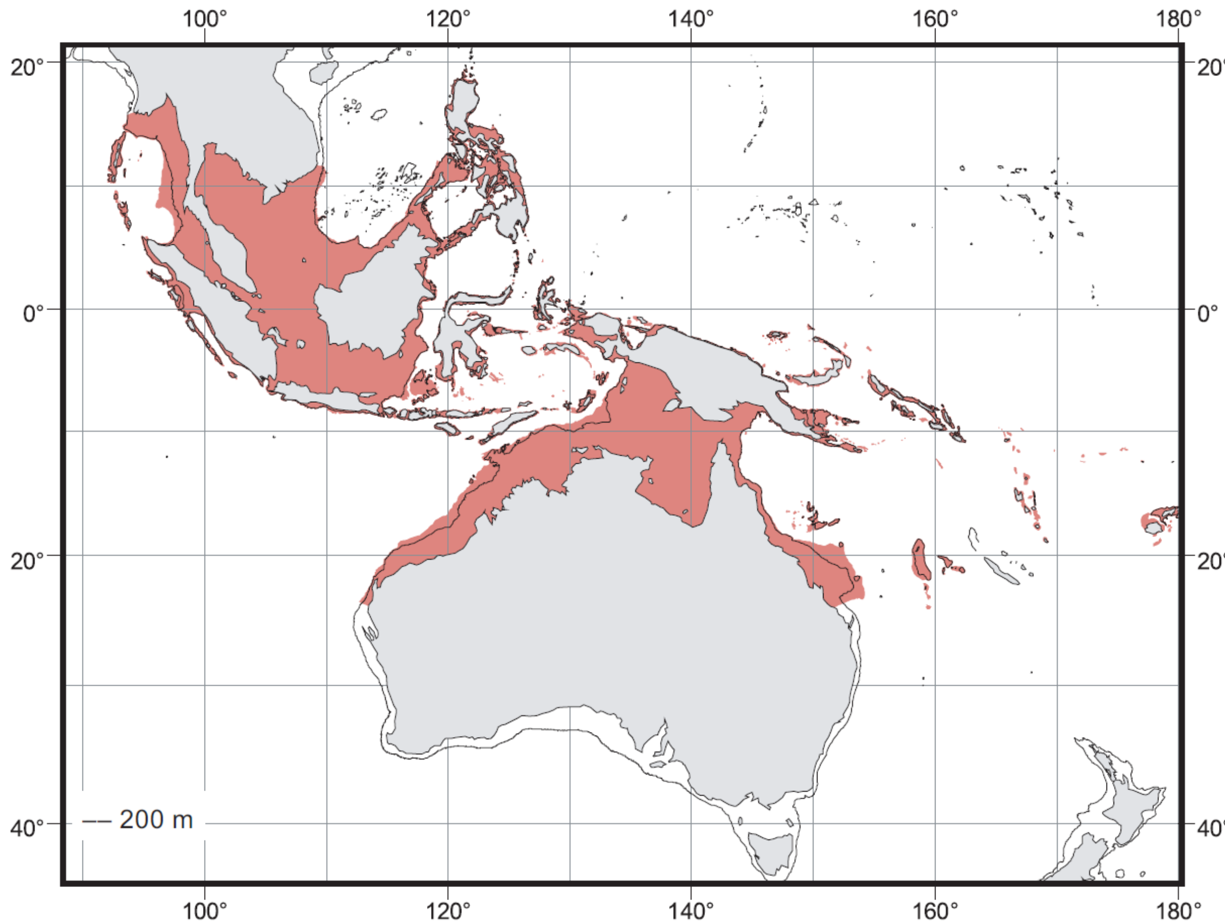
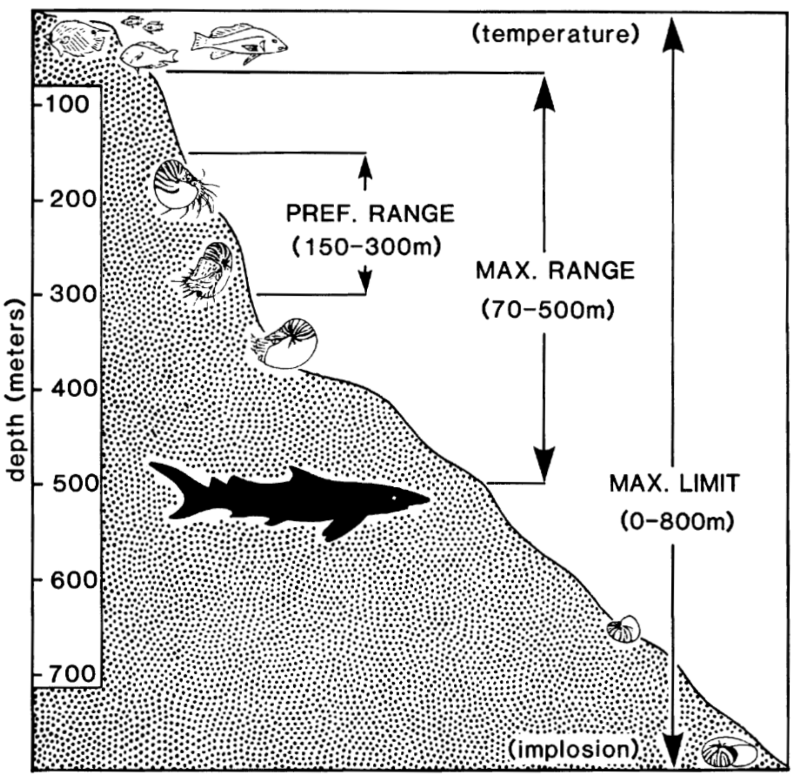


Figure 2. Known distribution (orange shade) of chambered nautilus (*Nautilus pompilius*) throughout the Indo-Pacific. The species is restricted to deep benthic habitats of the shelf platform across the region. *Map after Jereb (2005).*

3.5. Habitat

Chambered nautiluses are extreme habitat specialists. The distribution of *N. pompilius*, as well as other extant nautiloids species and subspecies, is restricted to benthic tropical habitat of the Indo-Pacific region on steep coral reef drop-offs and coral seamounts typically within depths of 130-700 m (Ward and Martin 1980, Hayasaka et al. 1982, 1995, 2010, Saunders 1984, 1990, Ward 1987, Saunders and Ward 2010, Dunstan et al. 2011c). Chambered nautiluses are bottom-dwelling scavengers and opportunistic predator species with close association with deep fore-reefs and associated sandy, silty, or muddy substrates (Jereb and Roper 2005, Saunders and Ward 2010). In fact, substrate configuration and bathymetric topography seems to strongly control the vertical and horizontal distribution of the species within their preferable habitat (Hayasaka et al. 1982, 2010, Ward et al. 2016). As such, habitat is likely the primary factor in determining movements between areas (Ward et al. 2016). However, movement between areas is very limited and individuals stay in the same area over long periods of time (Ward et al. 2016).

Vertical and horizontal distribution of chambered nautiluses is restricted by shell architecture, constraints of species physiology, and predation pressure. The internal arrangement of the shell's chambers that are filled with gas limits their depth to 800 m due to excessive hydrostatic pressure that can lead to shell implosion and subsequent animal death (Kanie et al. 1980, Ward et al. 1980, Jereb and Roper 2005, Hewitt and Westermann 2010, Saunders and Ward 2010). Thus, waters deeper than 800 m constitute a geographical barrier to individual movement. In addition, studies indicate that the chambered nautilus must equilibrate at ~200 m to adjust it neutral buoyancy, otherwise chamber flooding can occur at ~250 m (Dunstan et al. 2011c). This finding may partially explain possible habitat preference for steep-slope terrace-like fore-reefs (Hayasaka et al. 1982, 1995, 2010). Based upon studies at Osprey Reef in Australia, populations of the chambered nautilus undergo strong vertical migrations between depth of 100 and 700 meters. During the day, chambered nautiluses seem to either rest (by attaching to reef structures) at relatively shallow depths of 160-225 m or forage below 490 m, while during the night active movement is observed within the full depth range between 100 and 700 m (Hayasaka et al. 1982, Kier 2010, Dunstan et al. 2011b, 2011c).



Vertical and horizontal migrations patterns (i.e., distribution range) may respond to optimal feeding substrate, nektobenthic life style (Ward and Martin 1980), predator avoidance (Saunders et al. 2010), resting requirements to maintain buoyancy (Dunstan et al. 2011c), upper temperature limitations of ~25 ºC (Carlson 2010), as well as the 800 m deep threshold that leads to shell implosion (Kanie et al. 1980, Ward et al. 1980) (Fig. 3).

Figure 3. Summary of factors limiting the vertical distribution of chambered nautiluses based on *N. belauensis*, Palau, and that also seems applicable to *N. pompilius* (Saunders and Ward 2010). *Figure from Saunders (1984).*

Chambered nautiluses seem to avoid waters shallower than 100 meters because visual predation by teleost fish and water temperature can exceed 25ºC (Hayasaka et al. 1982, 2010, Saunders 1984, Carlson 2010, Saunders and Ward 2010, Saunders et al. 2010, Dunstan et al. 2011c). It seems that temperatures above 25 ºC are too warm for chambered nautiluses to maintain adequate metabolism levels (Carlson 2010). However, chambered nautiluses have been found in waters as shallow as 5 m at night during winter when temperatures can drop to 22 ºC (Ward et al. 1984, Jereb and Roper 2005, Saunders and Ward 2010). These limitations constrain the migration capacity of chambered nautiluses by imposing physiological and ecological barriers and effectively isolating small localized populations resulting in restricted gene flow that leads to genetically distinct populations (Wray et al. 1995, Woodruff et al. 2010, Sinclair et al. 2011, Williams et al. 2012, 2015).

3.6. Genetic Structure

Genetic analysis suggests that the chambered nautilus (*N. pompilius*) populations are separated into three geographically distinct monophyletic clades or subspecies: West Australia/Indonesia, Northeast Australia/Papua New Guinea, and West Pacific including the Coral Sea in East Australia (Wray et al. 1995, Sinclair et al. 2007, 2011, Bonacum et al. 2011, Williams et al. 2012, 2015). Based on genetic analysis of the *cytochrome oxidase subunit 1(COx 1),* both east and west Australia populations are significantly genetically distinct and populations of the northern Great Barrier Reef (Northeast Australia), and the Coral Seas in northeastern and eastern Australia have also been diverging genetically (Sinclair et al. 2006, 2011). The ancestor population of the species seems to have originated around New Guinea approximately two million years ago with a group radiating southeast towards New Caledonia, Fiji, and American Samoa, another group migrating south towards Australia's Great Barrier Reef and the Coral Seas, and a third group migrating north and northwest towards Palau, the Philippines, and Indonesia (Bonacum et al. 2011). In fact, new genetic analysis based on both *COx 1* and *16S rDNA* sequences corroborated this finding and show striking genetic differences among *N. pompilius* populations from the Philippines, Australia, Fiji, American Samoa, and Vanuatu (Fig. 4).

Chambered nautiluses show a high degree of genetic and morphological variations across the distributional range (Tanabe et al. 1990, Wray et al. 1995, Sinclair et al. 2007, 2011, Swan and Saunders 2010, Tanabe and Fukuda 2010, Woodruff et al. 2010, Bonacum et al. 2011, Williams et al. 2012, 2015, Ward et al. 2016). Geographical isolation due to their limited dispersal ability may have promoted genetic differences over the past five million years leading to phenotypic dissimilarities (Woodruff et al. 2010, Sinclair et al. 2011, Bonacum et al. 2011, Williams et al. 2015). For example, marked morphological differences have been observed between populations of *N. pompilius* of Fiji and Philippines (Tanabe et al. 1990, Swan and Saunders 2010, Tanabe and Tsukahara 2010).The distinct genetic and morphological differences among these regions are related to geographical and physical isolation over evolutionary time scales (Sinclair et al. 2011). Among the main effective dispersal barriers for the expansion of nautiloid species distribution outside and within the Indo-Pacific regions has been water temperature, depth, distance between adjacent continental and island shelf, and predation (Crick 1993).

These barriers may restrict the ability of the chambered nautilus (*N. pompilius*) to move among subregions, occupy suitable habitat, and re-colonize areas where populations have drastically declined or gone extinct due to overfishing. In fact, these populations may currently represent evolutionary diverging lineages and there is no evidence of contemporary gene flow among them and mixing seems to be unlikely (Sinclair et al. 2011). Dispersal among relatively small isolated populations may be sporadic and totally random due to chance such as drift via tropical storms. As such, genetically distinct populations of the chambered nautilus should be managed as discrete units because each subregion contains unique genetic diversity that are of high conservation value (Sinclair et al. 2011). Therefore, the survival of genetic distinct populations is critical for the conservation of the species.

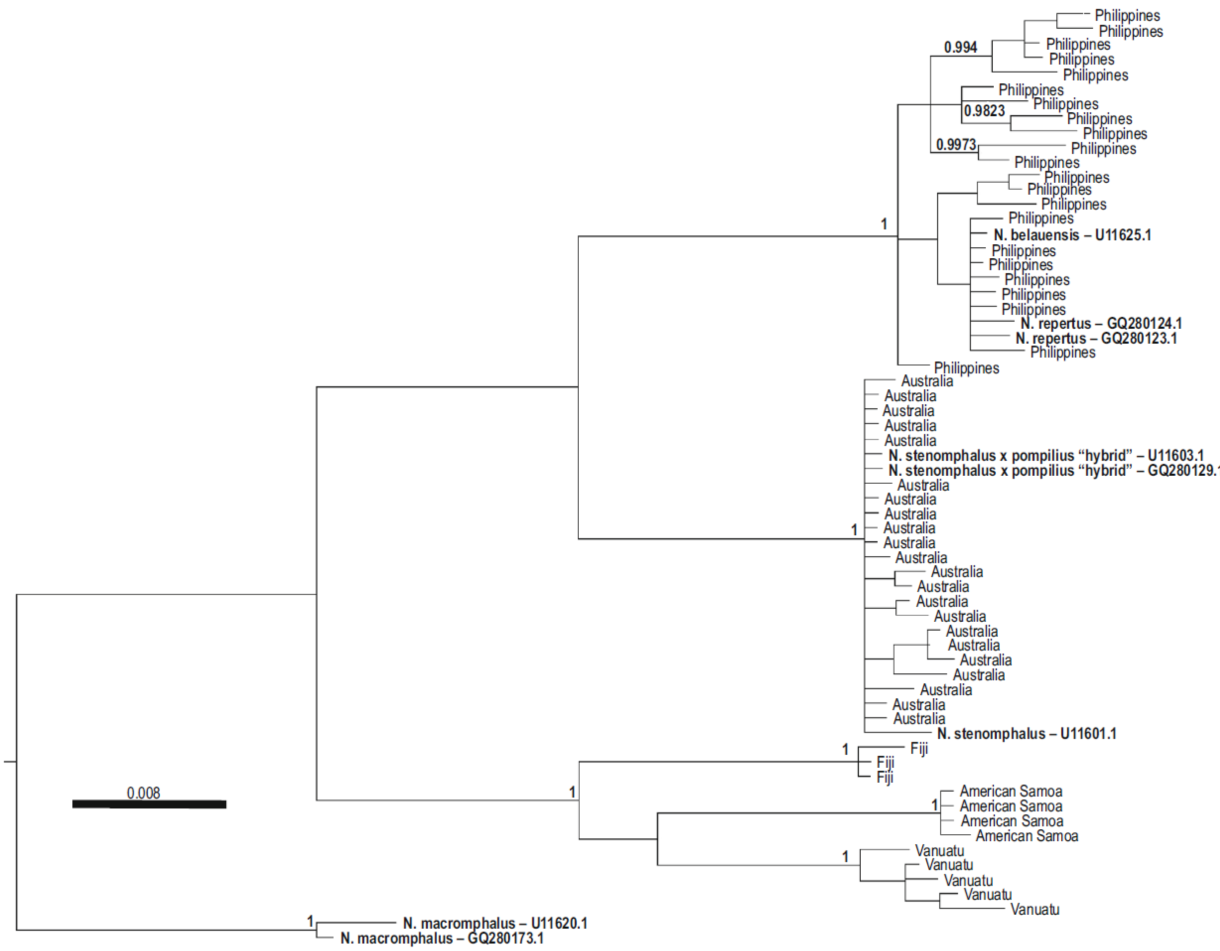


Figure 4. Bayesian inference tree of 16S rDNA sequences of *N. pompilius* sequences and sequences of other *Nautilus* species from GenBank. Posterior probabilities below 0.95 are not shown. Note that *N. belauensis, N. stenomphalus, N. repertus*, and *N. pompilius* do not fall into discrete clades while *N. macromphalus* does. As such, it is likely that the genus *Nautilus* may be comprised of only two species: *N. pompilius* and *N. macromphalus* (Ward et al. 2016). *Figure and legend modified after Ward et al. (2016).*

The limited ability for the chambered nautilus (*N. pompilius*) to disperse has isolated local populations by restricting gene flow leading to genetically distinct populations (Wray et al. 1995, Woodruff et al. 2010, Sinclair et al. 2011, Williams et al. 2012, 2015, Ward et al. 2016). Nautiloids do not produce larvae for dispersal, thus connectivity among regions is precluded across oceans expanses that are deeper than 800 m (Saunders and Ward 2010). This depth limitation created an effective dispersal barrier that restricts the distribution and colonization of the species as gene flow depends mostly on adult movements and ocean currents (Saunders and Ward 2010) colder than 25ºC (Carlson 2010). Currents can further affect individuals' position on their reef habitat (O'Dor et al. 1993). The animals are slow and weak swimmers and tend to avoid fast or jerky movements or strong currents (Hayasaka et al. 2010). Acoustic telemetry estimations have revealed that the species can travel at rates of up to 3.2 km per night from self propulsion and up to 6 km per night facilitated by currents (Dunstan et al., 2011a). Small scale navigation to familiar locations may be possible using simple visuals cues at shallower waters where light penetrates (Crook et al. 2009, Crook and Basil 2013). But chambered nautiluses seem to remain mostly close to the reef for protection from predators (Hayasaka et al. 2010, Saunders et al. 2010). Indeed, studies based on acoustic telemetry at Osprey Reefs in Australia suggest that *N. pompilius* tends to rest cryptically at around 200 m during the day with limited movement likely to avoid detection from predators (Dunstan et al. 2011c). Thus, movements of nautiluses between isolated archipelagos may be sporadic and limited to optimal dispersal events (Saunders and Ward 2010).

Fine genetic differences are also observed within regions and populations. Trapping analysis supports that specimens from different areas such as the Great Barrier reefs and the Coral Sea reefs show genetic differences (Sinclair et al. 2007). For example, within the Great Barrier Reef, individuals from relatively small populations of Osprey Reef and Shark Reef in the Coral Sea seem to be genetically isolated (Fst = 0.312 and 0.229, respectively) (Williams et al. 2015). These differences are related to the physical geography of the ocean floor (physiography) where depths of over 1,700 m divides Osprey reef and the Great Barrier Reef and has prevented mixing (Dunstan et al. 2011c). In contrast, populations from the Philippines and west Australian reefs that are more geographically separated shown small degree of genetic structure (Fst = 0.015) (Williams et al. 2015). Genetic similarities of these two geographically distant populations were not likely the result of current gene flow between regions, but rather due to genetic drift from formerly large populations (Williams et al. 2015). Now, those populations are dramatically in decline (Dunstan et al. 2010, 2011a, Barord et al. 2014). This lack of connectivity among regions suggests that local extinction from overfishing is highly possible as recolonization is unlikely because movement through open waters is limited by predation and physiological constraints (Yomogida and Wani 2013).

3.7. Feeding

The chambered nautilus is a nekton-benthonic opportunistic scavenger with as many as 90 small oral tentacles that are used for feeding on fish, crustaceans, other invertebrates, and detrital matter associated with deep benthic reef habitats (Ward and Wicksten 1980, Saunders 1984, Ward et al. 1984, 2016, Hayasaka et al. 2010, Saunders and Ward 2010). Based on these studies young hatchlings in aquaria feed immediately on shrimp or small food items, and in wild adults, crabs, echinoids, fish, and other cephalopods including nautilus have been identified in crop analysis. The buccal mass is well distinguished from other modern cephalopods by the presence of calcified deposits with denticles and shorter inner lamellae of the lower jaw which may reflect an adaptation to a crustacean and scavenger diet (Tanabe and Fukuda 2010). Chambered nautiluses can easily detect prey using chemoreception from significant distances (Barord et al. 2014). This sensitive sensorial adaptation is perhaps one of the reasons that bait traps are so effective in catching nautiluses by local and commercial fisheries (del Norte-Campos 2005, Dunstan et al. 2010).

3.8. Growth, Reproduction, and Lifespan

All chambered nautilus species are k-selected with life history traits of late maturity, low fecundity, and relatively long life span (Haven 1977, Saunders 1983, Arnold 2010, Collins and Ward 2010, Landman and Cochran 2010, Dunstan et al. 2011b). Chambered nautiluses have slow circumferential growth rate with ~0.12 mm/day for immature individuals and ~0.061 mm/day for submature and mature animals (Saunders 1983, Collins and Ward 2010, Dunstan et al. 2011b). In aquaria conditions, average growth rates are 0.1 to 0.16 mm/day, although abnormal shell formation is common (Westermann et al. 2004, Linzmeier et al. 2016). Chambered nautilus have relatively long life span of up to 20+ years reaching maturity relatively late at around 14-16 years (Landman and Cochran 2010, Dunstan et al. 2011b). These life history traits differ from the rest of coeloid cephalopods (i.e., octopus, squid, cuttlefish) that are short-lived (1-2 years) and highly fecund (Jereb and Roper 2005, Barord and Basil 2014a) making chambered nautilus highly vulnerable to mortality before reproduction.

Relatively little information is known about chambered nautilus reproduction in the wild and most information is based on captive animals. Chambered nautiluses reproduce sexually, locating and identifying mates in their dark environments via chemicals or odors produced by males and females and diffused by currents (Basil et al. 2000). In contrast to other cephalopods, nautiluses are iteroparous (i.e., they have multiple reproductive cycles over their lifetime) (Haven 1977, Arnold 2010). In males, four tentacles fuse to form a structure called the spadix used to transfer spermatophores (i.e., sperm reservoirs) to females during copulation (Jereb 2005). Copulation between males and females may happen for several hours with the male grasping the female tentacles (Haven 1977, Arnold 2010).

Egg-laying has not been directly observed in the wild. In captivity, females produce a relatively low number of eggs per year (10-20 eggs per year) which make them animals of lower fecundity in comparison with other cephalopod species (Uchiyama and Tanabe 1999). Based on captivity observations, females lay eggs on rocky substrate attaching them with a strong cement-like structure to the substrate (Barord and Basil 2014). Based on oxygen and carbon isotopes analyses of adult shells, females may lay the eggs in shallower (100-200 m) and warmer (22-24ºC) waters (Landman et al. 2001) and gestation is unusually long, lasting about 10 to 12 months (Arnold 2010, Barord and Basil 2014b). As with other extant coleoids, chambered nautiluses do not have larval stages which prevents wide dispersal throughout the oceans (Saunders and Ward 2010, Dunstan et al. 2011b). When the eggs hatch, hatchlings (~22-26 mm in shell diameter) exhibit already seven to eight internal chambers and migrate to deeper (300-400 m) and cooler waters (14 ºC) (Uchiyama and Tanabe 1999, Landman et al. 2001, Dunstan et al. 2011b). Live hatchlings have rarely been seen in the wild (Hayasaka et al. 1982, Dunstan et al. 2011b). Most information on life history characteristics related to reproduction, age, class structure, growth rate, maturation time, and lifespan have been gathered from field, captivity, and radiometric studies.

Demographic differences are important within chambered nautilus populations. Sexual dimorphism between sizes of males and females is observed with mature males relatively larger than females (Dunstan et al. 2011b). Most unexploited populations seem to be dominated (over 80%) by males (Dunstan et al. 2011b). This male/female ratio of 8:1 seems to be common across the geographic range and had been estimated at Osprey Reef in the Coral Seas, Australia (Dunstan et al. 2011a, 2011b), Phillipines (Haven 1977), Palau (Saunders and Spinosa 1978), New Caledonia (Ward and Martin 1980), and Papua New Guinea (Saunders et al. 1987, Saunders 1990). In addition, ~75% of all captured individuals are mature (Hayasaka et al. 1982, Saunders 1984, Arnold 2010, Dunstan et al. 2010, 2011a). However, chambered nautiluses are not segregated within their habitat by either size or sex (Dunstan et al. 2010), although seasonality in female presence may exist in some areas (Haven 1977). Juveniles seems to comprised less than 10-20% of the entire population and occupy the same habitat within vertical distribution as adults and sub-adults (Ward and Martin 1980, Hayasaka et al. 1982, Saunders 1983, 1990, Ward 1987, Tanabe et al. 1990, Dunstan et al. 2011b, 2011c). Previous studies have shown ontogenetic habitat partitioning (Haven 1977). Low abundance of juveniles in the population is another indication that chambered nautiluses have low fecundity (Dunstan et al. 2011a).

Captive breeding of chambered nautiluses (e.g., aquaria) over the past two decades has been mostly unsuccessful. Eggs that are produced under captivity are often infertile, and when hatching occurs offspring have very low and short survivorship. First embryos were observed at the Waikiki Aquarium in the United States in 1985 but the eggs did not hatch (Alrnold and Carlson 1986). Twenty years later, eggs of the chambered nautilus successfully hatched at the Henry Doorly Zoo (USA) in a closed artificial sea water system (Fields 2006). Although very few other hatching events have occurred in aquaria, none of the juveniles have survived over a year (Barord and Basil 2014b). These life history characteristics make them highly vulnerable to exploitation.

3.9. Importance of Chambered Nautilus in its Ecosystem

Chambered nautiluses are deep-sea opportunistic predators with scavenging generalist feeding habits (Ward and Wicksten 1980, Saunders 1984, Jereb and Roper 2005, Saunders and Ward 2010, Dunstan et al. 2011b). In fact, recent studies suggests that chambered nautiluses are likely obligate scavengers (Barord and Basil 2014a, Barord 2015). Deep sea scavengers play a crucial role in nutrient cycling, energy flow, and functioning of the deep sea food webs (Beasley et al. 2012). Broadly, chambered nautiluses are crucial in understanding cephalopodan evolution through genetic, paleontological, paleoecological, and paleoclimatological studies (Chamberlain et al. 1981, Crick 1993, Sinclair et al. 2006, Boyle and Rodhouse 2008, Woodruff et al. 2010, Barord 2015).

3.10. Population Abundance

Available information indicates that chambered nautilus population abundances are relatively low and drastically declining in some areas (Ward et al. 2016). Populations of chambered nautiluses are patchily distributed across their geographic region and site occupancy is irregular and can be unpredictable. There are no global population estimates for chambered nautiluses. Population density varies greatly among regions, but in general abundance is relatively low and can rapidly decline even further after few years of continued fishing (del Norte-Campos 2005, Dunstan et al. 2010, Barord et al. 2014). In fact, scientists studying chambered nautilus for the last 40 years with experience in trapping individuals throughout the geographical range (including Australia, American Samoa, Fiji, New Caledonia, New Guinea, the Philippines, and Vanuatu), report that most single traps yield relative low abundances that range from zero to five individuals (Ward et al. 2016).

In habitats where fishing occurs, chambered nautilus population abundance are notably low. Abundance of the chambered nautilus (*N. pompilius*) from unfished areas is relatively higher than from even lightly fished areas. Population estimates, based on baited remote underwater video systems ("BRUVS"), have shown relatively low abundance of less than one individual per squared kilometer (ind./km^2) from surveyed locations at Cairns-Lizard Island in the Great Barrier Reef (0.34 ind./km^2), Beqa Passage in Vitu Levu, Fiji (0.21 ind./km^2), and Taena Bank in American Samoa (0.16 ind./km^2) (Barord et al. 2014). In contrast, the lowest population abundance (0.03 ind./km^2) has been observed at heavily fished areas such as the Bohol Sea in the Philippines (Barord et al. 2014).

Other surveys indicate population abundance were two or three orders of magnitude lower than truly unexploited populations (i.e., no history of commercial fishing) in locations such as Osprey Reef in Australia (13.6-77.4 ind./km^2) (Dunstan et al. 2010, 2011a, Barord et al. 2014). However, population abundance calculated through BRUVS may actually overestimate natural abundance because baited traps tend to attract chambered nautilus species from very long distances and thus concentrate them around trap sites (Dorman et al. 2012, Barord et al. 2014). In fact, based on high percentage of recaptured individuals in studies of other nautilus species such as *N. belauensis* in Palau, chambered nautiluses seem to rapidly habituate to baited trapping sites (Hayasaka et al. 1995) which may inflate actual population abundances. Thus, populations of chambered nautiluses may actually be more dispersed with lower densities per unit of area than current estimations.

This dispersed structure and the relatively low abundances of unexploited populations may be representative of the chambered nautilus (*N. pompilius*) across their range and some scientists consider the species rare (Barord et al. 2014, Barord 2015, Ward et al. 2016). This hypothesis is also consistent with paleontological studies that indicate that due to the scarce fossil record, ancestors of chambered nautiluses were also likely rare (Ward 1984, Teichert and Matsumoto 2010). Thus, rarity, low abundance, and disperse populations make chambered nautiluses extremely vulnerable to unsustainable exploitation which can wipe out local populations in few decades.

3.11. Population Trend

Based on the best available science, chambered nautilus populations have declined in areas where fisheries currently occur or have occurred, including in the Philippines, India, Indonesia, and New Caledonia. Fisheries dependent data and survey studies show that *N. pompilius* populations in some areas within the Philippines have drastically declined due to overfishing and similar trends can be expected if fishing starts in other regions (Dunstan et al. 2010, Barord et al. 2014). For example, the population of *N. pompilius* in Tañon Strait, Philippines has declined by 80 % in trap yields and the species is believed to be locally extirpated (Dunstan et al. 2010, Barord et al. 2014). A questionnaire study in the Palawan region of the Philippines of 26 fishermen and seven traders suggests declines of up to 80% in catch per unit effort of *N.*

pompilius (and by inference other nautilus species) at some locations from 1980 to 2010 (Fig. 5) where effort was mostly comprised by just 3-4 local fishermen at each location (Dunstan et al. 2010). This study also reported crashes of chambered nautilus fisheries in Cagayancillo within the Palawan Province, in Tawi-Tawi Province, and in Tañon Strait (Dunstan et al. 2010). In the early 2000s, declines were reported anecdotally by some fishermen in the Visayan Regions where several fishing sites occur (Schroeder 2003). According to the Palawan Council for Sustainable Development and the Philippine Management Authority in Palawan, traders have also reported a decline in the number of *N. pompilius* shells provided by fishermen in the last five years.[8] Currently, Palawan waters in the Philippines continue to be heavily targeted by fishermen that operate around Panglao Island and Balabac Island (Freitas and Krishnasamy 2016).

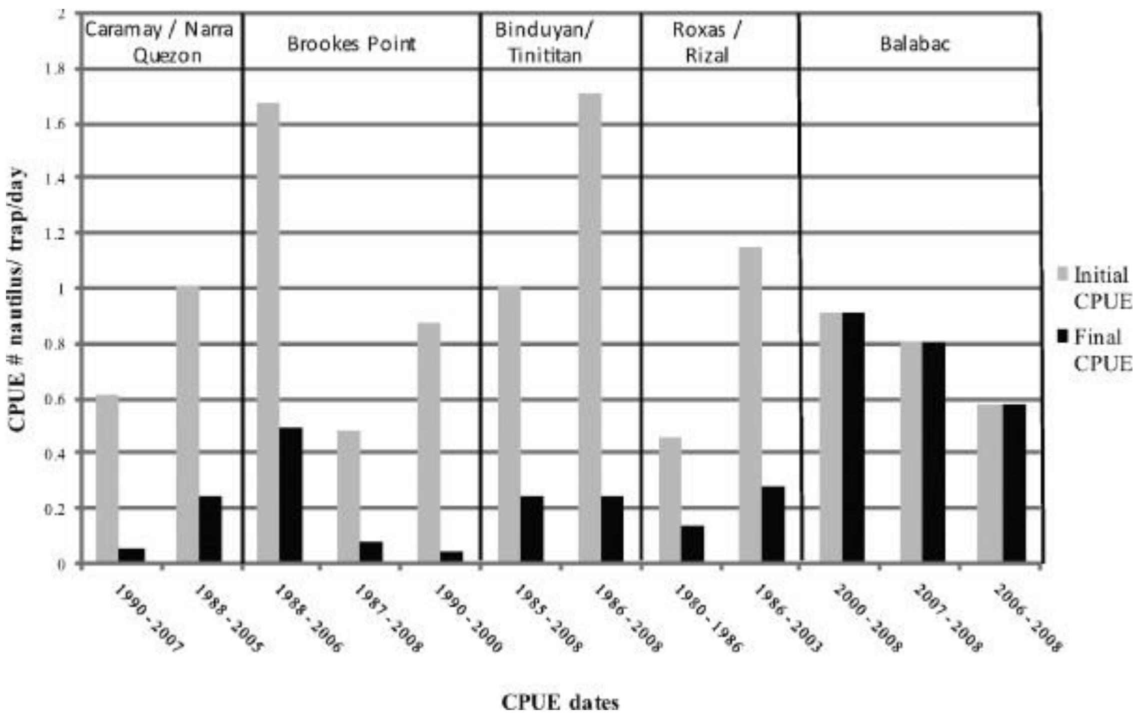


Figure 5. Changes in catch per unit effort (CPUE) over time for Palawan chambered nautilus fishery. CPUE changes from fisher reports between the start of fishing efforts to either current or last recorded (if fishing was discontinued) CPUE for chambered nautilus in the Palawan and Balabac regions of the Philippines. *Figure and caption after (Dunstan et al. 2010).*

Other studies and government agencies have reported declines of chambered nautiluses in India, Indonesia, and New Caledonia following several decades of intense harvest. For example, the Scientific Authority of India reported declines of *N. pompilius* in Indian waters after several

[8] Proposal: Inclusion of the Family Nautilidae (Blainville, 1825) in Appendix II in accordance with Article II paragraph 2 (a) of the Convention and satisfying Criterion B in Annex 2a of Resolution Conf. 9.24 (Rev. CoP16). http://www.fws.gov/international/cites/cop17/ussubmissions/chambered_nautilus_appendixII.pdf

years of intense harvest.[9] In Indonesia, *N. pompilius* harvests may be increasing and fishermen, traders, and species experts have reported substantial species decline in the wild and in markets in comparison with previous decades (Freitas and Krishnasamy 2016). In New Caledonia, past declines were reported for *N. pompilus* and *N. macromphalus* due to commercial harvest that occurred several years ago (Aguiar 2000).

Decline in catch rates over the last decades have also been reported from scientific studies. For example in the 1970s in the Tañon Strait, Philippines, chambered nautilus populations from scientific study sites that coincided with commercial fisheries showed declines in catch yields of ~27 % (5 to 1 individuals per trap) in a 5 year period when the number of fishermen increased and trapping was occurring deeper due to low yields (Haven 1977, Saunders and Ward 2010). In 1987, the chambered nautilus fishery in the Tañon Strait ceased (i.e., crashed) and a fishery independent study estimated catch yields of 0.01 chambered nautilus per trap which indicated a ~80% decline of the population in just about 15 years (Dunstan et al. 2010). By the late 1980s chambered nautilus was commercially extinct and likely extirpated from the Tañon Strait (Ward 1988, Alcala and Russ 2002). Similarly, scientists had indicated that capture-recapture fishery-independent studies in some reef areas of New Caledonia were harder to implement due to rapid decline of chambered nautiluses in some areas under intense harvest.[10]

Unexploited populations of chambered nautiluses live in resource limited environments where individuals within the population are sparsely distributed, population size is relatively low, fairly stable, and population growth rates do not exceed more than one individual per year (Sinclair et al. 2006, 2011, Saunders and Ward 2010, Tanabe and Tsukahara 2010, Dunstan et al. 2010). For example, the unfished but relatively small population of *N. pompilius* at Osprey Reef in Australia seems to have been stable for over a 12-year period (Dunstan et al. 2010). Given the peculiarities of their life history (i.e., slow growth, low reproduction, long gestation, lack of dispersal capabilities, geographic isolation, and low populations numbers), the chambered nautilus is thus extremely vulnerable to disturbances. In fact, any disturbance associated with habitat degradation or extraction of individuals from the population due to fishing will have a substantial and direct impact on the growth and long term population viability. Species experts that have studied the chambered nautiluses for decades consider that all the species within the family are highly susceptible to local extinction, particularly those very isolated and endemic populations throughout the geographical range (Saunders 1984, Landman and Cochran 2010, Dunstan et al. 2010, 2011a, 2011b, Barord et al. 2014, Barord 2015).

Chambered nautiluses are highly vulnerable to exploitation and local extinction even with light levels of fishing. In the Philippines, chambered nautilus fishing seems to be seasonal (6 to 9 months) depending on weather conditions, and fishing pressure is relatively low with a handful of local fishers at each location as well as few bait traps per fisher (del Norte-Campos 2005).

[9] Proposal: Inclusion of the Family Nautilidae (Blainville, 1825) in Appendix II in accordance with Article II paragraph 2 (a) of the Convention and satisfying Criterion B in Annex 2a of Resolution Conf. 9.24 (Rev. CoP16). http://www.fws.gov/international/cites/cop17/ussubmissions/chambered_nautilus_appendixII.pdf

[10] Proposal: Inclusion of the Family Nautilidae (Blainville, 1825) in Appendix II in accordance with Article II paragraph 2 (a) of the Convention and satisfying Criterion B in Annex 2a of Resolution Conf. 9.24 (Rev. CoP16). http://www.fws.gov/international/cites/cop17/ussubmissions/chambered_nautilus_appendixII.pdf

Harvest seems to be demand-driven mainly for the international shell trade and is characterized of a boom-bust cycle that only last for 10-15 years after which a population becomes depleted, fishing becomes unprofitable, and the fisheries is moved to a new location (Aguiar 2000, Dunstan et al. 2010). This indicates that even relatively low fishing pressure have a substantial negative effect on the population abundance of chambered nautiluses that can lead to drastic declines in less than two decades, especially for those species with very limited distribution ranges (del Norte-Campos 2005, Dunstan et al. 2010, Barord et al. 2014). Therefore, smaller, and very isolated populations are more vulnerable to overexploitation given the life history characteristics of the species. Research at other sites suggests that as the chambered nautilus declines in the Philippines, fishing pressure will likely shift to other countries such as Indonesia and elsewhere to fuel the international trade (Freitas and Krishnasamy 2016).

The abundance of presumably unexploited populations of the chambered nautilus across the geographic range can serve as a baseline that local managers could use as a reference point to evaluate conservation strategies. For example, unexploited populations of *N. pompilius* at Osprey Reef [11] in Australia seems to show the highest abundance within the geographical region and seem to represent the baseline for the species (Dunstan et al. 2010, 2011a, Barord et al. 2014). Based on capture-mark-recapture techniques, underwater video, and remotely operated vehicle surveys over six years from 2000 to 2006, Dunstan et al. (2011a) estimated that chambered nautilus population around the seamount was comprised of ~1,172 to 3,363 individuals (14.6-77.4 ind/km^2) depending on depth. Slightly lower values (13.6 ind./km^2) has also been estimated for Osprey reefs using other surveys methodologies such as BRUVS (Barord et al. 2014).

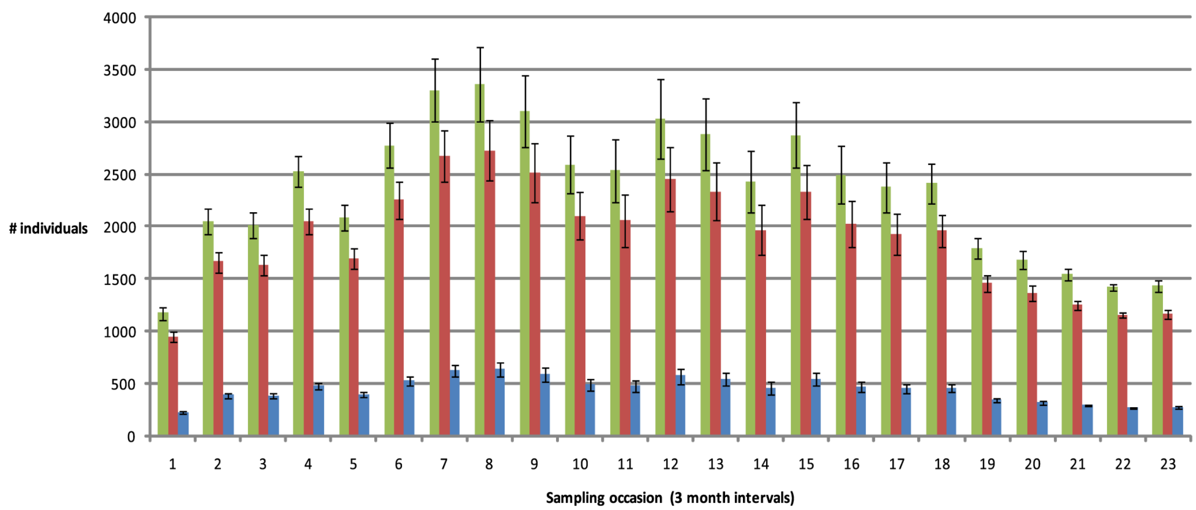


Figure 6. Temporal population estimates for total mature/sub-mature of chambered nautilus individuals (green bars), total males (red bars), and total females (blue bars) for each pooled three-month sampling occasion from the time-dependent model from the capture matrix with sex distinction. Error bars (1 standard error of the mean) are shown. Mean population estimates over the entire sampling period was 2344 mature/sub-mature Nautilus individuals (95% CI=1117 to

[11] Osprey Reef is a relatively small and isolated sea mount located 100 km from the outer edge of the Great Barrier Reefs rising from over 2000 m deep.

3570; SD=626); 1900 males (95% CI=906 to 2896; SD=508) and 443 females (95% CI=211 to 675; SD=118). *Figure and legend after Dunstan et al (2011a).*

Unlike other regions in the Indo-Pacific where chambered nautilus populations are well below one individual per squared kilometer, populations at Osprey Reef exhibit a hundred times more abundance. It is possible that the unfished population size at Osprey Reefs represents natural baselines abundance of wild populations (Barord et al. 2014). In this population, most individuals were mature (58%) and mostly males (male/female ratio: 83/17) with few juveniles (<10%) (Fig. 6) (Dunstan et al. 2011a). However, the low prevalence of juveniles may be sampling bias related to trap mesh size that allows juveniles to escape (Dunstan et al. 2011b). These data indicate that *N. pompilius* is sparsely distributed around the unfished island but with relatively low abundance. As such, this population can be use as a potential reference point through which local managers can evaluate population trends and conservation strategies.

4. Threats to the Species and Factors for Listing

Under the ESA, NMFS must analyze all factors that threaten the populations of the chambered nautilus throughout its range. The main threats that face the chambered nautilus populations include direct harvest for commercial international shell trade, habitat degradation throughout most of its range, predation, climate change, and small population sizes. Below is a detailed description of the factors that must be analyzed.

4.1. Present or Threatened Destruction, Modification, or Curtailment of its Habitat or Range

4.1.1. Habitat degradation

Destructive fishing practices, pollution, coastal development, sedimentation, and changes in water temperature and pH negatively impact the habitat of chambered nautiluses. Over half the reef areas off China, Indonesia, Malaysia, Myanmar, the Philippines, Thailand, and Vietnam are already threatened with habitat degradation (Bustamante et al. 2000, WRI 2011, De Angelis 2012, Freitas and Krishnasamy 2016) (Fig 7).

Indiscriminate and destructive fishing practices that use explosives (e.g., blast fishing with dynamite) and poison such as cyanide throughout the chambered nautilus's native range can substantially destroy and directly degrade the reef habitats that chambered nautiluses depend on (Fig 8). Although chambered nautiluses occupy mostly deeper reefs (100-500 m) where destructive fisheries do not generally reach, these practices in shallower reefs indirectly impact the entire food web that chambered nautiluses rely upon for food sources. Unselective and destructive fishing practices that kill unintended species are commonly used across the chambered nautilus range including waters off Fiji, China, Indonesia, the Philippines, and Vietnam (Rubec 1986, Pet-Soede et al. 1999, Mous et al. 2000, Boonstra and Bach Dang 2010, Burke et al. 2011) (Fig 8).

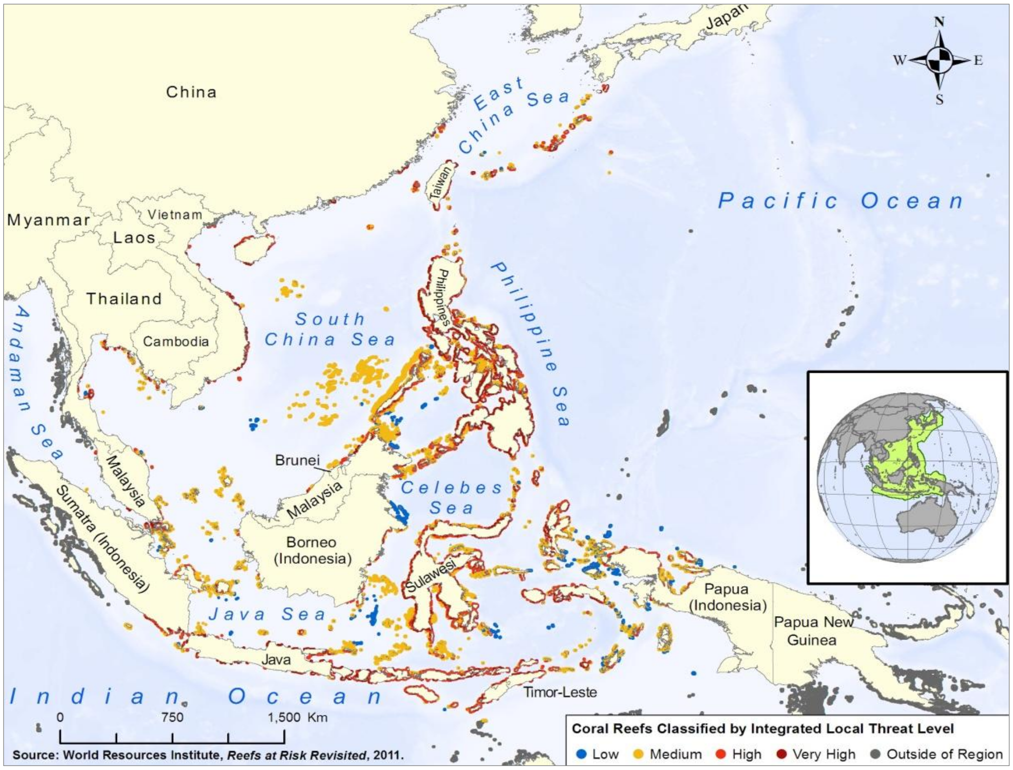


Figure 7. Reefs threatened by habitat degradation across Southeast Asia which including part of the distribution range of chambered nautilus. Map from WRI (2011).

Cyanide fishing for food and the aquarium trade has been used for several decades particularly in the Philippines and Indonesia with devastating consequences for their coral reef ecosystems (Rubec 1986, Mous et al. 2000, Halim 2002)[12]. This technique is highly destructive to coral reef ecosystems because it not only kills non-targeted fish, but also corals and invertebrates species (e.g., crustaceans, echinoderms, and worms) that are an important food source for fish communities. Based on the areas of observed destructive fishing practices, these reef locations are likely to support chambered nautilus fishing (Fig. 8). Although the Philippines Cyanide Fishing Reform Program was established to address this problem, cyanide fishing continues occurring across the Philippines (WRI 2011). The impacts of these destructive practices on the adjacent deeper reef habitats where chambered nautiluses live are unexplored.

The main driver for these destructive fishing practices is the traffic of live reef fish to satisfy Asian seafood markets and to supply the growing aquarium trade in Europe and North America that has drastically increased over the last four decades especially in Indonesia, New Caledonia, Papua New Guinea, the Philippines, and Vanuatu (Wood 2001, Petersen et al. 2004, Raubani 2007, Rhyne et al. 2012, 2014, Schwerdtner Máñez et al. 2014). Chronic removal of reef fishes and live corals from shallower reef areas (adjacent to nautilus's preferred habitat) may decrease biodiversity and deprive less productive deeper habitats of food sources necessary to sustain opportunistic scavenging species such as chambered nautiluses.

[12] *See* Center for Biological Diversity, et al. Petition to Prevent the Import of Illegally Caught Tropical Fish into the United States and Require Testing and Certification (March 8, 2016).

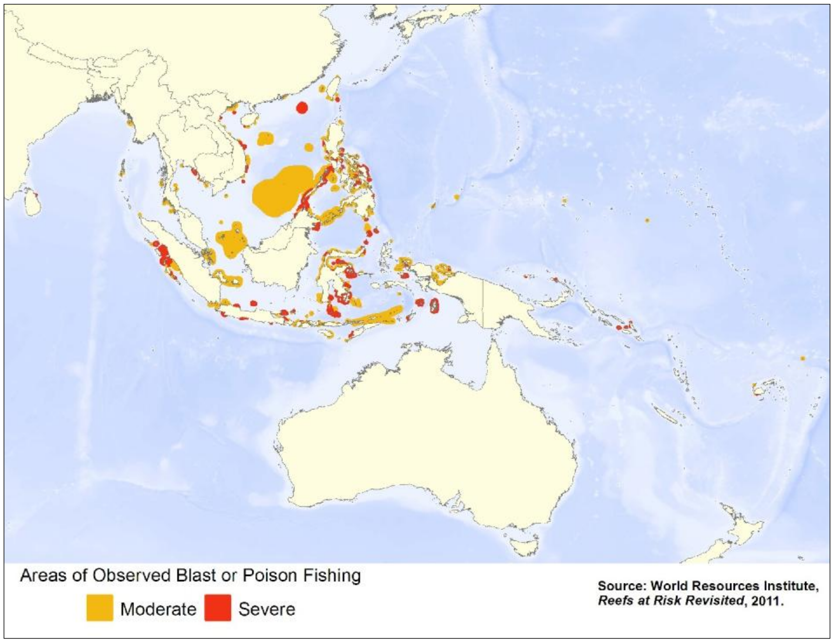


Figure 8. Areas of observed blast fishing and cyanide fishing coincided with the distributional range of chambered nautilus. Map from WRI (2011).

4.1.2. Pollution and Sedimentation

Pollution and sedimentation affect reef areas within the distribution range of the chambered nautilus and may directly affect their habitat and their physiology. In general, pollution and sedimentation compromise the health of reef communities by destroying habitat and decreasing biodiversity (Rogers 1990, Edinger et al. 1998, Fabricius 2005, Burke et al. 2006). Cephalopods are highly sensitive to pollution and can accumulate heavy metals (Danis et al. 2005, Seixas et al. 2005, Storelli et al. 2006, Dorneles et al. 2007, Pierce et al. 2010). Higher concentrations of pollutants may potentially bioaccumulate in longer lived species such as chambered nautiluses but more studies to address the impact of toxic chemicals have on population viability are needed (Bustamante et al. 2000, Pernice et al. 2009).

Large portions of the fore-reef off Australia, China, Fiji, New Caledonia, Solomon Islands, the Philippines, Vanuatu, Vietnam, and Western American Samoa are impacted by sedimentation and localized pollution, which could reach deeper reef slopes in areas where the platform is narrow (Raubani 2007, Ah-Leong and Sapatu 2009 p., Kere 2009 p. 200, Sykes and Morris 2009, Todd et al. 2010, Chen et al. 2010, Burke et al. 2011). Most wastewaters released to the oceans from these countries are untreated (Nellemann et al. 2008), but the potential direct effects on chambered nautiluses population have been unexplored.

Habitat destruction, sedimentation, and pollution from deep sea mining also occur within the chambered nautilus habitat and can directly affect the species. For example, waste products and mining tailings from some coastal areas in Australia and Papua New Guinea can directly flow or a released into the chambered nautilus habitat. [13] In addition, deep see mining leads to deep sea

[13] See Habitat Trend section in the Proposal: Inclusion of the Family Nautilidae (Blainville, 1825) in Appendix II in accordance with Article II paragraph 2 (a) of the Convention and satisfying Criterion B in Annex 2a of Resolution

habitat degradation and directly destroys the seabed communities that are highly sensitive to disturbances (Halfar and Fujita 2007, Rosenbaum and Grey 2015). Unfortunately, associated environmental impacts statements from some of the companies (e.g., Nautilus Minerals) that are involved in deep sea mining in Papua New Guinea have downplayed the high risk that local communities and the marine environment face due to these destructive activities (Dover 2011, Rosenbaum and Grey 2015).

4.2. Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

4.2.1. Overfishing

Chambered nautiluses are fished for the international shell trade and wholesale commerce (Aguiar 2000, Dunstan et al. 2011a, De Angelis 2012, Freitas and Krishnasamy 2016). The international demand has been met by targeted harvesting from commercial, subsistence, and artisanal fisheries that has occurred or is occurring throughout Indo-Pacific countries including India, Indonesia, New Caledonia, Papua New Guinea, the Philippines, and potentially in China, Palau, Thailand, and Vanuatu (Aguiar 2000, De Angelis 2012, NMFS 2014, Freitas and Krishnasamy 2016, LEMIS 2016).

Chambered nautiluses are highly vulnerable to light levels of overexploitation because of intrinsic biological traits (e.g., limited distribution, k-selected life history strategy, low fecundity, late maturity, long life span, and small populations) and extrinsic threats associated with targeted fishing, unregulated captures, destructive fishing practices, and bycatch related to deep sea reef fisheries (Dunstan et al. 2010, 2011a, Ward 2014, Barord et al. 2014). In fact, they face similar threats to other k-selected charismatic species targeted by fishing such as oceanic sharks and sea turtles.

Overfishing is the major threat to the continued survival of chambered nautiluses that can drive the extinction of small populations in significant portions of the range within the foreseeable future (Dunstan et al. 2010). Although *N. pompilius* is the most exploited and traded species within the family (De Angelis 2012, NMFS 2014, Freitas and Krishnasamy 2016), other chambered nautilus species are also at risk of overfishing in other locations such as, Papua New Guinea and Palau if shell demand and fisheries continue (Dunstan et al. 2010). Fishing is unsustainable in several significant portions of the chambered nautilus (*N. pompilius*) range and there is evidence that local extinction has already occurred. Overfishing is also among the main threats to the reef ecosystems within the chambered nautilus range (Lovell et al. 2002, Alcala and Russ 2002, Green et al. 2003, Cinner et al. 2006, Cinner and McClanahan 2006, Russ and Alcala 2010). In fact, in the coral triangle, which comprised several countries where chambered nautiluses occupy such as Indonesia, Malaysia, Papua New Guinea, the Philippines, and the Solomon Islands, over 90 percent of their natural reef resources are threatened by overfishing and unsustainable fishing practices (Coral Triangle Initiative 2016).

Overfishing of the chambered nautilus has occurred and is already occurring in several significant areas in Philippines and there is evidence that is happening in other significant

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http://www.fws.gov/international/cites/cop17/ussubmissions/chambered_nautilus_appendixII.pdf

portions of the species ranges including Indonesia. Small and large scales fisheries have been ongoing in Indonesia, the Philippines, and possibly in New Caledonia since the 1970s (Haven 1977, Alcala and Russ 2002, del Norte-Campos 2005). Sustainable fishing practices are not established in these regions and broad scale fishing restrictions or conservation plans are not in place. For example, exploitation of the species in areas of west central Philippines may have existed for decades (del Norte-Campos 2005). However, there is no cultural or historical fishing tradition for chambered nautiluses in the Philippines or in other regions and there is little or non-existent local demand (Dunstan et al. 2010). In some fishing communities, where chambered nautilus harvesting occurs, fishermen are commonly taught by traders how to trap chambered nautiluses and traders can even subsidize the fisheries by providing harvesters with transport and fishing gear (Dunstan et al. 2010, NMFS 2014). Without fisheries regulations and local management, local fisheries become non-viable just after 10-20 years because the abundance of chambered nautiluses drastically declines (Dunstan et al. 2010, 2011a, Barord et al. 2014).

Anecdotal evidence describing population declines due to overfishing and even local extinctions may have occurred in two traditional chambered nautilus fishing grounds within Philippines: Bohol Sea and Tañon Strait (Ward 1988, Alcala and Russ 2002, Barord et al. 2014). In fact, populations of the chambered nautilus in the Tañon Strait may have disappeared by 1987 (Ward 1988, Barord et al. 2014). Other regions of the Philippines such as Tawi Tawi, and Cayagancillo have shown populations crashes and fishing has become unprofitable (Dunstan et al. 2010). Informational data from a detailed interview questionnaire of traders and fishers on the chambered nautilus in Palawan, Philippines showed that up to 80% declines in catch per unit effort occurred in this region from 1980 to 2010 (Dunstan et al. 2010). Fishing pressure was extremely high during a short fishing season, reaching in average a total annual harvest of 12,200 individuals per year (6.6 metric tons per year of whole animals including shell) in a single area in the Philippines (del Norte-Campos 2005). However, lack of monitoring has prevented a comprehensive understanding on the effects of fishing on localized chambered nautilus populations (Barord et al. 2014). Nonetheless, based on our knowledge of life history strategies and information of other fisheries is likely that high fishing pressure will have devastating consequence for population viability since recovery is unlikely.

Commercial fisheries for chambered nautilus use baited fish traps made of bamboo or wire placed at depth from 60 to 250 m (Fig. 9), and baits consist of a wide variety of locally available meat such as chicken, stingray, eel, fish, shark, dog, monitor lizard, dolphin, triggerfish, pig, turtle, frog toad, and even snakes (del Norte-Campos 2005, Jereb and Roper 2005, Dunstan et al. 2010, Freitas and Krishnasamy 2016). The indirect impact of the fisheries in the local fauna is unknown but bait availability may drive fishing pressure (Dunstan et al. 2010). Life history traits such as late maturity (Saunders 1983, Dunstan et al. 2011b), long gestations (Arnold 2010), low fecundity (Arnold 2010) and long life span (Landman and Cochran 2010, Dunstan et al. 2011b) make nautiluses species particularly vulnerable to trap fisheries and overfishing. Although the species has relatively low abundance, individuals are easily attracted to baited traps due to their sense of smell, can be habituate to feeding sites, and thus can be efficiently captured by fishers (Basil et al. 2000, Dunstan et al. 2010, Crook and Basil 2013, Barord et al. 2014). Certain habits such as nocturnal vertical migrations can also facilitate capture. Chambered nautilus trap fisheries removed predominantly males, which is consistent with male-biased catch ratios obtained from scientific studies (Saunders and Spinosa 1978, Dunstan et al. 2010).

Figure 9. Chambered nautilus shells and bamboo traps used for fishing in Balabac, Philippines. *Photo credit: Jürgen Freund and WWF/TRAFFIC*

Baited trap fishing for chambered nautilus is fairly economical and cost effective since the product is non perishable. The only limiting factor in local trap fisheries seems to be depth and bait availability (Dunstan et al. 2010). Trap fishing is fairly inexpensive because traps and ropes can be reused from other fisheries or can be easily purchased locally (del Norte-Campos 2005, Dunstan et al. 2010). Similarly, boats that are already used for other fishing activities can be used for chambered nautilus fishing (del Norte-Campos 2005). In addition, baited traps are very effective because chambered nautiluses have a great chemoreception sensorial capabilities and can detect odors at very low concentration and thus long distances (Basil et al. 2000). As many as 60 nautiluses can be captured in a trap (1 m^3) deployed in a single night (Carlson 2010) which highlights their ability to detect odors over very long distances rather than reflecting local population abundances (Barord et al. 2014).

Chambered nautiluses are fished unsustainably in the Philippines, New Caledonia and in other Indo-Pacific areas, for the international shell trade (del Norte-Campos 2005, Dunstan et al. 2010, De Angelis 2012). Chambered nautilus fisheries seems to target mature individuals and are generally short in duration lasting approximately a decade or two before becoming commercially unprofitable or unviable (Dunstan et al. 2010). In fact, a small-scale fishery in Philippines has substantially reduced chambered nautilus abundance based on catch rates declines in less than 20 years (Dunstan et al. 2010). Fisheries declines in the Philippines have also been reported from specific areas such as Central Visayas (Green 2004), Northwestern Panary Island (del Norte-Campos 2005) and the species seems to have disappeared from Tañon Strait since the later 1980s (Alcala and Russ 2002). In some areas in the Philippines this fishery seems to be targeted and seasonal due to bait availability and weather conditions related to southwest monsoons (del

Norte-Campos 2005). Declines of fisheries yields over the past decades have been observed in New Caledonia (Saunders and Ward 2010). Chambered nautiluses can also be found in bycatch from other fisheries (Green 2004). Nautilus shells found in commercial trade may also derive from incidental collection of drift shells such as in Papua New Guinea (Saunders et al. 1991) and Fiji (Jereb and Roper 2005). Several commercial and recreational fisheries in Philippines associated with deep fore-reef habitat have also identified chambered nautilus individuals in bycatch (Alcala and Russ 2002).

Based on their life history traits, chambered nautiluses showed low resilience and high inability to withstand commercial fishing pressure (Jereb and Roper 2005, Boyle and Rodhouse 2008). As in other fish and invertebrate species with similar life history traits and that inhabited fore-reef slope such as Orange Roughy, large crabs, and deep water Eteline snappers, targeted fisheries can rapidly reduce their populations (Armstrong et al. 1998, Clark 2001, Williams et al. 2013, Barord et al. 2014). The long term effects of overfishing on chambered nautilus population and their ability to recover from fishing has not been studied through the entire range, but there is substantial evidence that fishing can wipe out entire populations in few decades or even few years (Dunstan et al. 2011a).

Nautilus fisheries tend to disproportionally remove more males than females due to the male to female ratio abundance (8:1) that is observed in unexploited populations. Although non-fished populations show a 8:1 male to female ratio (Dunstan et al. 2011a), fished populations in areas of Philippines shows a 1:1 male to female ratio which indicates that fishing selectively remove more males than female from the population (Barord et al. 2014). Since we have an incomplete understanding of the species behavior and reproduction in the wild, the impact that male removal have on the reproduction capacity of small populations is unknown. We know that their limited and geographically isolated distribution, limited dispersal abilities, poor population connectivity among regions and vulnerable life history trade suggest that even light levels of overfishing can lead to local extinctions (De Angelis 2012) and dramatic declines (Dunstan et al. 2010, Barord et al. 2014). The fact that some populations have been extirpated almost years ago (Ward 1988) and have not recovered, indicates that fishing is a serious threat that causes local extinctions of the species (Barord et al. 2014). Relatively isolated populations are inherently highly vulnerable to overexploitation and fishing may exponentially reduce new recruitment as subsequent immigration from external populations is very limited. Local extinctions due to fishing not only reduce metapopulation abundance but also reduce the genetic diversity that is unique in isolated populations.

4.2.2. International Trade

The distinctive pearly and coiled shells of chambered nautiluses are common in the international trade (De Angelis 2012, Freitas and Krishnasamy 2016). Whereas *N. pompilius* is the most common species reported in trade, all species of chambered nautilus are found in the international trade (De Angelis 2012, Freitas and Krishnasamy 2016). International trade for chambered nautilus shells is the main driver of the major threat for the species, overfishing (Freitas and Krishnasamy 2016). In general, there is no local demand of chambered nautilus species (Dunstan et al. 2010, De Angelis 2012, Freitas and Krishnasamy 2016). The international shell trade is a major indirect threat to the species similar to the threat that the international fin trade partially drives the unsustainable and irresponsible fishing for sharks.

The chambered nautilus and other nautilus species are traded internationally as live specimens or as dead animals via whole shells, part of shells, or exotic meat (del Norte-Campos 2005, Jereb and Roper 2005, De Angelis 2012, Freitas and Krishnasamy 2016). Live specimens are traded for the aquarium industry, for the pet trade, and by research institutions (Freitas and Krishnasamy 2016). In certain markets, collectors can pay higher prices (over $300 USD) for live animals or shells or rare chambered nautilus species (Freitas and Krishnasamy 2016) which can drive the demand for these rare species (Dunstan et al. 2010, NMFS 2014). Whole shells, worked and unworked shells are traded for curio products, jewelry, handicraft products, home décor items, and buttons for the clothing industry (Freitas and Krishnasamy 2016) (Fig. 10). Meat of chambered nautilus is traded in exotic food markets in Asia and may be eaten locally (del Norte-Campos 2005, Jereb and Roper 2005, De Angelis 2012) (Fig. 10).

The consumer markets for chambered nautilus products are spread across the entire world including North and South America, Eastern and Western Europe, Africa, the Middle East, Eastern and Southeast Asia, Australia, and Oceania (Fig. 11) (De Angelis 2012, Freitas and Krishnasamy 2016, LEMIS 2016). Thus, it is highly likely that demand for chambered nautilus products is high through the entire world (Freitas and Krishnasamy 2016). Quantitative trade data at global scale do not exit but trade information can be found from market survey reports, web advertisements, major online retailers (e.g., ebay, amazon, alibaba), personal communications, trade data obtained from the U.S. Fish and Wildlife Service Law Enforcement Management Information System (LEMIS 2016), and more recently from the comprehensive TRAFFIC/WWF report on the international trade of chambered nautiluses (Freitas and Krishnasamy 2016).

Figure 10. Chambered nautilus shells and shell products traded in the international commercial market. Photos posted in the online retailers eBay and Amazon.

The trade for chambered nautilus shell products is growing, and fishing for chambered nautilus to supply the international shell trade demand may be increasing. Although most reported chambered nautilus trade comes from fisheries in Philippines (del Norte-Campos 2005, Dunstan et al. 2010, De Angelis 2012, Freitas and Krishnasamy 2016, LEMIS 2016), over the past decades trade has increased from Indonesia (del Norte-Campos 2005, Saunders and Ward 2010, Dunstan et al. 2010, De Angelis 2012, 2012, Freitas and Krishnasamy 2016, LEMIS 2016). In addition, chambered nautilus shells are often collected for the ornamental and souvenir trade in Fiji, likely supplied by incidental collection (Carlson 2010).

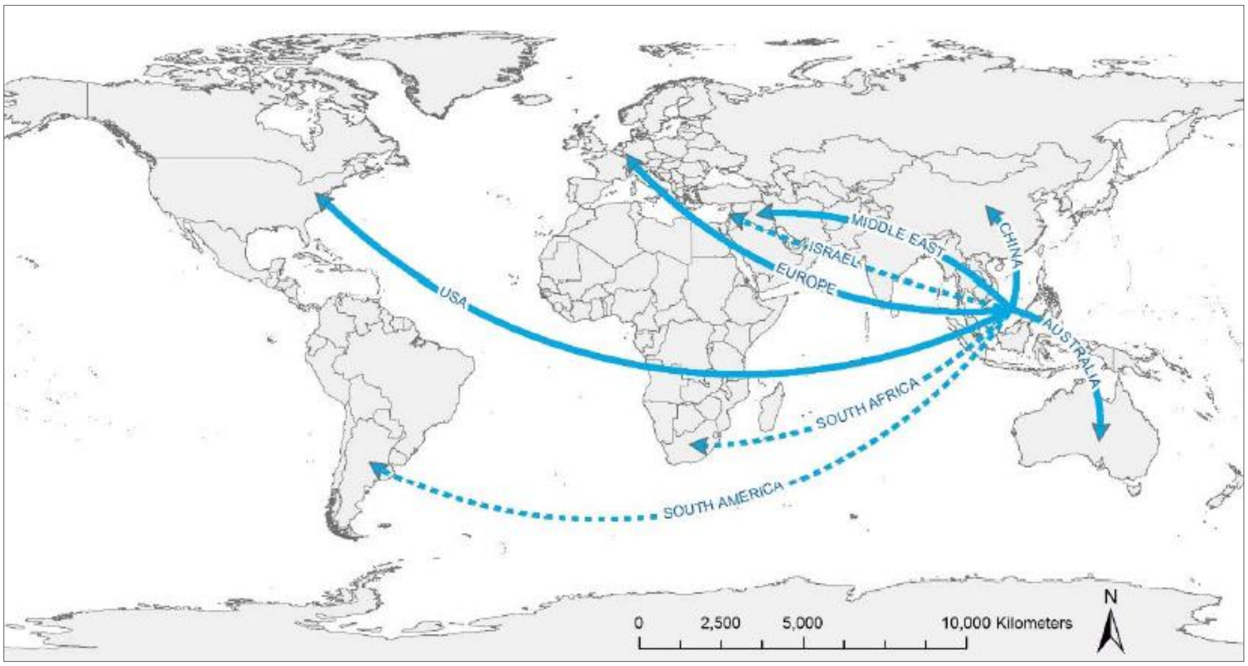

Figure 11. Major consumer destinations for chambered nautilus products coming from the Indo-Pacific. Dashed lines indicate regions where consumer markets are suspected because nautilus products have occasionally been observed for sale in local markets. Major known consumer markets include the U.S. and the E.U., with additional reported consumption of chambered nautilus products in China, Australia, and the Middle East. *Figure after Freitas and Krishnasamy (2016).*

Detailed information about the volume of harvest from these countries is very scarce or absent, but declines have been reported from fishermen and traders (del Norte-Campos 2005, Dunstan et al. 2010, De Angelis 2012, Freitas and Krishnasamy 2016). For example, a 12-month catches survey of Panay fishermen in 2001-2002 estimated a total annual harvest of about 6.6 metric tons (including whole animal) which is equivalent to 12,200 chambered nautiluses per year (del Norte-Campos 2005). As many as 25,000 specimens may have been exported from Indonesia to China between 2007 and 2010 based on personal accounts of scientists working on the region (see De Angelis 2012). In Palawan, Philippines alone, about 9,091 animals were fished in 2013 and up to 37,341 in 2014.[14] In fact, some exporters claimed that between 1000 and 1500 pieces are harvested from this region six times a year; and one exported even claimed that before 2005 more than 2000 pieces of nautilus commodities were exported to the U.S. up to four times a year (Freitas and Krishnasamy 2016). In recent years many exporters reported that such volumes have considerably declined due to abundance decline from fisherman (Freitas and Krishnasamy 2016).

The Philippines and Indonesia are among the Indo-Pacific countries where most of chambered nautilus products originate (De Angelis 2012, Freitas and Krishnasamy 2016, LEMIS 2016). Demand from local and international buyers is driving the ongoing development and decline of chambered nautilus fisheries in the Philippines (Dunstan et al. 2010). Although chambered nautilus fisheries represent an additional income to local fishers, locals do not have a history of nautilus fishing (Dunstan et al. 2010). Local trade for meat consumption or demand of shell products do not seem to be important and appears to be a market driven by outside demand (del Norte-Campos 2005, Dunstan et al. 2010). The fishery seems to have been introduced by fishers and traders after chambered nautilus fisheries from other locations had already crashed (Dunstan et al. 2010). A local questionnaire study from fishers in Palawan, Philippines showed that main international buyers include the United States, China, Hong Kong, Hawaii, Taiwan, Australia, and Europe (Dunstan et al. 2010). Trading information from Southeast Asia indicates that chambered nautilus consumer market for the Philippines includes North and South America, Eastern and Western Europe, Eastern and Southeast Asia, Africa, the Middle East, and Oceania (De Angelis 2012, Freitas and Krishnasamy 2016).

Trade of chambered nautilus products from Indonesia seems to be growing (Freitas and Krishnasamy 2016). Although most nautilus shell products originated from the eastern portion of Indonesia, the main trade, distribution, and export areas are in the western islands of the country (e.g., Java, Bali, Sulawesi, and Lombok) (Nijman et al. 2015, Freitas and Krishnasamy 2016). However, interviews with vendors and collectors across Indonesia suggest that the number of nautilus harvested in the country have declined over the last 10 years likely due to stock declines or increasing law enforcement (Freitas and Krishnasamy 2016).

Chambered nautilus products have been identified in China, Hong Kong, and Taiwan despite prohibitions on harvesting (Freitas and Krishnasamy 2016). For example, small numbers of whole shells were found in markets of southern China (e.g., Fujian, Guangdong, and Hainan) and even nautilus meat has been observed for sales in seafood markets of Guangzhou (Freitas and Krishnasamy 2016). In Hong Kong, a small trade of live specimens for aquaria exists but shells and products are rare in markets (Freitas and Krishnasamy 2016). In contrast, in Taiwan, nautilus products sold in markets seem to be relatively low and are mostly found in fishing ports and in tourist's souvenir shops and beaches. Some interviews with local traders suggest nautilus products comes from the Philippines (Freitas and Krishnasamy 2016).

Trade regulations of chambered nautilus products across Indo-Pacific countries are mostly absent and in those countries with limited regulation prosecution and data gathering is inadequate and

[14] See Commercial Harvest section in the Proposal: Inclusion of the Family Nautilidae (Blainville, 1825) in Appendix II in accordance with Article II paragraph 2 (a) of the Convention and satisfying Criterion B in Annex 2a of Resolution Conf. 9.24 (Rev. CoP16).
http://www.fws.gov/international/cites/cop17/ussubmissions/chambered_nautilus_appendixII.pdf

highly undereported (Freitas and Krishnasamy 2016). For example, from 2003 to 2004, Indonesia confiscated 22 individuals and ten shell products of chambered nautilus (Ministry of Forestry 2005) which grew by at least 213 shells in 2008 (Wisnu 2008). However, this is likely an underestimation of the actual trade. Within Indonesia, smuggling attempts of chambered nautilus shells are common and local authorities often disrupt attempts to sell chambered nautilus shells and other mollusks shells by local and non-locals at the Ngurah Rai International Airport (Wisnu 2008). In the U.S. alone about 4,488 shipments of nautilus products were reported by customs between January of 1999 to April of 2016 (LEMIS 2016).

4.2.2.1. Imports of chambered nautilus commodities into the United States

In the United States alone, import data of chambered nautilus products over the past 17 years highlights that the international trade is a global problem despite the absence of global trade data. These data were compiled from the U.S. wildlife custom declaration forms that are required for import or export of fish and wildlife (LEMIS 2016). The U.S. trade data recorded in the LEMIS 2016 database indicates that approximately 1,569,881 chambered nautilus commodities (i.e., whole shells, shell products, trims, live animals, etc) and 8,732 kilograms in shell parts were imported into the U.S. from at least 36 countries between January 1999 and April 2016 (LEMIS 2016) (Table 1). However, the bulk (~80%) of the trade has come from the Philippines where scientific evidence shows drastic declines in the chambered nautilus populations.

The Philippines, China, and Indonesia account for over 90% of total imports of chambered nautilus (*N. pompilius*) commodities into the U.S. Over the last 17 years, most shipments of chambered nautilus commodities have come from the Philippines (~83 %) and Indonesia (~6.4 %) with less than 10 % of shipments from Fiji (~1.7%), Japan (~1.4 %), India (~1.4%), and China (~1%). The number of chambered nautilus commodities imported into the U.S. has been strongly correlated with the number of shipments ($r = 0.997$, $p<0.00001$). As such, the greatest amount of chambered nautilus commodities over the last 17 years came from the Philippines (~79 %), China (5.9 %), Indonesia (~5.5 %), India (3.7 %), and Japan (3.5%) (Table 1). The rest of the countries imported less than one percent of the total trade. It is important to note that nautilus commodities imported from China are likely funneling through this country since the presence and fisheries practices of chambered nautilus in China are unconfirmed. Over 99 % of chambered nautilus commodities imported into the U.S. in the last 17 years consisted of shell products (47 %), jewelry (31 %), trims such as decorative shells (11 %), and whole shells (10%). Interestingly, the total combined imports of live specimens for aquarium and museums, or specimens for scientific purposes represented less than 0.06 % of the total commodities.

The total annual imports of chambered nautilus commodities into the U.S. have substantially declined over the last 17 years (Fig. 12, *note that y axes are in log scale*). This declining trend is more likely to represent a decline in supply than a lack of demand in the commercial market since international demand seems to be increasing (Freitas and Krishnasamy 2016). The average total number chambered nautilus commodities imported into the U.S. between 1999 and 2007 was ~133,550 items per year (Fig. 12). However, the average total annual imports from 2007 to 2015 have declined considerably reaching the lowest point in 2015 with ~9,868 imported commodities (Table 1, Fig. 12). This represents a decline of approximately 93 % of imported chambered nautilus commodities into the U.S. alone in comparison with the first half of the 2000s

Table 1 Summary of total number of chambered nautilus (*N. pompilius*) commodities imported to the United States between January 1999 and April 2016 from the top 12 exporting countries sorted by major exporters. Totals and percentage include values from countries not shown in this table with less than 0.1 % of imports. Values for chambered nautilus commodities that were reported as weight are not included in this table, but see Fig. 11 for general trend. Data was analyzed from LEMIS (2016) which is also attached with this petition.

Ctry	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**
PH	61,166	96,905	73,966	82,095	120,231	72,356	149,145	112,833	145,670	47,880
CN*	13,841		16	6,830	62,268	60	15	4,588	3,441	1,270
ID	1,083		676	518	116	531	12,316	29,558	16,378	5,462
IN	3,954	11,279	10,102	29,370	1,976				192	
JP	894			42,688	10,634	4	22	12	2	16
KR					8,000					
TW*	5			94	1,304			2,881		
FJ			2		4					
XX	4		2		2	50	3	13	2,032	902
TH		187		254	1	398	21	1	1,887	74
AU						288			2,287	
NZ								1,682		
Total	**81,597**	**108,988**	**84,880**	**162,324**	**204,590**	**73,874**	**161,534**	**151,647**	**172,520**	**55,801**

Table 1. Cont.

Ctry	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**Total**	**%**
PH	168,560	48,017	18,251	14,599	11,112	11,717	9,068	1,924	**1,245,495**	**79.34**
CN	34		54	67	180	1	0		**92,665**	**5.90**
ID	1,619	4,299	3,116	9,267	680	1,063	196	14	**86,892**	**5.53**
IN	1		3		1,627	2			**58,506**	**3.73**
JP	23	21	8	254	37	30	4	25	**54,674**	**3.48**
KR									**8,000**	**0.51**
TW									**4,284**	**0.27**
FJ			587	1,087	803	1,106	462	88	**4,139**	**0.26**
XX	3	40	3	2		110	84	2	**3,252**	**0.21**
TH	155	9	14	8	3	4	3		**3,019**	**0.19**
AU	2		1				12		**2,590**	**0.16**
NZ			5						**1,687**	**0.11**
Total	**170,529**	**52,421**	**22,252**	**25,966**	**14,623**	**14,366**	**9,868**	**2,101**	**1,569,881**	

Countries are, PH: Philippines, CN: China, ID: Indonesia , IN: India, JP: Japan, KR: South Korea, TW: Taiwan, FJ: Fiji, XX: Unknown, TH: Thailand, AU: Australia, NZ: New Zealand.
**China and Taiwan as native range of the chambered nautilus is uncertain. Thus it is possible that some international trade is being funneled through this county.*

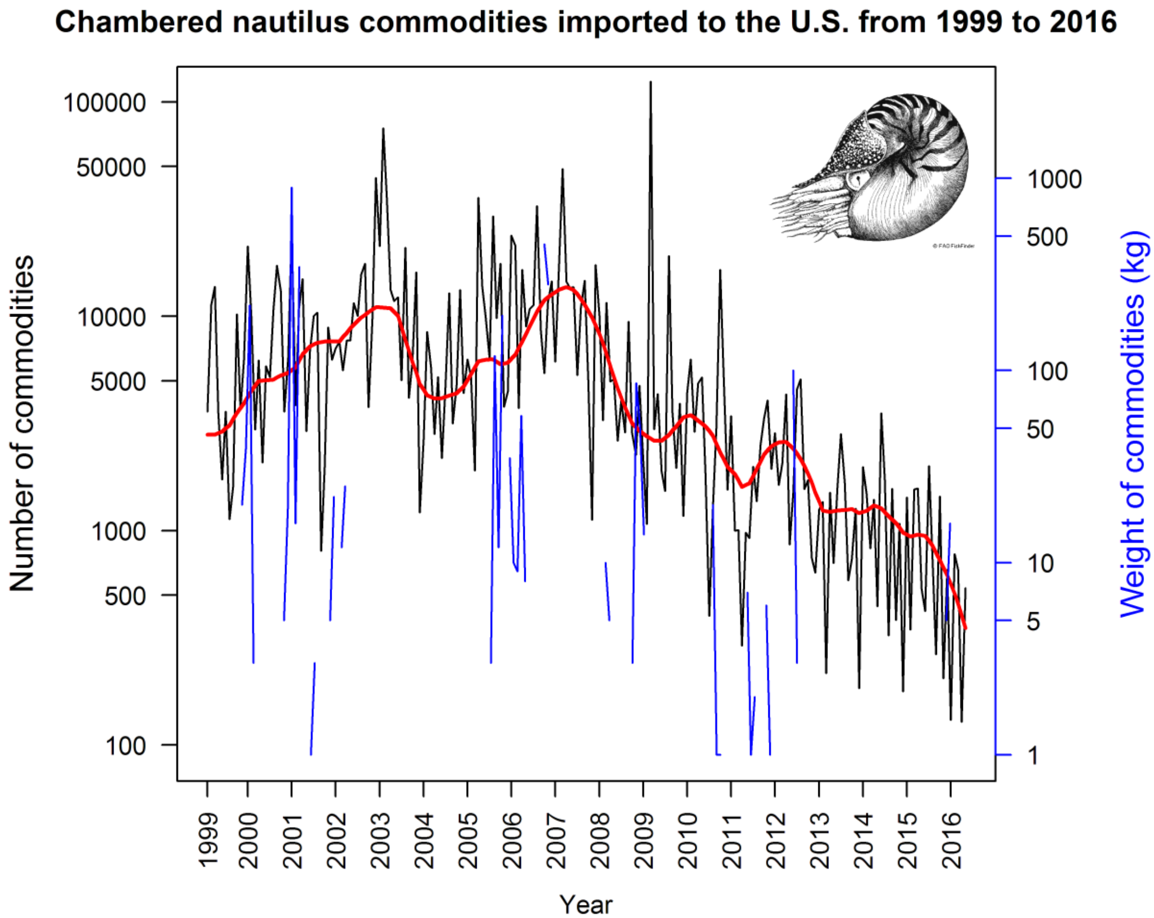

Figure 12. Temporal trend of number (left axis, black) and weight (right axes, blue) of chambered nautilus (*N. pompilius*) commodities per year imported into the United States from January 1999 to April of 2016 based on the U.S. Fish and Wildlife Service Law Enforcement Management Information System Data (LEMIS 2016). Commodities include whole shells, shells parts, ornaments, jewelry, trims, etc. Red line is a smoothing curve (lowess with span of 0.1) for a better visual representation of the trend. Note that the **y** axes are in log scale. Raw data and analysis code are attached with this petition. Analysis and graphing was performed in the statistical computing language R (R Core Team 2015).

The decline in chambered nautilus commodities imported into the United States may respond to either a decline of demand or most plausibly, a depletion of wild stocks in the Indo-Pacific region, especially in the Philippines. Based on the price increases of nautilus shell products over that last few years, demand may be increasing (Freitas and Krishnasamy 2016). Thus, a decline in supply due to a decline of chambered nautilus populations in the wild may be the most plausible explanation for decreasing imports. This analysis is based only on U.S. imports and likely underestimates international global trade numbers. For an in depth analysis of current international trade of chambered nautilus commodities refer to the recent published report by Freitas and Krishnasamy (2016).

Several factors suggest that U.S. import data of the chambered nautilus (*N. pompilius*) products likely underestimate the actual trade volumes of whole nautilus specimens into the country. Only

~20 percent of the imports were either whole shells or trim products from individuals shells (LEMIS 2016). The rest of the imported commodities were shell parts which makes it difficult to identify the correct nautilus species and determine the exact number of individual nautilus traded. Chambered nautilus commodities may be also categorized as shell products from other mollusk species, unidentified nautilus species, or erroneously categorized as other nautilus species (see LEMIS 2016 data). For example, ~6 % (in number) and 9% (in weight) of chambered nautilus commodities imported into the U.S. in the last 17 years were categorized as unidentified nautilus species (LEMIS 2016). Customs declarations of wildlife products rely upon the veracity of traders or consumers when passing through port of entry and misidentification is common (De Angelis 2012, Freitas and Krishnasamy 2016). Finally, determining the number of individuals from shell products based on weight is also complicated since shell sizes vary.

Worldwide growth in sales of whole shells, shell parts, jewelry, and ornaments derived from chambered nautilus shells may respond to worldwide demand, higher profits, and widespread and increasing online sales. Although shells are sold for a couple of dollars in some local stores in Indo-Pacific countries, prices are substantially higher outside the region and from online retailers (Freitas and Krishnasamy 2016). Sales of nautilus products are common in online retailers from Asia, Europe (France, Germany, and the UK), and North America (Freitas and Krishnasamy 2016). For example, on the online retailers such as eBay and Amazon, relatively small chambered nautilus shells are sold as earrings and pendants for $20-25 US dollars. Relatively large shells are sold for up to $5-60 US dollars, and are frequently polished and bisected to display the mesmerizing chambers. Large whole shells from rare chambered nautilus species can reach well over $300 US dollars. Jewelry made of the opalescent shells' inner surface can be sold as earrings for $80, bracelets for $225, and up to $490 for delicate necklaces. The iridescent shell are often worked and sold as "Osmeña pearls" or "rare nautilus pearl" for higher prices (Freitas and Krishnasamy 2016).

Nautilus shell commodities from online sales of U.S. based retailers (e.g., Ebay and Amazon) are currently shipped directly from Indo-Pacific countries including, China, India, Philippines, Indonesia, Malaysia, Solomon Islands, Thailand, and Vietnam. In the U.S. alone, more than 500 nautilus products (whole shells and shell parts) were for sale in a month (November to December) from over 40 different vendors in 2013 (Freitas and Krishnasamy 2016). In fact, a quick Ebay search on May of 2016 for nautilus products resulted in over 440 listing of nautilus shells and over 679 nautilus shell jewelry (pendant and necklaces) ready to be shipped mainly from Singapore and Indonesia. In addition, these retailers usually have supplies that often exceeds the amount available online at any moment, thus even online sales are likely to underestimate actual trade volumes (Freitas and Krishnasamy 2016).

International shell trade information is useful to partially understand the scope of nautilus harvesting in their geographic region and highlights the magnitude of the issue globally. Currently, the substantial harvesting and trade of *N. pompilius* in Philippines, the growing illegal harvest and trade in Indonesia, and trade from China over 90 % of all the nautilus commodities entering into the U.S. and may likely represent international patterns (De Angelis 2012, Freitas and Krishnasamy 2016, LEMIS 2016) (Table 1). Unfortunately, there is an absence of custom codes that makes almost impossible to precisely track international trade. Moreover, the lack of market measures to ensure the legality of the trade mask the actual volume of harvest that is occurring throughout the geographic range of the species (Freitas and Krishnasamy 2016).

The most concrete information about shell trade that can be linked directly to fisheries is the data of whole shell and live animals. Over the past 17 years, over 178,756 whole chambered nautilus specimens were imported into the U.S. alone (LEMIS 2016). Given that the U.S. is only one country in the international trade, it is very likely that hundreds of thousands of whole chambered nautilus and derived products are being trade annually without oversight across the globe (De Angelis 2012, Freitas and Krishnasamy 2016). The full extent of the impact of global trade on local chambered nautilus populations is difficult to determine, but it is clear that the volume of chambered nautilus shell products moving throughout the international trade is substantial and has likely pushed chambered nautilus population to local extinction and drastic declines.

4.2.3. Ecotourism

Some ecotourism operations in Palau use traps to deliberately catch chambered nautiluses to be used as trophy photographs during diving activities (NMFS 2014) (Fig. 13). Although most individuals are thought to be released into shallow waters after photographs are taken, this practice may increase predation risk of chambered nautilus as animals must swim to deeper waters during the day (NMFS 2014). In fact, scientific capture-release studies have shown that when chambered nautiluses are released during the day in shallow waters, predatory fish (e.g., triggerfish) quickly attack them as they descend to deeper and darker waters (Ward 1987, Saunders et al. 2010, NMFS 2014). As such, handling practices in scientific studies have changed and most scientists release chambered nautiluses in deeper waters to minimize predatory encounters (Dunstan et al. 2011c). In addition, captured chambered nautilus may quickly overheat in warmer shallow waters or out of the water, and after release they may experienced difficulty descending to deeper waters due to bubble formation (NMFS 2014). Thus, ecotourism through catch and release practices is likely to increase predation risk and promote physiological problems on chambered nautiluses that increase mortality rates.

Figure 13. Diver in Palau posing for a photograph with two Palau nautiluses, *N. belauensis*. Photo: Guido Floren.

4.3. Diseases or Predation

Natural predators of chambered nautiluses include teleost fishes, octopuses, and sharks (Saunders 1984, Ward 1987, Saunders et al. 1991, 2010, Saunders and Ward 2010, Yomogida and Wani 2013). Chambered nautiluses are highly vulnerable to predation by teleost fishes when unsheltered in shallow waters during the day (Saunders and Ward 2010, Saunders et al. 2010, Yomogida and Wani 2013). Nautiloids species are particularly vulnerable to predation in early ontogenetic stages (Yomogida and Wani 2013), which might be one of the reason that juveniles represent less than 10% of captured individuals during surveys in the wild through their geographical region (Saunders and Ward 2010, Dunstan et al. 2011a). Conversely, since intense harvesting targets relatively large individuals, fishing indirectly may increase predation risk in the population by leaving behind smaller and more vulnerable individuals. For example, a recent analysis found that fished areas from Bohol and New Caledonia had substantially higher number of shells with scars from predators than unexploited populations in Australia and Papua New Guinea (Ward 2014).

Predation substantially limits chambered nautilus movement within their preferred habitat. Chambered nautiluses have adapted to a cryptic life style associated with benthic structures probably as evolutionary response to predation. The most common response to predation attacks by fishes is retraction into their shells and closing their mantle with no defense or escape behavior (Saunders and Ward 2010, Saunders et al. 2010). Vertical migrations of the chambered nautilus (*N. pompilius*) may reflect predator avoidance behavior against teleost fishes during the day (Dunstan et al. 2011b, 2011c). In general, chambered nautiluses migrate to shallow waters (up to 100 m) at night and swim back down to deeper water at dawn (Saunders 1984, 1990, Dunstan et al. 2011c) which may indicate an adaptation to reduce predation risk in shallow waters during the day (Ward 1987, Saunders et al. 2010, Dunstan et al. 2011c). However, the frequency and extent of these vertical migrations may vary depending on food availability, habitat, and predator presence (Ward and Martin 1980, Ward et al. 1984, Dunstan et al. 2011c). In addition, chambered nautilus remain close to the substrate and avoid swimming in the open water column where they are more vulnerable to predation (Saunders 1984, 1990, Barord 2015). Vulnerability to predation combined with physiological depth limitation prevents geographical dispersion of the species through open oceans making isolated populations highly vulnerable to declines from fishing.

Chambered nautiluses, as in other shelled mollusks, grow their shells by accretion, thus unsuccessful predatory attacks and subsequent shell repair are preserved on their shells throughout ontogeny (Yomogida and Wani 2013). Based on the shapes and sizes of shell breakage and scars due to sublethal predation, predatory fishes seems to be among the most common natural threats, especially during juvenile stages (Ward 1987, Saunders et al. 1991, 2010, Yomogida and Wani 2013). Although the sizes of shell scars due to sublethal predation are relatively similar throughout their ontogeny, the numbers of scars is higher on smaller whorls. This indicates that a specific but unknown predatory fish is preferentially preying upon nautilus throughout their life particularly during early ontogeny stages and thus smaller individuals (Yomogida and Wani 2013).

Predation pressure is also variable across the geographical range. In addition, fishing pressure may disproportionally increase natural predation prevalence in juveniles by reducing the abundance of mature adults in a population (Ward et al. 2016). Octopus may be one of the main natural predators of chambered nautiluses in their preferable habitat during adult stages. For example, Saunders et al. (1991) found that over 50% of drift shells in Papua New Guinea showed bore holes, evidence of predation by octopus. In fact, around 2-8% of live-caught animals showed evidence of octopus drilling (Saunders et al. 1991). In contrast, predation evidence in Fiji reefs seems to be lower (Ward 1987). Importantly, predation scars and shell breaks tend to occur more common in fished than unfished sites (Ward et al. 2016). Thus, it is likely that chambered nautilus fishing alters predator/prey interactions in the deep sea because by reducing mature adults abundance, predation pressure indirectly increases in juveniles and subadult individuals (Ward et al. 2016).

4.4. Inadequacy of Existing Regulatory Mechanisms

4.4.1. Domestic Protections

Chambered nautiluses lack adequate regulatory protection across their range and the limited exiting protections are inadequately enforced. For example, in the Philippines, chambered nautiluses are protected under the Fisheries Administrative Order No. 168 Rules and regulations governing the gathering, culture and exploration of shelled mollusk that loosely prohibits the collection of mollusk without permits (Floren 2003). However, these restrictions seems to be poorly enforced (De Angelis 2012, Freitas and Krishnasamy 2016) and recent declines in regions within Philippines have not triggered any meaningful conservation actions. There are also no known fishery management plans for chambered nautiluses across the range. Thus in the Philippines, nautilus fisheries remain unregulated without controls in harvest or trade (Freitas and Krishnasamy 2016). In fact, the recent TRAFFIC/WWF report shows that more than half of 162 shops and markets visited by investigators in the Philippines had nautilus products for sale targeted towards tourists and potential traders (Freitas and Krishnasamy 2016). During that investigation, which last for only a year, over 18,500 nautilus pieces of whole nautilus shells (natural or processed) were counted through markets in the Philippines, especially in Luzon, and Western and Central Visayas (Freitas and Krishnasamy 2016).

Similarly, Indonesia has prohibited the harvest and sale of chambered nautiluses since 1990 through the Act of the Republic of Indonesia No. 5 concerning the Conservation of Living Resources and their Ecosystems (Undang-undang Republik Indonesia No 5 tahun 1990). However, trade in Indonesia is not controlled or even monitored with enforcement mostly lacking and products are widely available for sale domestically and for the international market (Nijman et al. 2015, Freitas and Krishnasamy 2016). For example, nautilus products were found in five of the seven provinces surveyed in Indonesia during the TRAFFIC/WWF's investigation between March 2013 to March 2014, and over 30 shops, markets, stalls, warehouses, and individual traders had nautilus commodities for trade (Freitas and Krishnasamy 2016). Based on this study, most shops selling nautilus shell commodities were located in areas that target local and foreign tourists, often unaware of the illegality of the trade, who buy these products to import them to their home countries (Freitas and Krishnasamy 2016).

Despite the general lack of law enforcement on the trade and selling of chambered nautilus products, confiscations may occur at Indonesian ports. Over 3,000 chambered nautilus (*N. pompilius*) shells were seized from 2008 to 2013 by Indonesian port authorities with a value of

$60,000 USD (Nijman et al. 2015). About two-thirds of this trade was destined to the international commercial markets which include mostly the United States and the Asia-Pacific countries (Nijman et al. 2015). It is possible that due to these limited actions in Indonesia, the shell trade may have shifted from street shops and markets openly displaying nautilus products to online sales that are more difficult to track and regulate (Freitas and Krishnasamy 2016). In addition, the sale of entire and recognizable nautilus shells may have declined while shell products such as jewelry and shell parts incorporated into furniture and handicraft items may be increasing (Freitas and Krishnasamy 2016).

Further, China protects chambered nautiluses and prohibits harvest; yet enforcement is also believed to be problematic or absent (Freitas and Krishnasamy 2016) because large shipments of nautilus commodities have reached U.S. ports in the last 17 years (LEMIS 2016).

The current deficiency of data on the species' biology and lack of understanding of their response to fishery pressure have likely inhibited the development of appropriate regional and local legislative mechanisms to protect the species from overexploitation and decline. Current U.S. trade data suggest that whole shell, part shells, and jewelry trade from Indonesia and Philippines is ongoing and unregulated (LEMIS 2016).

The absence of migration among chambered nautiluses population of Philippines, Western Australia/Indian Ocean, and Eastern Australia/Pacific Ocean underscores the need for conservation strategies that protect these populations as discrete conservations units (Williams et al. 2015). Specifically, adequate protection for the Philippines's chambered nautilus is imperative for the future existence of the species in this region as fishing continues to deplete the population and most trade products are coming from this country (see above). Strong evidence suggests lack of migration towards or from this region, indicating that repopulation is unlikely to recover if ongoing overfishing leads to population extinction (Williams et al. 2015). Fishing for chambered nautilus can drastically increase as fin fish stocks decline in heavily fished areas across Indo-Pacific countries. Thus comprehensive and enforceable regulations are urgently needed to protect the species.

4.4.2. International Union for the Conservation of Nature Red List Criteria

Chambered nautiluses are not listed under any red list criteria from the International Union for the Conservation of Nature (IUCN). The IUCN has not yet assessed the status of chambered nautilus. However, Dunstan et al. (2010) found "strong evidence that if the IUCN criteria were applied to information for *N. pompilius* off the Philippines . . . it would be placed in the endangered category." Additionally, the authors noted that IUCN guidelines allow for extrapolation based on analogous populations, and the "international demand for Nautilus shells, the ease with which local Indo-Pacific communities have adopted unsustainable fishing practices…, and the ecology and life history of the animal provide strong arguments towards IUCN globally endangered Red List categorization" (Dunstan et al. 2010). The lack of information on population estimates and trends have precluded a comprehensive evaluation of population status. Thus, estimates of the species' population size and density across its distribution range are urgently needed to determine population status to inform local managers.

4.4.3. Convention on the International Trade of Endangered Species (CITES)

Despite the apparent high risk of extinction that the species faces due to overfishing and commercial trade, chambered nautiluses are not currently listed under any of the CITES appendices. Protection of all species of chambered nautiluses (within the genera *Nautilus* and *Allonautilus*) under CITES will benefit the conservation of the species by regulating the ongoing chambered nautilus trade and will substantially decrease the incentive for ongoing exploitation, especially in the Philippines, Indonesia and other Indo-Pacific countries. All species of chambered nautilus qualify for Appendix II of CITES because they are vulnerable to overharvest and threatened by the international shell trade, significant commercial fishing in some areas, habitat degradation, and overfishing in other reef fisheries across their range.[15]

In preparation for the seventeenth Conference of the Parties (CoP17) the U.S., Fiji, India, and Palau, submitted a proposal to include the family Nautilidae under CITES Appendix II.[16] We are very grateful to the United States for co-sponsoring this proposal and for NMFS and the Fish and Wildlife Service's commitment of staff, time, and resources in assisting in developing and supporting the proposals at the upcoming CoP. We strongly support the listing of all Nautilidae species on Appendix II, as such a listing is both warranted and necessary. Each Nautilidae species clearly meets the CITES Appendix II standard, because it can be inferred that regulation of trade in each species is required to ensure that the harvest of specimens from the wild is not reducing wild populations to a level at which survival might be threatened by continued harvesting or other influences.[17]

We are hopeful the Appendix II proposal will be adopted by the Parties at CoP17. However, if the Appendix II listing is rejected, there will be no applicable international regulatory mechanisms to protect nautilus and thus international regulation must be deemed inadequate under the ESA. In contrast, if the CITES Appendix II proposal is adopted, international, commercial trade may only continue if it is not detrimental to the species' survival. While we firmly hope these CITES controls will help reduce unsustainable trade, the ongoing trade from the Philippines, Indonesia and China – despite domestic prohibitions – suggests that an illegal market already exists. Thus, additional ESA restrictions on trade, including a potential ban, will ensure trade is tightly regulated. Further, CITES regulations only require the exporting nation to make a non-detriment finding, and ESA listing would provide the U.S. the authority to review and substantiate those findings. Finally, while CITES restrictions would regulate the import of chambered nautilus in the U.S., without ESA protections, interstate sale (including from American Samoa) would continue unregulated. Thus, even if Nautilidae are included on CITES Appendix II at CoP17, regulatory mechanisms will likely remain inadequate to ensure the chambered nautilus's survival.

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[15] Proposal: Inclusion of the Family Nautilidae (Blainville, 1825) in Appendix II in accordance with Article II paragraph 2 (a) of the Convention and satisfying Criterion B in Annex 2a of Resolution Conf. 9.24 (Rev. CoP16). http://www.fws.gov/international/cites/cop17/ussubmissions/chambered_nautilus_appendixII.pdf

[16] Proposal: Inclusion of the Family Nautilidae (Blainville, 1825) in Appendix II in accordance with Article II paragraph 2 (a) of the Convention and satisfying Criterion B in Annex 2a of Resolution Conf. 9.24 (Rev. CoP16). http://www.fws.gov/international/cites/cop17/ussubmissions/chambered_nautilus_appendixII.pdf

[17] Res. Conf. 9.24. Annex 2a.

4.4.4. Potential Conservation Strategies

Natural isolated refugia and aquaculture could facilitate the conservation of chambered nautilus populations across the geographical range. Unfished isolated populations throughout the geographical range can be by de facto refugia for the species. But most of these isolated populations have not been monitored and population abundance and trends are unknown. In addition, small isolated populations may suffer from genetic drifts and could go extinct with drastic changes in environmental conditions (see below). Alternatively, aquaculture can potentially relieve wild populations from fishing pressure from commercial harvesting. However, captive breeding have been mostly unsuccessful as offspring do not survive to reproductive age and thus it is not a viable option to restore depleted populations (see above). In addition, within aquaria conditions, new produced shell is deformed or irregular, with black lines due to excess of minerals such as copper and zinc, which might reflect stress to new environmental conditions (Moini et al. 2014). Thus currently, aquaculture is an unlikely solution to protect the species.

Fishery and trade bans of chambered nautiluses or at least substantial reductions in fishing and trade are perhaps the best approach to prevent local and regional extinction of the species. Limiting fishing efforts to sustainable levels will drastically reduce catch rates. Ultimately, trade bans of chambered nautilus products will be highly necessary to lower demand and reduce or stop fishery pressure throughout the native region (NMFS 2014). Trade bans will be more effective in countries where chambered nautiluses inhabit and are heavily fished. However it is unknown how fast chambered nautilus population can rebound.

Programs that promote incentive payment initiatives and allow funding for education and secure livelihood independently of chambered nautilus fisheries could be an alternative strategy to reduce or even eliminate the shell trade. Such programs have worked before for other species such as sea turtles (Ferraro and Gjertsen 2009). Chambered nautilus fisheries is a low-investment additional source of income and local profits are not substantial (del Norte-Campos 2005, Dunstan et al. 2010), thus this issue has concrete solutions.

Finally, stock assessments and reporting of harvesting species should be conducted to determine the status of exploited populations and the level of impact that overharvesting is having or have had in localized chambered nautilus populations. Ideally, catch documentation that can trace the origin of nautilus products should be adopted and regulated in those countries where harvesting occur (e.g., the Philippines and Indonesia) to verify whether nautilus products are legally trade. Similarly, custom codes must be standardized to adequately trace, record, and monitor the fate of nautilus products that leave the country of origin and enter the international market (Freitas and Krishnasamy 2016). However, adequate amount of resource and enforcement is crucial for these programs to effectively work and ultimately is up to the country governments to facilitate nautilus conservation through regulations and raising awareness among traders about conservation concerns (Freitas and Krishnasamy 2016).

4.4.5. Inadequacy of greenhouse gas controls

International initiatives are currently inadequate to effectively address climate change threats such as warming and ocean acidification that may affect chambered nautilus species. The United Nations Framework Convention on Climate Change (UNFCCC), negotiated in 1992, provides the forum for international climate change negotiations. In the Framework Convention, signed and ratified by the United States, the world agreed to take the actions necessary to "prevent dangerous anthropogenic interference with the climate system." Parties to the Convention also agreed as a matter of fairness that the world's rich, developed countries, having caused the vast majority of emissions responsible for the problem, would take the lead in solving it.

The Kyoto Protocol was the first concrete, legally binding agreement for reducing emissions which required the world's richest countries to reduce emissions an average of 5 percent below 1990 levels by 2012, while asking developing nations to take steps to reduce emissions without being subject to binding emissions targets as they continue to raise their standard of living. The United States was the only industrialized country in the world that did not ratify the Kyoto Protocol. However, carbon emissions continued to steadily increase.

The 2009 UNFCCC conference in Copenhagen called on countries to hold the increase in global temperature below 2 °C, which is a level of warming which will still cause extreme disruption and danger to both human communities and natural ecosystems (Hansen et al. 2015, Tschakert 2015, UNFCCC 2015). However, the non-binding "Copenhagen Accord" that emerged from the Copenhagen conference and the subsequent "Cancún Accords" of 2010 and "Durban Platform" of 2011 failed to enact binding emissions reductions to reach the 2 °C goal.[18]

Currently, there is a legally binding global climate agreement that was discussed at the Paris Climate Conference in December 2015 and that was recently ratified by over 190 countries including the United States and that is due to enter in full effect by 2010. The agreement sets out a global action plan to reduce carbon emissions and avoid dangerous climate change by limiting global warming well below 2 degrees Celsius. Although these countries announced their proposed emission reduction targets, called "intended nationally determined contributions" or INDCs, such pledges are still inadequate to reach the 2 °C target, and are likely to lead to a global temperature rise of 3.1 °C[19]. The U.S. INDC would cut greenhouse pollution economy-wide by 26-28 % below 2005 emissions levels by 2025, which equates to reductions of just 14 to 16 % below 1990 levels by 2025. As discussed above, developed countries must reduce their economy-wide emissions by an average of 42 to 68 % below 1990 levels by 2030 with the range of reductions depending on the equity and sharing principles, for a likely probability of limiting warming to 2 °C (Climate Action Tracker 2014). Thus, U.S. efforts to reduce greenhouse gas emissions in the international sphere must also be considered inadequate.

4.5. Other Natural or Manmade Factors, Affecting its Continued Existence

[18] The non-legally binding Copenhagen Accord of 2009 and Cancún Accords of 2010 recognize the objective of limiting warming to 2°C above pre-industrial temperatures, but do not enact binding regulations to achieve this goal (http://cancun.unfccc.int/cancun-agreements/main-objectives-of-the-agreements/#c33; *unfccc.int/resource/docs/2009/cop15/eng/11a01.pdf). According to the Durban Platform, developed and developing nations agreed to a process to develop a* "new protocol, another legal instrument, or agreed outcome with legal force that will be applicable to all Parties to the UN climate convention"; this legal instrument must be developed as of 2015 and will not take effect until 2020 (*unfccc.int/resource/docs/2011/cop17/eng/l10.pdf).*

[19] Climate Action Tracker, 2016, http://climateactiontracker.org/. Climate Action Tracker is a joint project of Climate Analytics, Ecofys, Potsdam Institute for Climate Impact Research, and the New Climate Institute.

4.5.1. Small Population Size

Small population size is also a major threat that can increase the risk of localized species extinction. As explained throughout this letter, chambered nautilus populations seem to be generally small, dispersedly distributed across their range, and reproductively-isolated in geographically-separated populations (Sinclair et al. 2011, Dunstan et al. 2011a, Barord et al. 2014, Williams et al. 2015). Extinction risk is generally amplified if species occupy a small geographic range with low population abundance (Purvis et al. 2000, Hutchings and Reynolds 2004). Intense harvesting in some areas (e.g., Bohol Sea and Tañon Strait, Philippines) has already caused localized population extinctions (Ward 1988, Alcala and Russ 2002, Barord et al. 2014) and populations in other areas may follow the same trend (Dunstan et al. 2010, 2011a). As with other species that are adapted to stable deep sea environments, small and isolated populations of chambered nautilus can be highly vulnerable to drastic changes associated with fishing (decline in abundance or demographic shifts), habitat degradation, environmental fluctuations, and reduce reproductive capacity (Koslow et al. 2000, Roberts 2002, Morato et al. 2006, Hughes et al. 2015). Due to the reproductive isolation among geographically separated populations and the probability that these are genetically distinct and unique populations, the loss of any population throughout the geographical range could result in the loss of species diversity and even of potential subspecies.[20]

4.5.2. Climate Change and Ocean Acidification

Ocean warming and acidification in tropical Indo-Pacific region will affect the deep habitat of chambered nautilus and are threats to the species (NMFS 2014). Chambered nautiluses may be threatened by ocean warming and acidification which can have direct negative effects on distribution, foraging, growth and reproduction. Chambered nautilus depth distribution is limited to waters colder than 25 ºC (Carlson 2010). Global warming in tropical and subtropical waters has deepened the thermocline in the Indo-Pacific region (Vecchi and Soden 2007, Tokinaga et al. 2012) which may squeeze the vertical migration of deep water animal species such as chambered nautilus to narrow swabs of available habitat. Therefore warming could constrain foraging grounds for chambered nautiluses as shallower waters with greater food availability and diversity become too warm for the species.

Ocean acidification results in lower pH of seawater leading to corrosive conditions that directly affects species that produce calcium carbonate shells (Ries et al. 2009, Doney et al. 2009). Given that chambered nautiluses rely on calcium carbonate (specifically aragonite) uptake, storage, and deposition for growing (Cochran et al. 1981, Saunders 1983, Landman and Cochran 2010) they could be particularly vulnerable to sea water chemistry conditions that are unfavorable to calcification. As oceans continue to warm and pH of seawater continues to decrease (as more carbon dioxide is absorbed into the oceans), nautiluses' shell, especially juveniles', may be more susceptible to dissolution. Ocean acidification and warmer temperatures affect calcification

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during the early development of other cephalopods such as cuttlefish (Gutowska et al. 2010, Dorey et al. 2012). Ocean acidification in deeper and colder waters is predicted to substantially affect calcium carbonate shell deposition, and shelled species will likely decrease in growth rates and produce thinner and weaker shells that are more vulnerable to predation throughout the entire ontogeny (Feely et al. 2008, 2009, Doney et al. 2009, Gazeau et al. 2013). In addition, acidic waters may disrupt the ability of nautiluses to detect prey by chemoreceptor and avoid predators as observed in fishes (Simpson et al. 2011, Chung et al. 2014, Munday et al. 2014, Barner et al. 2015, Pistevos et al. 2015). Ocean acidification and warming can also increase the uptake of heavy metals in early life stages of cephalopods as observed in cuttlefish and squid (Lacoue-Labarthe et al. 2009, 2011, Kaplan et al. 2013).

5. Conclusions

Populations of the chambered nautilus, *N. pompilius*, have been extirpated or have drastically declined in significant portions of their geographical as a result of overexploitation to fuel the international shell trade market. The best scientific and commercial information that strongly supports the need to protect the species have become available in the last five years (Dunstan et al. 2010, 2011a, Bonacum et al. 2011, Williams et al. 2012, 2015, De Angelis 2012, Barord et al. 2014, Freitas and Krishnasamy 2016). Overexploitation of chambered nautiluses to fuel the commercial shell trade is the most important and current extinction threat that the species faces. In addition, a combination of extrinsic and intrinsic factors such as habitat degradation, climate change, vulnerable life history strategy, and geographic isolated small populations make the species highly vulnerable to local extinction.

Listing the chambered nautilus as threatened or endangered under the ESA could result in a permanent ban or restrictions on the import and sale of chambered nautiluses commodities into the U.S.. The decline of the species abundance in fisheries of the Philippines and indirectly in imports to the U.S. over the past decades may be a proxy of population decline in the wild. The evaluation of the species for consideration under the ESA must analyze current genetic studies which finely characterize populations throughout the current distribution. This is important to determine adequate management strategies for declining populations. Listing the species under the ESA would also support the evaluation of chambered nautiluses under CITES and red listing under the IUCN. The ESA listing of the chambered nautilus will create more awareness for the need to protect the species by local governments and environmental groups in Indo-Pacific countries where the species occur. This petition offers substantial information indicating that threatened or endangered species listing for the chambered nautilus (*N. pompilius*) may be warranted. The chambered nautilus urgently needs the legal protections to prevent the extinction of one of the oceans most enigmatic and iconic species.

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