

ENDANGERED SPECIES ACT STATUS REVIEW REPORT:

Chambered Nautilus

(Nautilus pompilius)



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DISCLAIMER

This document does not represent a decision by the National Marine Fisheries Service (NMFS) on whether this species should be proposed for listing as threatened or endangered under the Endangered Species Act of 1973 (ESA).

EXECUTIVE SUMMARY

This report was produced in response to a petition received from Center for Biological Diversity on May 31, 2016, to list the chambered nautilus (*Nautilus pompilius*) as endangered or threatened under the Endangered Species Act (ESA). On August 26, 2016, the National Marine Fisheries Service (NMFS) announced in the *Federal Register* that the petition presented substantial information in support, such that a status review for the species should be conducted (81 FR 58895). This report is the status review for the chambered nautilus. This report summarizes the best available data and information on the species and presents an evaluation of its status and extinction risk.

The chambered nautilus, *Nautilus pompilius*, is found in tropical, coastal reef, deep-water habitats of the Indo-Pacific. Within its range, the chambered nautilus has a patchy distribution and is unpredictable in its area of occupancy. The species is considered to be an extreme habitat specialist, physiologically limited by both temperature and depth. It is found in association with steep-sloped forereefs and cannot tolerate temperatures above approximately 25 °C or depths exceeding around 750-800 meters (m).

The global abundance of *N. pompilius* is unknown, with no available historical baseline population data. The species likely exists as small, isolated populations distributed throughout its range. However, abundance estimates of these fragmented populations are largely unavailable as the species is difficult to survey. Currently, population size has been estimated for *N. pompilius* off Osprey Reef in Australia using baited trap techniques (n = 844 to 4,467 individuals) and population density estimates (individuals / km²) are also available from Osprey Reef (13.6 to 77.4), the Great Barrier Reef (0.34), American Samoa (0.16), Fiji (0.21) and the Panglao region, Philippines (0.03).

The most significant threat to the chambered nautilus is overutilization through commercial harvest to meet the demand for the international nautilus shell trade. Chambered nautilus are targeted for their shells, which have a distinctive coiled interior, and are traded as souvenirs to tourists and shell collectors and also used in jewelry and home décor items (where either the whole shell is sold as a decorative object or parts are used to create shell-inlay designs). Based on the available trade data from the United States, and data garnered from seizures and research, it is clear that nautilus commodities are in high demand and nautilus products are globally traded likely in the hundreds of thousands.

Of the 10 nations where *N. pompilius* is known to occur, potentially half historically or currently have targeted nautilus fisheries. These waters comprise roughly three-quarters of the species' known range, with only the most eastern portion (e.g., eastern Australia, American Samoa, Fiji) afforded protection from harvest. The estimated levels of harvest

from many of these nautilus fisheries have historically led to extirpations of local *N. pompilius* populations. In fact, declines of 70 to 97 percent in the catch-per-unit (CPUE) have been estimated for populations from the Philippines and Indonesia, with observations of the serial depletion of populations based on anecdotal trapping reports and evidence of potential overfishing of the species in Indian waters. Commercial harvest of the species is also thought to occur in Papua New Guinea, East Asia, Thailand, Vanuatu, and Vietnam. Efforts to address overutilization of the species through regulatory measures appear inadequate, with evidence of targeted fishing of and trade in the species, particularly in Indonesia, Philippines, and China, despite prohibitions.

The continued harvesting of the species for the international nautilus shell trade and the subsequent serial depletion of populations throughout its range are placing the species on a trajectory to be at a high risk of extinction within the next couple of decades. The species' current demographic risks, including small and isolated populations, low productivity, habitat specificity, and physiological limitations that restrict large-scale migrations, means that as populations are depleted and extirpated, recovery and/or repopulation is unlikely. Many of the observed populations of the species are already on this path, with data indicating significant declines in abundance and even local extinctions. As the unsustainable harvesting of nautilus continues, with fisheries that follow a boom-bust cycle, and fishing efforts that serially exploit populations and then move on to new sites as the populations become depleted (particularly evident in the Philippines and Indonesia), this trend is unlikely to reverse in the foreseeable future. In fact, despite current domestic prohibitions on the harvest and trade of the species throughout most of the species' range (and particularly in the large exporting range states), these regulatory measures are largely ignored or circumvented through illegal trade networks. As such, although the species was recently listed on CITES Appendix II, the effect of this listing in terms of decreasing the threat of overutilization to the species through the foreseeable future cannot be determined at this time. Therefore, based on the best available information, we find that *N. pompilius* is at a moderate risk of extinction. Without adequate measures controlling the overutilization of the species, *N. pompilius* is on a trajectory where its overall abundance will likely see significant declines to the point where the species will be at a high risk of extinction throughout its range in the foreseeable future.

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INTRODUCTION

Scope and Intent

This document is the status review in response to a petition¹ to list the chambered nautilus under the Endangered Species Act (ESA). Under the ESA, if a petition is found to present substantial scientific or commercial information that the petitioned action may be warranted, a status review shall be promptly commenced (16 U.S.C. 1533(b)(3)(A)). National Marine Fisheries Service (NMFS) determined that the petition presented substantial information in support, such that a status review for the species should be conducted (81 FR 58895, August 26, 2016).

This document is the scientific review of the biology, population status, and future outlook for the chambered nautilus. It provides a summary of the available data and information on the species. In 2016, the United States, along with Fiji, India, and Palau, submitted a proposal for consideration at the 17th meeting of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Conference of the Parties to include all species of nautilus in Appendix II of CITES. This proposal was comprehensive in its portrayal of the species' biology and ecology as well as its discussion of potential threats to the species. We, therefore, cite extensively to this proposal throughout this status review (through directly quoted excerpts from the proposal, identified as "*Excerpt from CITES (2016)*") and provide updates based on new or missing information we have found since submission of this proposal. Based on this information, we present an evaluation of the species' status and extinction risk. The conclusions in this status review are subject to revision should important new information arise in the future. Where available, there are literature citations to review articles that provide even more extensive citations for each topic. Public comments, data and information were reviewed through July 2017.

¹ (1) Center for Biological Diversity to U.S. Secretary of Commerce, acting through the National Oceanic and Atmospheric Administration and the National Marine Fisheries Service, May 31, 2016, "A petition to list chambered nautilus (*Nautilus pompilius*) as endangered or threatened species under the Endangered Species Act."

LIFE HISTORY AND ECOLOGY

Taxonomy and Distinctive Characteristics

Nautilus taxonomy is controversial. Based on the Integrated Taxonomic Information System (ITIS), which has a disclaimer that states it “is based on the latest scientific consensus available . . . [but] is not a legal authority for statutory or regulatory purposes,” there are presently two genera within the family of Nautilidae: *Allonautilus* and *Nautilus*. The genus *Allonautilus* has two recognized species: *A. perforatus* and *A. scrobiculatus*. The genus *Nautilus* has five recognized species: *N. belauensis* (Saunders, 1981), *N. macromphalus* (Sowerby, 1849), *N. pompilius* (Linnaeus, 1758), *N. repertus* (Iredale, 1944), and *N. stenomphalus* (Sowerby, 1849). However, a review and analysis of recent genetic and morphological data suggests that perhaps only two of these five species are valid: *N. pompilius* and *N. macromphalus*, with the other three species more parsimoniously placed within *N. pompilius* (Vandepas et al. 2016; Ward et al. 2016). Similarly, Combosch et al. (2017), using genome-wide double digest restriction-site associated DNA data to re-analyze nautiloid species taxonomy, also suggested that *N. belauensis* and *N. repertus* be synonymized with *N. pompilius*. However, their findings indicate the existence of two undescribed *Nautilus* species (one from around American Samoa and Fiji and the other around Vanuatu) in addition to *N. macromphalus* in New Caledonia, *N. stenomphalus* found from the Great Barrier Reef to eastern Papua New Guinea, and *N. pompilius*, which occurs from Western Australia throughout Indonesia and the Philippines and west to Palau (Combosch et al. 2017). Saunders et al. (2017a) suggested that consensus may be trending towards treating *N. pompilius* as a “superspecies” taxonomically, with *N. stenomphalus*, *N. belauensis*, and *N. repertus* potentially as subspecies.

Because the taxonomy of the *Nautilus* genus is not fully resolved, with ongoing debate as to the number of species involved, for this status review we follow the latest scientific consensus of the taxonomy of the *Nautilus* genus as acknowledged by the ITIS, with *N. pompilius* as one of five recognized species:

Kingdom: Animalia

Phylum: Mollusca

Class: Cephalopoda

Order: Nautilida

Family: Nautilidae

Genus: *Nautilus*

Species: *pompilius*

belauensis

macromphalus

repertus

stenomphalus

Excerpt from CITES (2016):

All species of chambered nautilus are distinguished by their coiled external, calcium carbonate shell which is divided into compartments, called chambers. Embryonic shell development occurs similarly across all species (Arnold 1985; Arnold *et al.* 2010; Okubo *et al.* 1995), with shells containing at least 7 chambers in a newly-hatched chambered nautilus to 28 or more chambers in mature individuals (Arnold 1985; Arnold *et al.* 2010; Crick & Mann 2010; Dunstan *et al.* 2011c; Okubo *et al.* 1995; Shapiro & Saunders 2010; Ward 1987, 1988; Ward & Saunders 1997). They differ from other living cephalopods by having up to 90 retractable appendages that lack suckers (Fukuda 2010; Jereb & Roper 2005; MarineBio 2013). Chambered nautilus use their tentacles to scavenge by digging in the substrate to find food (Barord 2015) and to rest by attaching to reef surfaces (Dunstan *et al.* 2011b; Hayasaka *et al.* 1982; Kier 2010).

As the animal grows, its body moves forward and a wall called a septum is produced that seals off the older chambers. The body is contained within the newest and largest chamber, into which it can completely withdraw, closing the opening with a leathery hood (Jereb & Roper 2005). Researchers believe that these animals use their renal appendages to store calcium phosphate that is used in the formation of the septa and in outer shell development (Arnold 1985; Cochran *et al.* 1981; Landman & Cochran 2010; Ward 1987).

Cephalopods are distinguished from other marine mollusks by such features as a buoyancy mechanism, which facilitates movement, and a beak, which facilitates a carnivorous diet (Boyle & Rodhouse 2005). All cephalopods, including chambered nautilus, have well-developed brains capable of learning (Barord 2015; Crook & Basil 2008a, 2008b, 2012; Larson *et al.* 1997; Tanabe & Fukuda 2010).

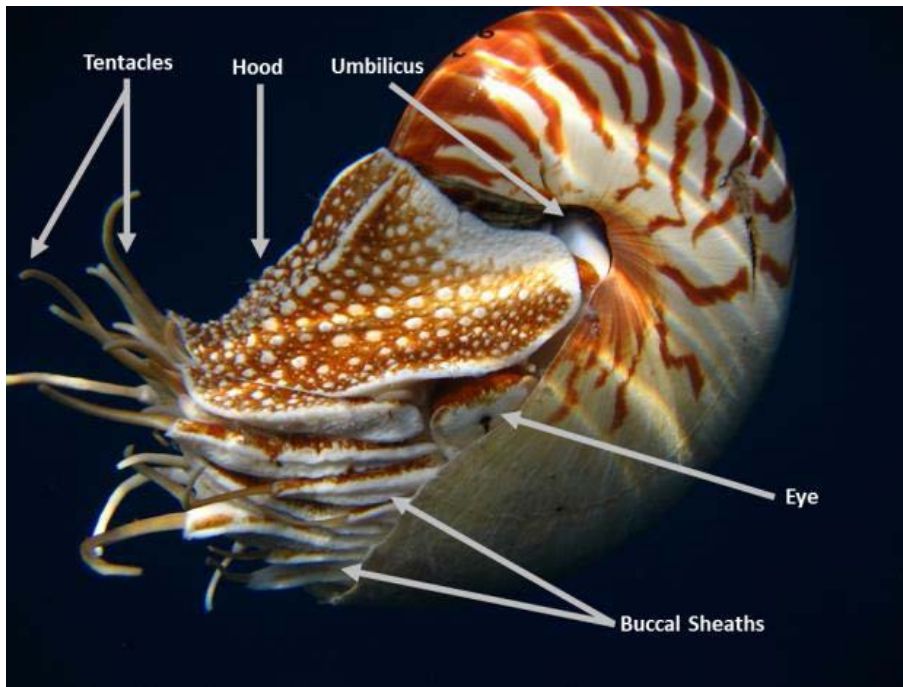


Figure 1. *Nautilus pompilius* with general anatomical features labeled. Source: Barord (2015).

The shell of the chambered nautilus can range in color from white to orange (Figure 1), and even purple, with unique color patterns (Barord 2015). Its distinctive coiled shell is what makes chambered nautilus a highly sought after commodity in international trade (CITES 2016).

Excerpt from CITES (2016):

Chambered nautilus are the last living representatives of the multi-chambered, externally-shelled cephalopods that appeared at least 450 million years ago (Boyle & Rodhouse 2005), and are often called "living fossils" (Crook & Basil 2008a, 2008b; Saunders & Landman 2010). Of the five Cephalopod subclasses – Actinoceratoidea, Ammonoidea, Coleoidea, Endoceratoidea, and Nautiloidea – three are extinct, including the last of the externally-shelled ammonoids which went extinct 65 million years ago possibly in response to predation following the rapid evolution of shallow-water teleosts during the Cretaceous (Saunders 1984b). Today, the soft-bodied octopus, squid, and cuttlefish exist as the only modern-day relatives to chambered nautilus (Boyle & Rodhouse 2005; Larson *et al.* 1997; Teichert & Matsumoto 2010). Chambered nautilus play a role in human understanding of molluscan evolution and are important to present-day paleontological, paleoecological, and paleoclimatological study (Allcock 2011; Arkhipkin 2014; Barord 2015; Biodiversity Clearing-House Mechanism of China *no date*; Boyle & Rodhouse 2005; Carlson 1985; Crook & Basil

2008a, 2008b, 2012; Crook *et al.* 2009; Larson *et al.* 1997; Mapes *et al.* 2010; Neumeister & Budelmann 1997; Ritterbush *et al.* 2014; Seuss *et al.* 2015; Sinclair *et al.* 2011; Wani *et al.* 2005).

Range, Distribution, and Habitat Use

Excerpt from CITES (2016):

Chambered nautilus are native to tropical, coastal reef, deep-water habitats of the Indo-Pacific, occurring variously on fringing reefs (for example, in Fiji), barrier reefs (as in Australia), and atolls (also in Australia) (Dunstan 2011a, 2011b; Hayasaka *et al.* 1982; Jereb & Roper 2005; Saunders 1981b; Saunders & Spinosa 1978; Saunders *et al.* 1989; Ward *et al.* 1977). *Nautilus pompilius* appears to have the broadest distribution, being native or possibly native to 16 countries.

Chambered nautilus populations have also been observed at seamounts in the Philippines, in Australia's Coral Sea (specifically Osprey, Bouganville Flinders, Holmes and Dart reefs), and the Great Barrier Reef (North and South Small Detached Reefs) (personal communication cited in Food and Agriculture Organization (FAO (2016))).

According to the information from the CITES (2016) proposal, the known range of *N. pompilius* includes: American Samoa, Australia, Fiji, India, Indonesia, Malaysia, New Caledonia, Papua New Guinea, Philippines, Solomon Islands, and Vanuatu. The chambered nautilus is also possibly native to China, Myanmar, Western Samoa, Thailand, and Vietnam. However, we note that the occurrence of *N. pompilius* in New Caledonia has not been confirmed. Available information on nautilus in New Caledonia waters (Aguilar 2000; Jereb 2005; Ward 2014) indicates that the only nautilus species found there is *N. macromphalus* (Saunders pers. comm. 2017). Therefore, we do not consider New Caledonia as part of the range of *N. pompilius*. Figure 2 provides a map of the range of all the nautilus species, including *N. pompilius*. Additionally, Saunders *et al.* (2017a) notes that traps set at *Nautilus* depths in Yap (Caroline Islands), Pohnpei and Majuro (Marshall Islands), Kosrae (Gilbert Islands), Western Samoa, and Tonga failed to catch any chambered nautiluses, providing "highly suggestive" evidence that the geographic range of *N. pompilius* may not extend out to these sites.

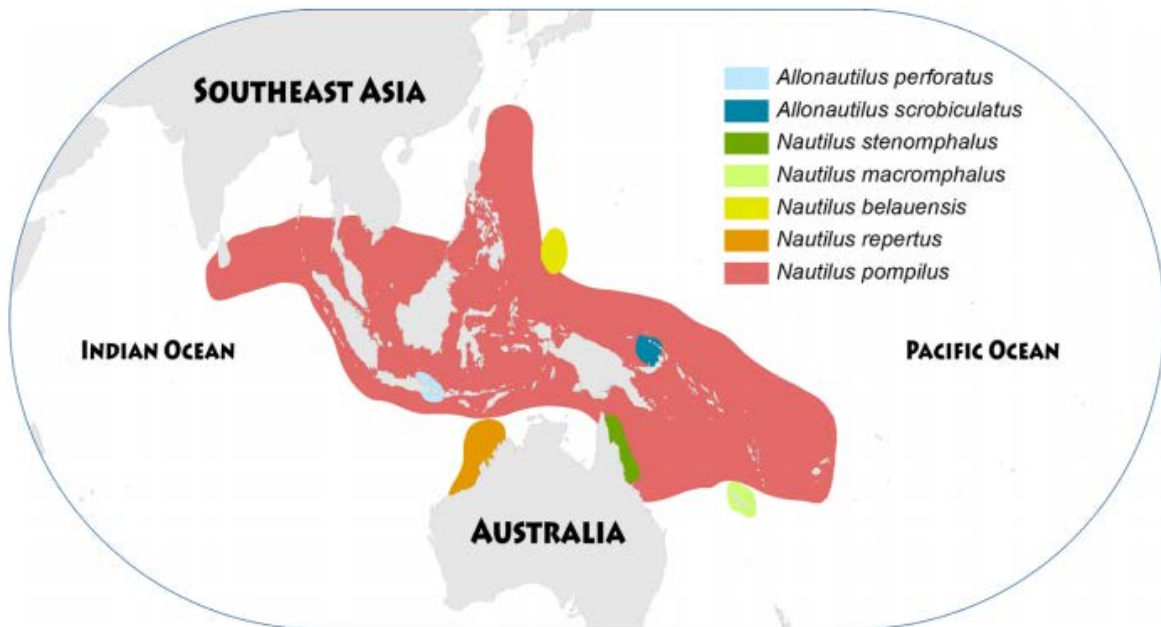


Figure 2. Range of nautilus species (including species from both the *Nautilus* and *Allonautilus* genera from the Nautilidae family). *Nautilus pompilius* is the most widely distributed nautilus, represented in the figure by the red shading. Note that American Samoa is not included as part of the shaded range of *N. pompilius* in this figure; however, the species is confirmed in American Samoa waters. Source: FAO (2016).

Excerpt from CITES (2016):

Within their range, chambered nautilus are irregular and unpredictable in their area of occupancy and, where they are known to occur, they are patchy in distribution (Saunders pers. comm. 2009). A preponderance of research indicates that these species are distributed erratically in association with coral reefs such that, where suitable habitat conditions exist, it cannot be presumed that chambered nautilus will occur there (Dunstan *et al.* 2011a; Jereb & Roper 2005; Reymont 2008; Saunders pers. comm. 2009; Saunders & Ward 2010; Saunders *et al.* 1989). Ecological research on populations in the Philippines and Fiji led researchers to conclude “that the distribution pattern of *Nautilus* is inferred [sic] not to be ubiquitous but rather restricted to some fixed small areas almost permanently” (Hayasaka *et al.* 1988, p. 18).

In terms of habitat, the chambered nautilus is limited in its horizontal and vertical distribution throughout its range because of physiological constraints, and, as such, is considered an extreme habitat specialist.

Excerpt from CITES (2016):

Chambered nautilus are extreme habitat specialists that live in close association with steep-sloped forereefs and associated sandy, silty or muddy-bottomed substrates, ranging from shallow water (rarely) to about 500 meters (m) (Jereb & Roper 2005; Saunders & Ward 2010). As noted by Hayasaka *et al.* (1982), the sea bottom configuration and bathymetric topography may be among “the most fundamental features controlling the distribution of chambered *Nautilus...*” (p. 72). Habitats with high concentrations of carbonate may also be an important characteristic of chambered nautilus’ habitat (Hayasaka *et al.* 1982).

Physiologically, chambered nautilus cannot withstand temperatures above approximately 25° C (Carlson 2010; Dunstan *et al.* 2011a; Hayasaka *et al.* 1982, 1985; Jereb & Roper 2005; Saunders pers. comm. 2009; Saunders 1984b; Saunders & Ward 2010; Saunders *et al.* 1989), which, within their geographic range is typically at about 100 m (Dunstan *et al.* 2011b; Hayasaka *et al.* 1982; Saunders 1984b). In areas where water temperatures drop seasonally, chambered nautilus will range into much shallower water nocturnally. For example, in New Caledonia, chambered nautilus [*N. macromphalus*] have been found in water as shallow as 5 m at night, but this only occurs in the winter when the water temperature is about 22° C (Jereb & Roper 2005; Saunders 1984b; Saunders & Ward 2010; Ward *et al.* 1984). Thus, shallow shelf areas where water temperatures exceed 25° C are not traversable and represent a geographic barrier to movement for these species (Hamada 1977; Hayasaka *et al.* 1985).

Hydrostatic pressure at depths exceeding 600 - 800 m will cause the shells of chambered nautilus to implode and the animal subsequently dies (Jereb & Roper 2005; Saunders 1984b; Saunders pers. comm. 2009; Saunders & Ward 2010; Saunders & Wehman 1977). Research indicates that chambered nautilus must equilibrate around 200 m “to regain neutral buoyancy” or chamber flooding will occur beginning at approximately 250 m (Dunstan *et al.* 2011b; Saunders & Wehman 1977). This may also help explain chambered nautilus’ apparent habitat preference for reef areas with “step-like” topography (Hayasaka 1985; Hayasaka *et al.* 1982, 1985, 1988, 2010; Shinomiya *et al.* 1985). Thus, water depth greater than 800 m is a geographic barrier to movement of chambered nautilus, except for rare shallow or mid-water vicarious drifting events. Suitable habitat for chambered nautilus may remain unoccupied when separated by depths greater than 800 m.

Though often described as pelagic, these species might best be characterized as mobile benthic bottom-dwelling fore-reef scavengers and opportunistic scavengers (Dunstan *et al.* 2011c; Jereb & Roper 2005; Nichols 1991; Saunders 1981a; Saunders & Ward 2010). Chambered nautilus do not swim in the open water column (where they are vulnerable to predation), but are nekto-benthic (or epibenthic), living in close association with reef slopes (along the reef face or fore reef) and bottom substrate

(Barord *et al.* 2014; Dunstan *et al.* 2010, 2011a, 2011b; Hayasaka *et al.* 1982, 1985; Nichols 1991; Saunders 1981a, 1984b; Saunders & Spinoso 1979; Saunders & Ward 2010; Ward & Martin 1980; Ward *et al.* 1977), and resting by attaching to the substrate with their tentacles (Dunstan *et al.* 2011b; Hayasaka *et al.* 1982; Kier 2010). Because chambered nautilus do not swim through mid-water, open ocean acts as a geographic barrier to movement between reefs.

Based on acoustic telemetry data, *N. pompilius* can travel distances of up to 6 km in a day facilitated by currents (Dunstan *et al.* 2011c). However, at the depths where these animals are generally active (>200 m), currents are weak and movements are primarily accomplished through self-propulsion, with observed *N. pompilius* distances of up to 3.2 km per day and maximum speeds of up to 1.18 km/h for short periods of time (less than 6 hours) (Dunstan *et al.* 2011a). In terms of descent and ascent movements, rates average 2.1 and 2.3 m/min, respectively, with maximums around 3.0 m/min (Dunstan *et al.* 2011c). While depths greater than 800 m have been shown to cause shell implosion in nautilus species, based on remotely operated vehicle observations of *N. pompilius* off the Great Barrier Reef in Australia, the species has the ability to descend to depths of up to 700 m, with juveniles sighted between 490 m and 608 m depths (Dunstan *et al.* 2011c).

In tracking studies conducted by Ward *et al.* (2016), the authors found that habitat may be the primary factor that influences nautilus movements within an area. For example, the depth profiles of two tagged *N. pompilius* off Panglao Island, Philippines, reflected the type of habitat within their area. Depth movements were more gradual when the animal was in the part of its habitat characterized by deep and sloping sandy bottoms with little structure, and varied when the animal was navigating through the portion of its habitat characterized by sharp, steep reef slopes with rocky bottoms and reef walls (Ward *et al.* 2016). Additionally, these nautilus were recaptured 3-5 months after release within a kilometer of their release point (Ward *et al.* 2016). The authors also found that temperature may play a role in nautilus migrations, with nautilus tracked in Vanuatu moving into shallower waters than those in Palau (Ward *et al.* 2016). In Vanuatu, water temperatures are cooler at shallower depths compared to similar depths in Palau, and thus may explain the presence of nautilus in these areas (Ward *et al.* 2016). Overall, Ward *et al.* (2016) found that, on average, nautilus move several kilometers each day, but that they tend to stay in one general area, with patterns of migrations influenced by habitat and potentially other local factors.

Despite the apparent temperature and depth constraints of the species, larger-scale migrations, although rare, have occurred. For example, an *N. pompilius* specimen was captured off southern Japan in the 1970s and assumed to have drifted 2,000 km in the Kuroshio Current from the Philippines (Saunders 2010). Saunders (2010) notes that these movements across large stretches of either shallow, warm water (<100 m, > 25°C) or deep

water (>800m) would likely be accomplished only by drifting or rafting (i.e., moving passively with ocean currents) through midwater or surface waters. However, the author notes that these movement events must have occurred “with sufficient frequency” to account for the species distribution across the Indo-Pacific.

Feeding and Diet

The chambered nautilus uses its 90 retractable appendages, or tentacles, to dig in the substrate and feed on a variety of organisms, including fish, crustaceans, echinoids, nematodes, cephalopods, other marine invertebrates, and detrital matter (Saunders and Ward 2010; Barord 2015). The chambered nautilus also has an acute sense of olfaction and can easily smell odors (such as prey) in turbulent waters from significant distances (of up to 10 m) (Basil et al. 2000).

Excerpt from CITES (2016):

Chambered nautilus have been characterized as deep-sea scavenging generalists and opportunistic predators (Dunstan *et al.* 2011c; Jereb & Roper 2005; Nichols 1991; Saunders 1981a; Saunders & Ward 2010). Deep sea scavengers are important in energy flow, nutrient cycling, and in stabilizing marine food webs (Beasley *et al.* 2012; Kaiser & Moore 1999). Recent research suggests that chambered nautilus may be strict or obligate scavengers (Barord 2015; Barord *et al.* 2014). If this is true, chambered nautilus would be among the largest obligate marine scavengers (Ruxton & Houston 2004).

Based on the movement of tagged *N. pompilius* individuals, Dunstan et al. (2011c) observed that the species forages during the day in deeper waters (below 489 m depths) and also at night, when they are primarily active and moving within their full depth range (between 100 m to over 700 m). This is in contrast to a study of nautilus individuals in Palau (*N. belauensis*), which showed a distinct diurnal pattern, with individuals remaining in deeper water (300 to 350 m) during the day and ascending to shallower waters and increasing activity at night (Ward et al. 1984). Dunstan et al. (2011c) attribute the differences in the observed patterns of diurnal vertical migrations of the species to the respective populations’ characteristics and habitat type. The authors suggest that diurnal patterns are likely influenced by a number of varying factors including location of preferred feeding habitat, requirements for buoyancy regulation, and avoidance of predators. Given that two different nautilus species were observed, differences in individual migration movements may also be species-specific.

Reproduction and Growth

Excerpt from CITES (2016):

Little is known about chambered nautilus reproduction in the wild. Female chambered nautilus produce one large egg at a time, which requires a lengthy incubation period (1 year) (Carlson 1985; Carlson *et al.* 1984; Collins & Ward 2010; Landman & Cochran 2010; Okubo *et al.* 1995; Uchiyama & Tanabe 1996; Ward 1983, 1987, 1988). Egg-laying has not been directly observed in the wild. Chambered nautilus are iteroparous (having multiple reproductive cycles over the course of its lifetime), but ecological information is insufficient to determine how many eggs a single wild female might lay over an entire year or if a female “lays more than one [egg] a season” (P. Ward, Professor, Department of Biology, University of Washington, Seattle, Washington, USA, pers. comm. 2010).

Observations of captive animals suggest that nautilus reproduce sexually and have multiple reproductive cycles over the course of their lifetime. Based on data from captive *N. belauensis* and *N. macromphalus* individuals, female nautilus may lay up to 10 to 20 eggs per year, which hatch after a lengthy embryonic period of around 10 to 12 months (Uchiyama and Tanabe 1999; Barord and Basil 2014; Carlson 2014). Embryos in the wild are thought to develop in shallow, warm water (around 100 to 200 m depths and 22 to 24°C) (Uchiyama and Tanabe 1999; Barord and Basil 2014; Carlson 2014). There is no larval phase, with juveniles hatching at sizes of 22 to 23 mm in diameter, and potentially migrating to deeper and cooler waters (Barord and Basil 2014); however, live hatchlings have rarely been observed in the wild.

The chambered nautilus is a slow-growing and late-maturing species, with age at maturity between 10 and 17 years and longevity thought to be at least 20 years (Dunstan *et al.* 2011b; Ward *et al.* 2016). Circumferential growth rate of the species is estimated to range from 0.053 mm/day to 0.23 mm/day and slows as the animal approaches maturity (Dunstan *et al.* 2010; Dunstan *et al.* 2011b). However, average size at maturity of *N. pompilius* appears to vary among regions, with smaller shell diameters noted around the Philippines, Fiji, and eastern Australia and larger diameters off Indonesia (Table 1). The species also exhibits sexual dimorphism, with males consistently growing to larger sizes than females (Saunders and Ward 2010).

Table 1. Shell size and weight of observed mature *N. pompilius* individuals. Where available, standard deviations (SD) are also provided.

Location	# of individuals	Year	Average size at maturity (mm)	Mature shell range (mm)	Average weight (for mature individuals; g)	Weight range (for mature individuals; g)	Citation
Indonesia: Ambon	44	1987	194.6 (SD: 5.7)	183.2 – 207	1,160 (SD: 996)	990 – 1,330	Saunders <i>et al.</i> (2017b)

Indonesia: Sumbawa	60	2011	199.8 (SD: 11.5)	150.5 – 218.2			Saunders et al. (2017b)
Philippines: Tañon Strait	268	1979, 1981	170 (males); 160 (females)	150 – 188	850		Saunders et al. (2017a); Saunders (2010); Tanabe et al. (1990)
Philippines: Sulu Sea	29		114	103 – 126			Saunders (2010)
Fiji: Suva	280	1983, 1986	150 (males); 140 (females)				Tanabe et al. (1990)
Fiji: Suva	22	1986	146 (males); 136.5 (females)	136.5 – 155	516.8	400 – 670	Saunders et al. (1989)
Fiji: Suva	74	1982–1983	>138				Zann (1984)
Papua New Guinea: Lae & New Ireland Province			144 (Lae); 169 (New Ireland Province)	124 – 199			Saunders (2010)
Papua New Guinea: Manus Region (Ndrova Island and Komuli)	129	1984 – 1985	178.2 (males); 157.2 (females)	142 – 198.5	830.6	445 – 1200	Saunders et al. (1987)
Australia: Osprey Reef	956	1998 – 2008	131.9 (males); 118.9 (females)	100 – 145			Dunstan et al. (2011b)
Australia: Queensland	5		153				Saunders (2010)
American Samoa: Taema Bank	11	1986	174.5 (males); 164.9 (females)	163 – 179.2	818.2	680 – 925	Saunders et al. (1989)

Population Structure

Isolated Populations

As noted in the CITES (2016) proposal, most of the recent genetic data suggest that *N. pompilius* “may be comprised of numerous as yet ‘unrecognized but separate sibling species’ that exist as genetically distinct, geographically- and reproductively-isolated

populations (Barord *et al.* 2014, p. 1; Bonacum *et al.* 2011; Dunstan *et al.* 2011c; Sinclair *et al.* 2011; Williams *et al.* 2012, 2015)."

In an examination of the genetic structure and degree of gene flow between an *N. pompilius* population off Western Australia and one off the Philippines, Williams *et al.* (2015) concluded that very little gene flow exists between the two populations. The authors note that the absence of migration between the Philippines and Western Australia indicates that recolonization would not be a possibility if the Philippines population were to be extirpated (Williams *et al.* 2015). However, the current range of *N. pompilius* does not appear to include much of Western Australia, and the sampled population from the Williams *et al.* (2015) study may actually have comprised both *N. pompilius* and *N. repertus* specimens.

On a smaller geographic/population scale, Sinclair *et al.* (2007) analyzed DNA sequence information from *N. pompilius* collected from the Coral Sea and the outer edges of the Great Barrier Reef in north Queensland ("Northern GBR") and found population-specific genetic differentiation. Through use of Random Amplification of Polymorphic DNA (RAPD) analysis and partial sequencing of the *CoxI* gene region, the authors determined that there is genetic divergence between the geographic lineages of "Northern GBR" and "Coral Sea," indicating distinct groups of populations and pointing to the potential for larger-scale geographic divergence of the species. In a follow-up study, Sinclair *et al.* (2011) found an even greater degree of genetic variation between populations on the east coast of Australia (using the "Northern GBR" and "Coral Sea" populations) and the west coast of Australia (Scott Reef), with phylogenetic analyses suggesting three genetically divergent populations.

In addition to genetics, other studies have looked at morphological differences to examine isolation between *N. pompilius* populations. For example, based on biometric analysis of *N. pompilius* from the Philippines and Fiji, Tanabe and Tsukahara (2010) concluded that the populations are morphologically differentiated. The samples were taken using baited fish traps from Tañon Strait, Philippines (n=52), and off Suva Harbor (n=101) and Viti Levu Island (n=62), Fiji. The authors found significant morphological differences in weight, size at maturity, and the slopes of allometric relationships of morphological characters between the two populations (Tanabe and Tsukahara 2010). The authors note that these results combined with the results from Masuda and Shinomiya (1983), which showed statistically significant differences in allele frequencies between these two populations, indicate that *N. pompilius* from the Fiji islands is genetically and morphologically differentiated from *N. pompilius* in the Philippines (Tanabe and Tsukahara 2010).

While it is thought that deep water largely serves as a barrier to movement of *N. pompilius*, explaining the isolation of the above populations, results from Swan and Saunders (2010) suggest it is more likely a combination of both depth and geographic distance. In their

study, Swan and Saunders (2010) examined the correlation between morphological differences and distances between populations in Papua New Guinea, including some that were separated by deep water (>1000 m). Their findings showed that adaptive equilibrium had not yet been attained, indicating that the populations are not completely genetically isolated (Swan and Saunders 2010). As such, the authors surmised that there is at least some degree of contact and gene flow between the Papua New Guinea populations, through potentially rafting or midwater movements, with the amount inversely related to the geographic distance between the populations (Swan and Saunders 2010).

Given the above information, it is reasonable to assume that populations separated by large geographic distances and deep water are genetically differentiated, with very little to no gene flow.

Diversity

In terms of genetic diversity, Williams et al. (2015) estimated large ancestral and current effective population sizes for the Philippines (current median size = 3,190,920) and Ashmore Reef (Western Australia) (current median size = 2,562,800) populations, indicating a low likelihood of the fixation of alleles and no evidence of significant genetic drift impacts in either population. Additionally, the authors found no significant difference in the allelic richness between the sampled locations in the Philippines and Western Australia. In other words, the data tend to suggest that the species may have high genetic diversity. These effective population sizes are similar to those recently reported by Combosch et al. (2017), who found large effective population sizes in the Indo-Pacific population (4.5×10^6 specimens; 3.2×10^6 for the Philippines subpopulation) and in the Coral Sea (7.2×10^6 for the Great Barrier Reef and 5.7×10^6 for Papua New Guinea). Combosch et al. (2017) estimated much smaller effective population sizes for nautilus populations within the South Pacific, with New Caledonia at 0.34×10^6 specimens, Vanuatu at 0.67×10^6 , and the American Samoa/Fiji population at 0.41×10^6 specimens. However, the authors of both studies caution that due to the low fecundity and long generation time of the species, genetic responses to current exploitation rates (such as decreases in genetic diversity) may not yet be detectable in these effective population size estimates (Williams et al. 2015; Combosch et al. 2017). In fact, using *CoxI* sequences from *N. pompilius* across its range and Tajima's *D* test to examine departures from population equilibrium, Vandepas et al. (2016) found significant negative Tajima's *D* values for the populations in Western Australia, New Caledonia and Papua New Guinea. These results indicate an excess of rare alleles or high-frequency polymorphisms within the populations, suggesting they may be currently recovering from possible bottleneck events. While not statistically significant, the Tajima's *D* values for the rest of the sampled populations with the exception of Palau and Eastern Australia (i.e., Fiji, Indonesia, Vanuatu, Philippines and American Samoa) were also negative, suggesting that the species potentially has low genetic diversity across its range.

Overall, given the available and somewhat conflicting information, the level of genetic diversity needed to maintain the survival of the species and the current level of genetic diversity across the entire range of the species remains highly uncertain. Further morphological and genetic tests examining differences within and among populations are needed.

Sex-Ratios and Population Structure

In terms of population structure, the available information suggests chambered nautilus populations are comprised mainly of male and mature individuals. Based on trapping data, including mark-recapture studies, male *N. pompilius* appear to dominate the catch, with proportions of 75 to 80 percent (CITES 2016). In addition, a large proportion of those captured (around 75 percent) are mature, with juvenile *N. pompilius* individuals rarely caught (CITES 2016).

Excerpt from CITES (2016):

There are consistently few juveniles in the populations studied (Hayasaka *et al.* 1982; Saunders & Spinoso 1978; Ward & Martin 1980). Detailed age class distribution information from the 12-year study of the unfished population in Osprey Reef, Australia, found fewer than 10 percent of the population were juveniles, indicating that chambered nautilus exhibit low fecundity in the wild (Dunstan 2011a) and affirming previous field studies which found that juvenile chambered nautilus represent less than 10-20 percent of the population (Carlson & Degruy 1979; Havens 1977; Saunders 1983, 1990; Saunders & Landman 2010; Tanabe *et al.* 1990; Ward 1987; Ward & Martin 1980; Ward *et al.* 1977; Zann 1984).

The male-biased sex ratio could reflect the natural equilibrium for these populations. While population theory suggests it is the females that are the critical sex for population growth, there are examples where population growth which may be male-biased density-dependent (as summarized by Caswell & Weeks 1986; Hamilton 1967; Rankin & Kokko 2007). A male-biased sex ratio and high genetic diversity within populations may be indicative of a population structure based on multiple paternity, as with loggerhead sea turtles (Lasala *et al.* 2013). Chambered nautilus experts have noted the high levels of morphological and genetic variation (Bonacum *et al.* 2011; Sinclair *et al.* 2007, 2011; Swan & Saunders 2010; Tanabe & Fukuda 2010; Tanabe *et al.* 1985, 1990; Ward & Saunders 1997; Williams *et al.* 2012, 2015), and research in the 1980s on the genetic structure of *N. pompilius* populations in Papua New Guinea found high levels of genetic variation within populations, indicating that individuals within that population were freely interbreeding (Woodruff *et al.* 2010). If males of the species are the critical sex for population growth, the trapping of mostly adult males to supply international trade is of particular concern to the sustainability of the species.

In fact, Saunders et al. (2017a) argues that examination of this male-female sex ratio and composition of mature individuals in populations provides clues to the current stability of the population. In the authors' study, they compared 16 nautilus populations from "unfished" areas (in Papua New Guinea, Australia, Indonesia, Fiji, Palau, American Samoa, New Caledonia, and Vanuatu) to two populations in the Philippines that have been subject to decades of uncontrolled exploitation and provided an estimate of quantitative measures to illustrate demographic disturbance, or "disequilibrium," in a nautilus population. Specifically, Saunders et al. (2017a) found that the mean percentage of mature animals in the unfished nautilus populations (n=16) was 73.9 percent (SD: 21.8, SE: 5.1) and the mean percentage of males was 75.0 percent (SD: 16.4, SE: 4.1). The authors suggested that these proportions could be used as a baseline for determining whether a population (of n > 100 individuals) is at equilibrium (Saunders et al. 2017a). In contrast, the intensely fished Philippine population from Tañon Straits (n=353 individuals) had a male proportion of only 28 percent and mature individuals comprised only 26.6 percent of the population, which the authors suggest are levels that signal pending collapse of the local fishery (Saunders et al. 2017a). Ultimately, the authors indicate that these ratios obtained by examining the sex and maturity composition of a population could be used as a basis for determining whether management and conservation measures are appropriate. However, a caveat to this method is that it is unclear if the male-biased sex ratio reflects the natural equilibrium for chambered nautilus populations. Because these population studies tend to use baited traps to capture chambered nautiluses, there may be an aspect of sampling bias in terms of the size and sex of individuals attracted to the traps. For example, laboratory studies by Basil (2014) suggest that female *N. pompilius* may repel each other. Potentially, this female avoidance of one another may explain why fewer females are found in the baited-trap field studies. In fact, in a study of *N. pompilius* drift shells that were collected between 1984 and 1987 in Papua New Guinea (n=1,329), 54 percent were male, suggesting a much different sex ratio than those determined from baited studies (Saunders et al. 1991). Given the conflicting information, further research on sex ratios in the wild, as well as a better understanding of the population structure of the species, is needed.

ABUNDANCE AND TRENDS

The global abundance of *N. pompilius* is unknown, with no available historical baseline population data. In fact, the first study to estimate baseline population size and density for the species in a given area was only recently conducted by Dunstan et al. (2011a). This study examined the *N. pompilius* population at Osprey Reef, an isolated coral seamount off Australia's northeastern coast with no history of nautilus exploitation. Based on data collected from 2000 to 2006, the authors estimated that the population at Osprey Reef consisted of between 844 and 4,467 individuals, with a density estimate of 14.6 to 77.4 individuals per square kilometer (km²) (Dunstan et al. 2011a). Subsequent research,

conducted by Barord et al. (2014), provided abundance estimates of nautiluses (species not identified) from four locations in the Indo-Pacific: the Panglao region of the Bohol Sea, Philippines, with 0.03 individuals per km², Taena Bank near Pago Pago Harbor, American Samoa, with 0.16 individuals per km², the Beqa Passage in Viti Levu, Fiji, with 0.21 individuals per km², and the Great Barrier Reef along a transect from Cairns to Lizard Island, Australia, with 0.34 individuals per km² (Table 2). With the exception of the Bohol Sea, these populations are located in areas where fishing for nautiluses does not occur, suggesting that nautiluses may be naturally rare, or that other unknown factors, besides fishing, may be affecting their abundance. The authors also indicate that the population estimates from this study may, in fact, be overestimates as they used baited remote underwater video systems to attract individuals to the observation area (Barord et al. 2014). In either case, these very low population estimates suggest that chambered nautiluses are especially vulnerable to exploitation, with limited capacity to recover from depletion. This theory is further supported by the comparison between the population density in the Panglao region of the Bohol Sea, where nautilus fishing is occurring, and the unfished sites in American Samoa, Fiji, and Australia, with the Bohol Sea density less than 20 percent of the smallest unfished population (Barord et al. 2014) (Table 2).

Recently, Williams et al. (2015) and Combosch et al. (2017) used genetic modelling to estimate current effective median population sizes for *N. pompilius* from locations in the Indo-Pacific, Coral Sea, and South Pacific. Specifically, the authors examined genetic markers and used Bayesian clustering methods to estimate median effective population sizes. Williams et al. (2015) estimated a population size for the Australian Ashmore Reef population (which the authors note may possibly contain the entire Australian northwest shelf nautilus population) at 2,562,800 individuals and a median size for the Palawan region, Philippines, population at 3,190,920 individuals. Similarly, Combosch et al. (2017) estimated a median effective population size for the Philippines of 3.2×10^6 individuals, and for the entire Indo-Pacific population this estimate was 4.5×10^6 individuals. Other current median effective population sizes estimated by Combosch et al. (2017) include 7.2×10^6 individuals for the Great Barrier Reef population, 5.7×10^6 individuals for the Papua New Guinea population, 0.34×10^6 individuals for New Caledonia, 0.67×10^6 individuals for Vanuatu, and 0.41×10^6 individuals for the American Samoa/Fiji population.

Williams et al. (2015) recognize that the use of different methods to generate population density estimates (such as those used by Barord et al. (2014)) will produce “predictably dissimilar abundance data” (Williams et al. 2015). Additionally, the authors suggest that the large estimates from the genetic methods (with no evidence of population reduction) may indicate that the genetic response to exploitation (e.g., a decrease in allelic richness) has not had enough time to become detectable yet, unlike the trapping data from the above studies (Williams et al. 2015).

Table 2. Population density estimates for fished and unfished *N. pompilius* populations from Australia, American Samoa, Fiji, and the Philippines (based on data from 2011-2013).

Location	Total number trapped	Population Density (ind/km ²)	Fished Population?	Reference
Australia: Osprey Reef	68	13.6 – 77.4	No	Dunstan et al. (2011a); Barord et al. (2014)
Australia: Great Barrier Reef	92	0.34	No	Barord et al. (2014)
Australia: Great Barrier Reef		7 - 67	No	Combosch et al. (2017)
American Samoa: Taema Bank	22	0.16	No	Barord et al. (2014)
Fiji: Beqa Passage	20	0.21	No	Barord et al. (2014)
Philippines: Panglao region, Bohol Sea	6	0.03	Yes	Barord et al. (2014)

Overall, abundance information is extremely spotty and limited to only a select number of locations (Table 3). Additionally, it is difficult to make comparisons between these locations using the available abundance and catch-per-unit-effort (CPUE) information (e.g., number of individuals caught per trap) because the methods of collecting the data varies greatly by study. For example, most of the studies listed below are based on trapping data where multiple traps can be set and left over multiple nights, or one trap can be set for one night, and the particulars of the trapping methods are generally not available from the anecdotal or study descriptions. As such, the reported data below is hard to standardize across studies. It should also be noted that the majority of the data are over two decades old, with no available recent trapping estimates (Table 3). Furthermore, though not yet confirmed by research, many nautilus experts hypothesize that chambered nautilus likely occur in locations where they are not currently observed (NMFS 2014), suggesting abundance may be underestimated. However, these experts agree that current abundance

estimates cannot be extrapolated across the species' range without considering suitable habitat and likelihood of nautilus presence (NMFS 2014), which has yet to be done.

Table 3. Reported average number of *N. pompilius* individuals caught per trap during sampling events in various locations throughout the chambered nautilus' range.

Location	Year Sampled	Average number of Individuals/Trap	Reference
Australia: Osprey Reef	1998 – 2008	5.7 – 7.9	Dunstan et al. (2011a)
American Samoa: Taema Bank	1986	Range: 3 – 29	Saunders et al. (1989)
Fiji: Suva	1984	3.1 (Range: 1–8.3)	Zann (1984)
Papua New Guinea: Kavieng (New Ireland)	1984	5 (8 – 9 in deeper waters)	Saunders and Ward (2010)
Papua New Guinea: Port Moresby	1985	7	Saunders and Ward (2010)
Papua New Guinea: Manus (Ndrova Island & Komuli)	1984 – 1985	Not stated; but maximum reported as 30 in one trap overnight	Saunders et al. (1987)
Vanuatu: Efate Island	1987	2.6	Blanc (1988)

In terms of current trends in abundance, *N. pompilius* populations are generally considered stable in areas where fisheries are absent (e.g., Australia) and declining in areas where fisheries exist for the species; however, recent CPUE data from Fiji indicate a decline despite no active fishery (FAO 2016). In the unfished Australian Osprey Reef population discussed above, Dunstan et al. (2010) used mark-recapture methods to examine the trend in CPUE of individuals over a 12-year period. Analysis of the CPUE data showed a slight increase of 28 percent from 1997 to 2008, and while this increase was not statistically significant, the results indicate a stable *N. pompilius* population in this unexploited area (Dunstan et al. 2010).

In locations where fisheries have operated or currently operate, anecdotal declines and observed decreases in catches of nautilus species are reported (Table 4). Citing multiple personal communications, the CITES (2016) proposal noted declines of *N. pompilius* in Indian waters, where commercial harvest occurred in the past for several decades, and in Indonesian waters, where harvest is suspected to be increasing. In fact, traders in Indonesia have observed a significant decrease in the number of nautilus collected over the past 10 years, which may be an indication of a declining and depleted population (Freitas and Krishnasamy 2016). In the Philippines, Dunstan et al. (2010) estimated that the CPUE of *Nautilus* from four main nautilus fishing locations in the Palawan region has decreased by an estimated average of 80 percent in less than 30 years. Anecdotal reports from fishermen that once fished for *N. pompilius* in the Sulu Sea note that the species is near commercial extinction, forcing fishermen to move to new areas in the South China Sea (Freitas and Krishnasamy 2016). Furthermore, in Tawi Tawi, Cayangacillo, and Tañon Strait/Cebu, Philippines, fisheries that once existed for chambered nautilus have since been discontinued because of the rarity of the species, with Alcala and Russ (2002) noting the likely extirpation of *N. pompilius* from Tañon Strait in the late 1980s. The fact that the species has not yet recovered in the Tañon Strait, despite an absence of nautilus fishing in over two decades, further evidences the susceptibility of the species to exploitation and its limited capability to repopulate an area after depletion.

Table 4. Available abundance trends for *N. pompilius* throughout its range.

Location	Trend	Data	Time Frame	Reference
Australia (Osprey Reef)	Stable/increasing (28 percent)	CPUE	12 years (1997-2008)	Dunstan et al. (2010)
Indonesia	“Significant decrease”	Trader observation of numbers collected for trade	Past 10 years	Freitas and Krishnasamy (2016)
Indonesia (Luk – Sambik Bongkol village – Gangaa, North Lombok)	70 – 93 percent decline	CPUE (Anecdotal reports) 10 – 15 individuals (ind)/night 1 – 3 ind/night	Past 10 years	Freitas and Krishnasamy (2016)
Indonesia (Bali)	Unknown decline	CPUE (Anecdotal reports) 10 – 20 ind/night Much less now	Past 10 years	Freitas and Krishnasamy (2016)
Indonesia (East Nusa Tenggara)	93 – 97 percent decline	CPUE (Anecdotal reports) Up to 30 shells after a storm Only 1 or 2 now	Past 10 years	Freitas and Krishnasamy (2016)

Philippines (Palawan Region)	70 – 94 percent decline	CPUE (Anecdotal reports) 1 ind/trap 0.2 ind/trap	6 – 24 years (variable dates, from 1980s to 2008)	Dunstan et al. (2010)
Philippines (Sulu Sea)	Near commercial extinction	Anecdotal reports		Freitas and Krishnasamy (2016)
Philippines (Tañon Strait/Cebu)	97 percent decline; possible extirpation	CPUE (Traps) 3.5 ind/trap 0.13 ind/trap	40 years	FAO (2016); Haven (1977)
Philippines (Siquijor)	100 percent decline; extirpation	CPUE (Traps)	~30 years (1985 – 2014)	FAO (2016)
Fiji	~66 percent decline	CPUE (Traps) [Note: variable estimates throughout the years, ranging from 1 ind/trap (2013) to 3.1 ind/trap/day (1983)]	37 years (1976 – 2013)	FAO (2016)
Papua New Guinea (Manus Island)	90 percent decline; however, data is questionable	CPUE (Traps) 20 ind/3-night set to 1.5 ind/trap	31 years (1984 – 2015)	FAO (2016); Saunders (pers. comm. 2017)
India	Unknown (few beached dead specimens and rare in bycatch)	Landings/Traps (Anecdotal)	Several decades	FAO (2016)

ANALYSIS OF ESA SECTION 4(A)(1) FACTORS

The ESA requires NMFS to determine whether a species is endangered or threatened because of any of the factors specified in section 4(a)(1) of the ESA. The following provides information on each of these five factors as they relate to the status of the chambered nautilus. For each relevant factor where information is available, its impact on the extinction risk of the species is evaluated, whether minor or significant, with “significant” defined as increasing the risk to such a degree that it affects the species’ demographics (i.e., abundance, productivity, spatial structure, diversity) either to the point where the species is strongly influenced by stochastic or compensatory processes or is on a trajectory toward this point.

Present or Threatened Destruction, Modification, or Curtailment of Habitat or Range

Excerpt from CITES (2016):

Much of the chambered nautilus habitat is impacted by human activities, including destructive fisheries, pollution, sedimentation, and changes in water temperature and pH. More than half the reef areas in China, India, Indonesia, Malaysia, Myanmar, the Philippines, Thailand, and Viet Nam are considered to be at risk from these threats, in addition to coastal development (Burke *et al.* 2002; De Angelis 2012).

Below we explore the various threats to the habitat of *N. pompilius* and evaluate the likely impact on the status of the species.

Harvest of Coral Reef Species and Destructive and Unselective Fishing Practices

Excerpt from CITES (2016)

The coral reef habitat of chambered nautilus is home to a variety of other species that are harvested for human use or consumption, including shrimp, crabs, and anemones (Hayasaka 1985; Hayasaka *et al.* 1982; Saunders 1984b); stony and hard coral, starfish relatives, hermit crabs, a variety of sea snails and ornamental fish (Burke *et al.* 2002; CCIF 2001; Hayasaka *et al.* 1982; Suzuki & Shinomiya 1995; Sykes & Morris 2009). Fish include those typically associated with coral reefs, such as parrotfish (Scaridae family) and butterflyfish (Chaetodontidae family), as well as teleosts such as herring relatives (Clupeidae family) and those associated more typically with silty sea bottoms, such as stargazers (Uranoscopidae family) and flounders (Pleuronectidae family) (Hayasaka *et al.* 1982; Shinomiya *et al.* 1985).

Harvest of coral and live rock for the aquarium trade contributes directly to the destruction of coral reefs and decreases the biodiversity of the reef ecosystem (Burke *et al.* 2002; Conservation & Community Investment Forum (CCIF) 2001; Lal & Cerelala 2005; Sykes & Morris 2009). The bustling trade in live reef fish to satisfy high-end Asian food markets has been on the rise since the 1970s (Petersen *et al.* 2004). Most marine products in the aquarium trade are sourced from coral reefs worldwide (Lal & Cerelala 2005). Harvest for the food aquarium trade occurs within nautilus habitat, including in Indonesia, New Caledonia, Papua New Guinea, the Philippines, Vanuatu (Aguilar 2000; Manez *et al.* 2015; Raubani 2009; Saunders pers. comm. 2014).

In some cases, unselective and destructive fishing practices are used to satisfy these industries. Unselective fishing techniques, such as the use of dynamite and poison kill unintended species, degrade or destroy habitat, and negatively impact the marine ecology of the ecosystem (Burke *et al.* 2002). Such techniques are used variously

throughout the chambered nautilus' range—to a lesser extent in Fiji, where only a few fishermen employee [sic] blast fishing and to a greater extent in the waters off China, Indonesia, the Philippines, and Viet Nam (Aguiar 2000; Barber & Pratt 1997, 1998; Uthicke & Conand 2005; Wilkinson 2008; Burke *et al.* 2002; World Resources Institute (WRI) 2008).

Blast and poison fishing (based on survey observations and expert opinion) are evident throughout much of the range of the chambered nautilus (WRI 2011) (Figure 3). Although illegal, the use of these destructive practices continues. For example, in a September 2016 article in the Jakarta Post, Amnifu (2016) reports that blast fishing, a common occurrence in East Nusa Tenggara waters, and particularly around Sumba Island, has recently expanded to parts of the Sawu Sea National Park's conservation area.

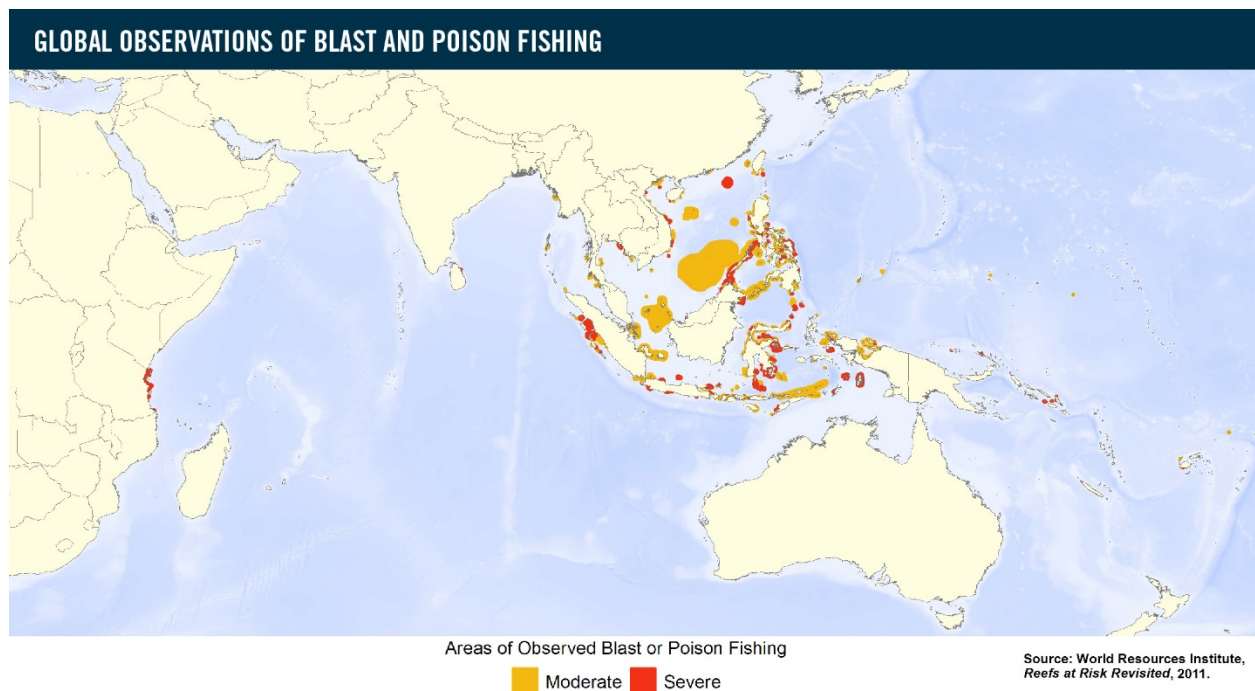


Figure 3. Global observations of blast and poison fishing. Areas highlighted in yellow (under moderate threat) represent those places where blast and/or poison fishing occurs occasionally (i.e., once a month). Areas highlighted in red (under severe threat) represent those places where blast and/or poison fishing occurs frequently (i.e., once a week or more often). Source: WRI (2011).

Blast fishing is particularly destructive as it not only destroys coral reefs but also indiscriminately kills their marine inhabitants. A “typical” blast will shatter corals and turn them into rubble within a 1 to 1.5 m diameter of the blast site and can kill marine organisms, including invertebrates, within a 20 m radius (Pet-Soede and Erdmann 1998; Njoroge 2014). Because blast fishing is generally conducted in shallow reef waters (e.g. 5 to

10 m depths) (Fox and Caldwell 2006), *N. pompilius* is unlikely to experience direct mortality from these destructive practices given that they generally inhabit much deeper waters. However, the indirect impact, such as changes in coral reef community structure and loss of fish biomass (Raymundo et al. 2007), could decrease the availability of food resources for the scavenging chambered nautilus. Additionally, depending on the extent of the coral reef destruction, *N. pompilius*, because of its physiological constraints, may be incapable of finding and exploiting other suitable habitat with greater prey resources. Additional research is needed to determine the effects of blast fishing on the deeper-water inhabitants of these impacted coral reefs.

Another primarily illegal fishing practice that destroys coral reefs is cyanide, which is used to stun and capture live reef fish. When exposed to cyanide, coral respiration rates decrease and can cease altogether, with corals observed expelling their zooxanthellae and resulting in coral bleaching and mortality events (Rubec 1986; Jones 1997).

Excerpt from CITES (2016):

Cyanide is used to harvest both food fish and aquarium fish in various regions of the Indo-Pacific. This is destructive to the coral reef ecosystems, because it kills non-target fish, coral, and reef invertebrates (Barber & Pratt 1997, 1998; CCIF 2001). This technique was developed in the 1960s in the Philippines and spread to Indonesia in the 1990s by Filipino divers in search of new sources of live fish for the food trade who trained local fishermen (Barber & Pratt 1997, 1998). According to the Conservation and Community Investment Forum, cyanide fishing has been used there for so long that it is commonly thought of as “traditional” (CCIF 2001). Locations where use of cyanide and destructive fishing practices are known or suspected to occur correspond to the majority of chambered nautilus’ range countries (Barber & Pratt 1997; WRI 2008). Notably, the Philippines Cyanide Fishing Reform Program is attempting to address this problem by providing training in alternative fishing techniques (WRI 2008).

Similar to blast fishing, cyanide fishing is unlikely to result in direct mortality of *N. pompilius*, given the species’ preferred depth range; however, changes in coral reef community structure and loss of fish biomass (Raymundo et al. 2007) could decrease the availability of food resources for the chambered nautilus. Additional research is needed to determine the effects of cyanide on the deeper-water reef habitats.

Overall, given the uncertain effects of blast and cyanide fishing on nautilus populations, and the patchy and largely unknown distribution of the species and its habitat preferences, the best available information does not indicate that habitat degradation from the harvest of coral reef species and destructive and unselective fishing practices are likely significant threats to the species. Further research is needed to determine the extent of nautilus habitat degradation and the impacts on the status of the species.

Pollution and Sedimentation

Excerpt from CITES (2016):

Pollution and sedimentation impacting large portions of coral reefs, especially the coastal reefs areas, are reported in parts of Australia, China, Fiji, New Caledonia, Solomon Islands, the Philippines, Vanuatu, Viet Nam, and Western Samoa, potentially impacting chambered nautilus habitat (Ah-Leong & Sapatu 2009; Burke *et al.* 2002; Kere 2009; Raubani 2009; Sykes & Morris 2009; Wantiez *et al.* 2009). Between 80-90 percent of the wastewater dumped into Indo-Pacific waters is untreated (Nelleman *et al.* 2008). Increased sedimentation compromises the health and composition of the coral community on the reef, destroying habitat (International Society for Reef Studies (ISRS) 2004). Habitat destruction and pollution from deep sea mining occurs within or impacts chambered nautilus habitat; for instance, in Australia and Papua New Guinea, effluent and mining tailings from coastal areas either flow into or are dumped into chambered nautilus habitat (A. Dunstan, Queensland Government Department of Environment and Heritage Protection, Raine Island Recovery Project, Australia, pers. comm. 2010).

Cephalopods are sensitive to chemical pollution and have low tolerance for salinity changes (Beeton 2010). Bioaccumulation and transfer of heavy metal pollutants up the food chain have been reported for three cephalopod relatives of chambered nautilus: the common octopus (*Octopus vulgaris*), the common cuttlefish (*Sepia officinalis*), and the European squid (*Loligo vulgaris*) (as summarized in Pierce *et al.* 2010; Rjeibi *et al.* 2014). Despite their differences in life histories, it is possible that chambered nautilus are similarly affected, as they share certain physiological characteristics with their coleoid counterparts. For example, chambered nautilus have blood chemistry similarities with octopuses and giant squid (*Architeuthis* spp.) (Brix *et al.* 1994); oxygen-diffusing capacities similar to octopuses (Eno 1994); and genetic structural similarities of hemocyanins with octopuses (Bergmann *et al.* 2006).

Evidence of the impacts of pollution and sedimentation on chambered nautilus habitat and the effects to the species is speculative or largely unavailable. For example, in their review of the nautilus CITES proposal, the fifth FAO expert advisory panel (FAO panel) hypothesized that an observed 60 percent decline in a local *N. pompilius* population in Fiji was potentially because of pollution of its habitat (FAO 2016). This assumption was largely based on the fact that no known local utilization of the species and no commercial fishery exists in this area. Therefore, the FAO panel speculated that the decline was attributed to local habitat degradation as they noted the population is in close proximity to a major port (Suva) and its potentially small and fragmented characteristics made it especially vulnerable to habitat destruction (FAO 2016).

Although mining may also contribute to the pollution of chambered nautilus habitat, it appears that the extent of this pollution, and its subsequent impacts on nautilus populations, may be largely site-specific. For example, in a study comparing bioaccumulation rates of trace elements between nautilus species located in a heavily mined location (i.e., *N. macromphalus* in New Caledonia) versus a location not subject to significant mining (i.e., *N. pompilius* in Vanuatu), Pernice et al. (2009) found no significant difference between the species for trace elements of Ag, Co, Mn, Ni, Pb, Se, V, and Zn. The authors concluded that the geographical origin of the nautilus species was not a major contributor to interspecific differences in trace element concentrations (Pernice et al. 2009). Additionally, the authors noted that, based on the study results, the heavy nickel mining conducted in New Caledonia does not appear to be a significant source of contamination in the oceanic habitat of the nautilus, suggesting that the lagoons in New Caledonia likely trap the majority of the trace elements from the intense mining activities (Pernice et al. 2009).

It is worth noting that the species mentioned above (*N. macromphalus*) in the CITES (2016) excerpt regarding heavy metal pollutant bioaccumulation tend to occur in highest abundance in much shallower depths than the chambered nautilus. For example, the common octopus is generally found from the coast to the outer edge of the shelf, up to 200 m depths, and the common cuttlefish is most abundant around 100 m depths (Jereb et al. 2015). In fact, the shell of the common cuttlefish implodes between 150 and 200 m depths (Jereb et al. 2015). While the European squid may be found in depths of up to 500 m, most reports suggest the species is most common in water shallower than 100 m (Jereb et al. 2015). Given the coastal distribution of these species, they are likely much more susceptible to chemical pollution through industrial, domestic, and agricultural practices compared to the deeper-dwelling chambered nautilus. As such, using these species as proxies for potential bioaccumulation rates in *N. pompilius* may not be valid.

Additionally, many of the studies that have evaluated metal concentrations in cephalopods examined individuals outside of the range of the chambered nautilus (for example, Rjeibie et al. 2014, referenced in the CITES (2016) excerpt, studied tissues from cephalopods off Tunisia), with results that show that metal concentrations vary greatly depending on geography (Rjeibi et al. 2014; Jereb et al. 2015). As such, to evaluate the threat of bioaccumulation of toxins in chambered nautilus, information on concentrations of these metals from *N. pompilius*, or similar species that share the same life history and inhabit the same depth and geographic range of *N. pompilius*, is necessary. Presently, the biological impact of potential toxin and metal bioaccumulation in chambered nautilus populations is unknown. While the study by Pernice et al. (2009) indicated no significant difference in the bioaccumulation rates of trace elements between nautiluses located in areas of intensive mining (and, therefore, high heavy metal pollutants) compared to nautiluses in areas without

significant mining, there is no information on the lethal concentration limits of toxins or metals in the species. Additionally, evidence to suggest that current concentrations of environmental pollutants are causing detrimental physiological effects to the point where the species may be at increased risk of extinction is lacking. As such, the best available information does not indicate that present bioaccumulation rates and concentrations of environmental pollutants in *N. pompilius* are significant threats to the species.

Climate Change and Ocean Acidification

Excerpt from CITES (2016):

Coral bleaching caused by increased water temperatures has impacted reefs in Australia, Palau, and Thailand, exacerbating the negative impacts on coral reefs from pollution and overharvest (Burke *et al.* 2002; Golbuu *et al.* 2005; Nelleman *et al.* 2008; NOAA Satellite & Information Service 2010). Ocean acidification and warming increases uptake of heavy metals in early life stages, as documented in cuttlefish in the context of ocean acidification and ocean warming, as well as decreased salinity on hatching (Lacoue-Labarthe *et al.* 2009; Palmegiano & d'Apote 1983). Ocean acidification changes oxygen distribution and reduces pH (e.g. Hofmann *et al.* 2010; Stramma *et al.* 2010). Rising acidity increased the corrosiveness of the water to calcium carbonate (Turley & Boot 2010; Turley & Gattuso 2012). Such fluctuations may negatively impact chambered nautilus given their reliance on calcium uptake, storage, and processing as part of their physiological development and biological functions.

Given the strict temperature tolerance of the chambered nautilus, warming surface water temperatures may further restrict the distribution of the species, decreasing the amount of suitable habitat (particularly in shallower depths) available for the species. Perhaps more concerning may be the effects of ocean acidification. In terms of ocean acidification, which will cause a reduction of pH levels and concentration of carbonate ions in the ocean, it is thought that shelled mollusks are likely at elevated risk as they rely on the uptake of calcium and carbonate ions for shell growth and calcification. However, based on available studies, the effects of increased ocean acidification on juvenile and adult mollusk shell growth and physiology are highly variable (Gazeau *et al.* 2013). For example, after exposure to severe CO₂ levels (PCO₂ = 33,000 µatm) for 96 hours, the deep-sea clam, *Acesta excavata*, exhibited an initial drop in oxygen consumption and intracellular pH but recovered with both levels approaching control levels by the end of the exposure duration (Hammer *et al.* 2011). No mortality was observed over the course of the study, with the authors concluding that this species may have a higher tolerance to elevated CO₂ levels compared to other deep-sea species (Hammer *et al.* 2011). This is in comparison to intertidal and subtidal mollusk species, such as *Ruditapes decussatus*, *Mytilus*

galloprovincialis, and *M. edulis*, which exhibited reduced standard metabolic rates and protein degradation when exposed to decreases in pH levels (Gazeau et al. 2013).

In terms of the impact of ocean acidification on calcification rates, which is important for the growth of chambered nautilus, one relevant study looked at cuttlebone development in the cephalopod *Sepia officinalis* (Gutowska et al. 2010). Similar to nautilus, cuttlefish also have a chambered shell (cuttlebone) that is used for skeletal support and for buoyancy regulation. Results from the study showed that after exposure to 615 Pa CO₂ for 6 weeks, there was a seven-fold *increase* in cuttlebone mass (Gutowska et al. 2010). However, it should be noted that unlike *N. pompilius*, *Sepia officinalis* is not a deep-sea dwelling species but rather found in 100 m depths, and their cuttlebone is internal (not an external shell).

While the above were only a few examples of the variable impacts of ocean acidification on mollusk species, based on the available studies, such as those described in Gazeau et al. (2013), it is clear that the effects are largely species-dependent (with differences observed even *within* species). To date, we are unaware of any studies that have been conducted on *N. pompilius* and the potential effects of increased water temperatures or acidity on the biological status of the species. Therefore, given the species-specific sensitivities and responses to climate change impacts, and with no available information on chambered nautilus, we conclude that the best available information at this time does not indicate that impacts from climate change are posing significant threats or will pose significant threats to the existence of the species in the future.

Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

The primary threat to the chambered nautilus is overutilization for commercial purposes—mainly, harvest for the international nautilus shell trade. Chambered nautilus shells, which have a distinctive coiled interior, are traded as souvenirs to tourists and shell collectors and also used in jewelry and home décor items (where either the whole shell is sold as a decorative object or parts are used to create shell-inlay designs) (CITES 2016). The trade in the species is largely driven by the international demand for their shells and shell products since fishing for nautilus has been found to have no cultural or historical relevance (Dunstan et al. 2010; De Angelis 2012; CITES 2016; Freitas and Krishnasamy 2016). Nautilus meat is also not locally in demand (or used for subsistence) but rather sold or consumed as a by-product of fishing for the nautilus shells (De Angelis 2012; CITES 2016). While all nautilus species are found in international trade, *N. pompilius*, being the most widely distributed, is the species most commonly traded (CITES 2016).

Although most of the trade in chambered nautilus originates from the range countries where fisheries exist or have existed for the species, particularly the Philippines and

Indonesia, commodities also come from those areas with no known fisheries (such as Fiji and Solomon Islands). Other countries of origin for *N. pompilius* products include Australia, China, Taiwan, India, Malaysia, New Caledonia, Papua New Guinea, Vanuatu, and Vietnam (Freitas and Krishnasamy 2016). Known consumer markets for chambered nautilus products include the Middle East (United Arab Emirates, Saudi Arabia), Australia, Singapore, Malaysia, Indonesia, Philippines, Hong Kong, Russia, Korea, Japan, China, Taiwan and India, with major consumer markets noted in the European Union (Italy, France, Portugal), the United Kingdom, and the United States (Freitas and Krishnasamy 2016). In fact, between 2005 and 2014, the United States imported more than 900,000 chambered nautilus products (CITES 2016). The vast majority of these U.S. imports originated from the Philippines (85 percent of the traded commodities), followed by Indonesia (12 percent), China (1.4 percent), and India (1.3 percent) (CITES 2016).

Because harvest of the chambered nautilus is primarily demand-driven for the international shell trade, the intensive nautilus fisheries that develop to meet this demand tend to follow a boom-bust cycle that lasts around a decade or two before becoming commercially nonviable (Dunstan et al. 2010; De Angelis 2012; CITES 2016). Fishing for nautilus is fairly inexpensive and not labor-intensive, requiring a fish trap baited with locally-available meat (e.g., cow, duck, goat, offal, chicken, pufferfish) (Freitas and Krishnasamy 2016). These traps are usually set at 150 to 300m depths and retrieved after a few hours or left overnight (Freitas and Krishnasamy 2016). Given the minimal fishing gear requirements, and the fact that chambered nautilus exists as small, isolated populations, harvest of the species may continue for years within a region, with the fisheries serially depleting each population until the species is essentially extirpated from that region (CITES 2016). Commercial harvest of the species is presently occurring or has occurred in the Philippines, Indonesia, India and Papua New Guinea, and also potentially in China, Thailand and Vanuatu (CITES 2016). However, based on the number of commodities entering the international trade, it is likely that the Philippines and Indonesia have the largest commercial fisheries for chambered nautilus, with multiple harvesting sites throughout these nations (CITES 2016). Although information on harvest levels and the status of chambered nautilus populations within this portion of its range is limited, the available data, discussed below, provide extensive evidence of the significant negative impact of these fisheries and overutilization of the species.

Commercial Harvest

Philippines

Excerpt from CITES:

According to traders, harvest and trade of chambered nautilus has occurred here since at least the 1970s (Freitas & Krishnasamy 2016). Schroeder (2003) noted that while the fishery was targeted in some areas, bycatch occurred in others where the specimens were not marketed. Fishermen in Palawan and Bohol report that harvesting chambered nautilus is not a traditional subsistence fishing activity and that trapping techniques were learned from demand-driven shell traders (Dunstan 2010; NMFS 2014). More than 18,500 whole nautilus shells were encountered in a survey of 162 shops visited in Luzon, Visayas, Mindanao, Manila, Cebu, and Zamboanga, (Freitas & Krishnasamy 2016). Many of the shells are processed in Cebu City, Philippines, where there are many factories as well as an international airport that facilitates export (Devanadera pers. comm. 2016). The meat is less valuable but rather than discard it, fishermen will eat it or occasionally sell some of the meat in local markets (del Norte-Campos 2005; Freitas & Krishnasamy 2016). Traders indicate that international demand for chambered nautilus is primarily for the whole shell, including shells that are incorporated whole as curios (Freitas & Krishnasamy 2016). There appear to be no cultural, historical, or social connections to harvesting chambered nautilus in the Philippines, other than as a source of local income for the shell and meat trade (del Norte 2005; Dunstan *et al.* 2010).

According to a review by Saunders et al. (2017a), anecdotal accounts of fishing for *N. pompilius* in the southcentral Philippines indicate trapping of the species has actually occurred since the early 1900s. Specifically, these accounts suggest trapping in 1900 and 1901 would yield anywhere from 4-5 nautilus per trap to up to 20 animals (depending on the duration of the trap set) (Saunders et al. 2017a). In 1971, Haven (1972 cited in Haven (1977)) found that Tañon Strait, Philippines, was still an abundant source of *N. pompilius*. From 1971 to 1972, around 3,200 individuals were captured for study (Haven 1977). Prior to this time, *N. pompilius* was, for the most part, caught as bycatch in fish traps by Filipino fishermen (Saunders et al. 2017a). However, Haven (1977) notes that it was during this time when more fisherman began targeting this location, specifically for nautilus shells, with the numbers of fishermen tripling during subsequent years. Trap yields in 1972 were similar to those from the early 1900s, with fishermen reporting catches of zero to 19 nautilus, with an average of 5 animals per trap (Saunders et al. 2017a). However, by 1975, the impact of this substantial increase in fishing pressure on the species was already evident (Haven 1977). Fishermen in 1975 reported having to move operations to deeper water as catches were now rare at shallower depths, and the number of individuals per trap had also decreased (Haven 1977). Additionally, although the number of fishermen had tripled in those 3 years, and therefore fishing effort for the species intensified, the catch did not see an associated increase, indicating a likely decrease in the abundance of the species within the area (Haven 1977). From October to November of 1975, fishermen reported around 220 trapped individuals, a number similar to the 300

individuals caught by Haven (1977) in the month of October in 1971 and before the widespread establishment of the nautilus fishery. However, by 1979, trap yields had drastically fallen, to around 2 nautilus per trap, and only a few fishermen remained engaged in the fishery (Saunders et al. 2017a). CITES (2016) reports that around 5,000 chambered nautilus were trapped per year in Tañon Strait in the early 1980s, and by 1987, the population was estimated to have declined by 97 percent, with the species considered commercially extinct and potentially extirpated from the area (Alcala and Russ 2002). Based on 2014 data from baited remote underwater video station footage in the region, nautilus activity remains low and the population density still has yet to recover to pre-1970 levels (Saunders et al. 2017a). Similarly, other nautilus fishing sites that were established in the late 1980s, including at Tawi Tawi (an island province in southwestern Philippines), Cagayancillo (an island in the Palawan province) and Cebu Strait (east of Tañon Strait), have also seen harvest crash in the last couple decades (Dunstan et al. 2010). More recently, in the Central Luzon region, Bulacan and Pampanga Provinces were formerly collection and trade sites for nautilus species; however, collectors and traders noted that the last shipments from these areas were back in 2003 and 2007, respectively, indicating they are likely no longer viable harvesting sites (Freitas and Krishnasamy 2016).

The level of harvest (5,000 chambered nautilus individuals/year) that appeared to lead to local extirpations in Tañon Strait is being greatly exceeded in a number of other areas throughout the chambered nautilus' range in the Philippines. In Tibiao, Antique Province, in northwestern Panay Island, del Norte-Campos (2005) estimated annual yield of the chambered nautilus at around 12,200 individuals for the entire fishery (data from 2001 to 2002). In the Palawan nautilus fishery, 9,091 nautilus were harvested in 2013 and 37,341 in 2014 (personal communication cited in CITES (2016)). This level of harvest is particularly concerning given the significant declines already observed in these fisheries. In fact, in four of the five main nautilus fishing areas in this province, Dunstan et al. (2010) estimated a decline in CPUE of the species ranging from 70 percent to 90 percent (depending on the fishing site) over the course of only 6 to 24 years. The one main fishing region in Palawan that did not show a decline was the municipality of Balabac; however, the authors note that this fishery is relatively new (active for less than 8 years), with fewer fishermen, and, as such, may not have yet reached the point where the population crashes or declines become evident in catch rates (Dunstan et al. 2010). However, given that the estimated annual catches in the Balabac municipality ranged from 4,000 to 42,000 individuals in 2008 (Dunstan et al. 2010), this level of annual harvest, based on the trends from the other Palawan fishing sites (Dunstan et al. 2010), will likely lead to similar population declines of chambered nautilus in the near future.

In addition to the declines in harvest and CPUE of the species from observed fishing sites throughout the Philippines, the overutilization of *N. pompilius* in this area is also evident in

the available trade data. In a personal communication cited in CITES (2016), it was stated that over the past five years, shell traders in Palawan Province have seen a decline in the number of shells being offered to them by local harvesters. Similarly, harvesters and traders in the Visayan regions have noted increasing difficulty in obtaining shells, with this trend beginning in 2003 (CITES (2016) citing Schroeder (2003)). Based on U.S. trade data from the last decade, Philippine export and re-export of nautilus commodities to the United States has decreased by 92 percent since 2005 (Figure 4) (CITES 2016).

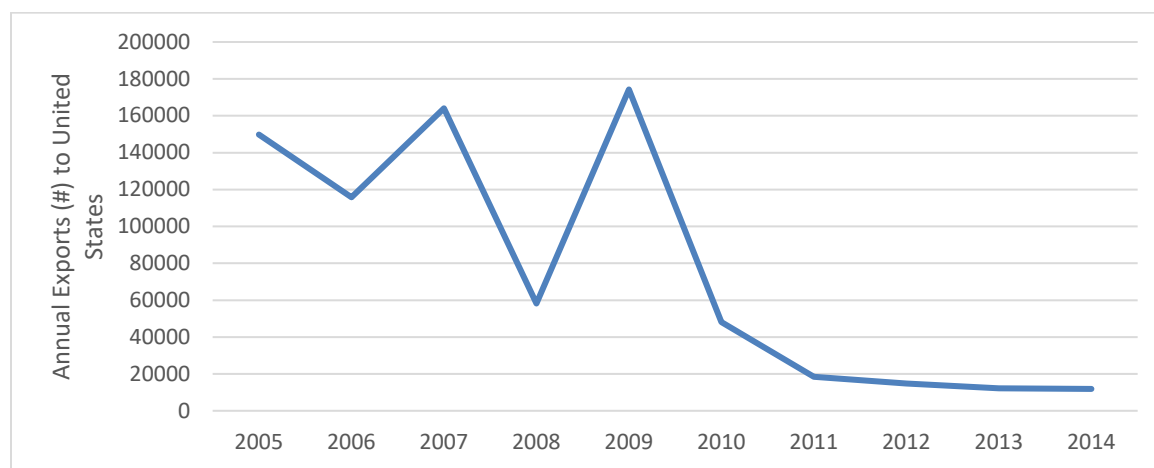


Figure 4. Philippine exports and re-exports of all nautilus commodities to the United States between January 2005 and December 2014. Source: CITES (2016).

Despite the extensive evidence of overutilization of the species throughout the Philippines, including the serial depletion and potential extirpation of local populations, harvest and trade in *N. pompilius* continues, with the Philippines still the number one supplier of nautilus commodities to the United States (based on figures from 2014).

Indonesia

Signs of decline and overutilization of chambered nautilus populations are also apparent off Indonesia. In fact, based on the increasing number of chambered nautilus commodities originating from Indonesia, it has been suggested that nautilus fishing has potentially shifted to Indonesian waters because of depletion of the species in the Philippines (CITES 2016). According to trade data reported in De Angelis (2012), the Philippines accounted for 87 percent of the nautilus commodities in U.S. trade from 2005 to 2010, whereas Indonesia accounted for only 9 percent. However, with the significant decline of nautilus exports coming out of the Philippines in recent years (2010 to 2014), Indonesia has become a larger component of the trade, accounting for 42 percent of the nautilus commodities in 2014, while the Philippines has seen a decrease in their proportion, down to 52 percent (CITES 2016).

Similar to the trend observed in the Philippines, a pattern of serial depletion of nautilus because of harvesting is emerging in Indonesia. Both fishermen and traders note a significant decline in the numbers of chambered nautilus over the last 10 years, despite a prohibition on the harvest and trade of *N. pompilius* that has been in place since 1999 (CITES 2016; Freitas and Krishnasamy 2016). For example, fishermen in North Lombok note that they used to trap around 10 to 15 nautilus in one night, but currently catch only 1 to 3 per night (Freitas and Krishnasamy 2016). Similarly, in Bali, fishermen reported nightly catches of around 10 to 20 nautilus until 2005, after which yields have been much less (Freitas and Krishnasamy 2016). While fishing for chambered nautilus has essentially decreased in western Indonesia (likely because of a depletion of the stocks), the main trade centers for nautilus commodities are still located here (i.e., Java, Bali, Sulawesi and Lombok). The sources of nautilus shells for these centers now appears to originate from eastern Indonesian waters (including northeastern Central Java, East Java, and West Nusa Tenggara eastward) where it is thought that nautilus populations may still be abundant enough to support economically viable fisheries, and where enforcement of the current *N. pompilius* prohibition appears weaker (Nijman et al. 2015; Freitas and Krishnasamy 2016). Data collected from two large open markets in Indonesia (Pangandaran and Pasir Putih) indicate that chambered nautilus are still being offered for sale as of 2013. Over the course of three different weekends, Nijman et al. (2015) observed 168 *N. pompilius* shells for sale from 50 different stalls in the markets (average price was \$17 USD/shell). In addition to catering to tourists, a wholesaler with a shop in Pangandaran noted that he also exports merchandise to Malaysia and Saudi Arabia on a bimonthly basis (Nijman et al. 2015). In total, Nijman et al. (2015) found evidence of six Indonesian wholesale companies that offered protected marine mollusks (and mostly nautilus shells) for sale on their respective websites (with two based in East Java, two in Bali, and one in Sulawesi). The company in Sulawesi even had a minimum order for merchandise of 1 metric ton, and company in Java noted that they could ship more than one container per month, indicating access to a relatively large supply of nautilus shells (Nijman et al. 2015).

The available U.S. trade data provide additional evidence of the likely overutilization and potential serial depletion of populations within Indonesia, although not yet as severe as what has been observed in the Philippines. Based on data from the last decade, Indonesian export and re-export of nautilus commodities to the United States has decreased by 23 percent since 2005 (Figure 5) (CITES 2016); however, large declines were seen between 2006 and 2009 before smaller increases in the following years. As noted above, these trends may likely be depicting the depletion of nautilus populations in western Indonesian waters and a subsequent shift of fishing effort to eastern Indonesian waters in recent years to support the nautilus trade industry.

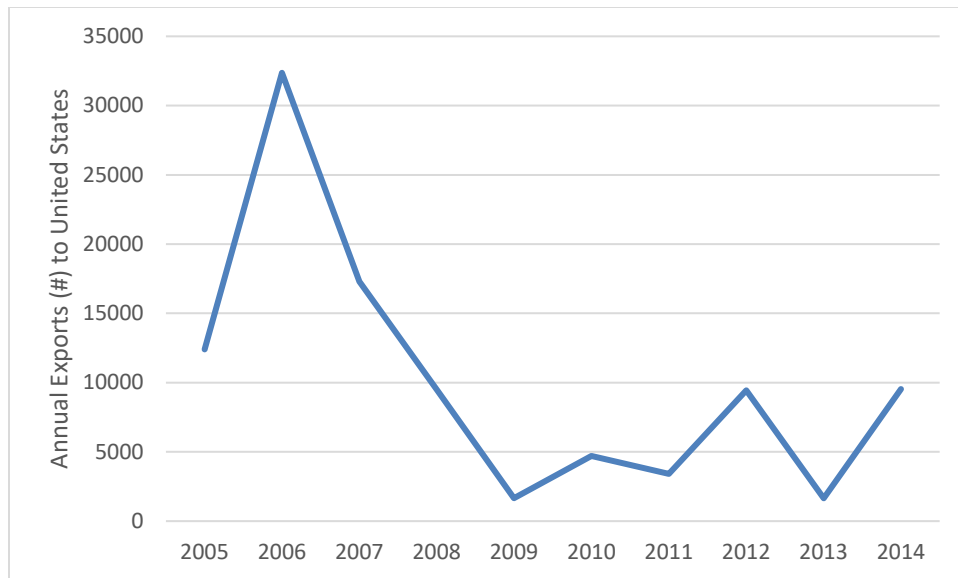


Figure 5. Indonesian exports and re-exports of all nautilus commodities to the United States between January 2005 and December 2014. Source: CITES (2016).

India

In India, CITES (2016) states that the chambered nautilus has been exploited for decades and is also caught as bycatch by deep sea trawlers. A 2007 survey aimed at assessing the status of protected species in the curio trade in Tamil Nadu confirmed the presence of *N. pompilius* shells and found them highly valued in the retail domestic markets (John et al. 2012). Out of 13 major coastal tourist curio markets surveyed, *N. pompilius* shells were found in 20 percent of the markets (n=40 shops) (John et al. 2012). Based on estimated sales from these markets, *N. pompilius* was the fourth highest valued species (n=25 total species), accounting for 7 percent of the annual profit from the protected species curio trade (John et al. 2012). During the survey, chambered nautilus shells sold, on average, for approximately 275INR each (7 USD in 2007 dollars) (John et al. 2012).

Interviews with the curio traders indicate that the Gulf of Mannar and Palk Bay, the island territories of Andaman and Lakshadweep, and Kerala are the main collection areas for the protected species sold in the curio trade (John et al. 2012). While the extent of harvest of *N. pompilius* is unknown, the fact that the nautilus shells sold in markets are nearly half the size of the reported common wild size (90 mm vs 170 mm) (John et al. 2012) suggests that this curio trade may be contributing to overfishing of the population, causing a shift in the local population structure. Compared to observed mature shell sizes elsewhere throughout the range of *N. pompilius* (average mature shell length range: 114 to 200 mm; Table 1), the Indian market nautilus shells are likely entirely from immature individuals. The removal of these nautilus individuals before they have time to reproduce, particularly for this long-lived and low fecund species, can have devastating impacts on the viability of the local

populations. While the authors note that curio vendors may strategically stock a larger number of undersized shells rather than fewer larger shells to meet the demand of the tourists, given the relative rarity of chambered nautilus shells in Indian waters (with only 9 shells sold during the 2007 survey) and the fact that larger shells generally obtain higher prices, it is likely that curio vendors are stocking whatever is available.

Although trend data are not available, the popularity of the species in the curio trade as well as information suggesting that the marketed shells are significantly smaller than wild-caught and likely belong to immature individuals indicate that this level of utilization may have already negatively impacted the local populations within India. The continued fishing and selling of *N. pompilius* within southern Indian waters will likely lead to overutilization of the species, as has been observed in other parts of its range, and potential extirpation of these small and isolated populations.

Papua New Guinea

Excerpt from CITES (2016):

Nautilus meat does not appear to be traditionally eaten locally (Kailola 1995). Shells might occasionally be kept as ladles, but it would be rare to find the shell being sold in the local market (Saunders *et al.* 1991). Trade from this country was believed to derive from incidental collection of drift shells because there had been no known chambered nautilus fishery or deep-water trapping prior to the 1990s (Saunders pers. comm. 2009; Saunders *et al.* 1991). Research data obtained on two populations in the early 1980s showed similar male:female ratios to unfished populations (Saunders pers. comm. 2014; Ward 2014). However, a fisheries resources publication later noted that chambered nautilus are collected in Papua New Guinea as ‘specimen shells’ (for shell collectors); such shells are generally collected from live animals to obtain undamaged shells. Shells are also used as inlay and the species may be caught as bycatch in deep-slope fisheries (Kailola 1995). New fishing sites may have opened in at least two locations around 2008, but the extent and impact of harvest have not been investigated.

Possible Commercial Harvest

East Asia (China, Hong Kong, and Taiwan)

Minimal numbers of nautilus shells are sold in art markets, home décor shops, small stores, and airport gift shops, with meat found in seafood markets (particularly in the south of China on Hainan Island, the large coastal cities of Fujian and Guangdong Provinces, and Taiwan) (Freitas and Krishnasamy 2016). There is also evidence of a small trade in live specimens for aquaria in Hong Kong; however, the origin of these live specimens is unclear (Freitas and Krishnasamy 2016). While the CITES (2016) proposal suggests that nautilus

harvest may occur on Hainan Island, we found no information to confirm that a fishery exists.

Thailand

Species experts note that targeted chambered nautilus fisheries have occurred and are occurring in Thailand (NMFS 2014), with past observations of shells found in gift shops (CITES 2016); however, we could find no published information on the current intensity or duration of such harvest (or confirmation that the fishery is still occurring).

Vanuatu

Species experts note that targeted chambered nautilus fisheries have occurred and are occurring in Vanuatu (NMFS 2014), with shells sold to tourists and collectors (Amos 2007). While we could find no published information on the current intensity or duration of such harvest (or confirmation that the fishery is still occurring), we note that the start of the fishery may have begun in the late 1980s. From March to June 1987, the Vanuatu Fisheries Department conducted a deep sea fishing trial, aimed at testing commercial fishing traps on the outer-reef slope of north Efate Island, Vanuatu (Blanc 1988). Results showed the successful capture of *N. pompilius*, with a CPUE of around 2.6 nautilus per trap per day, taken at depths greater than 300 m (Blanc 1988). In total, 94 traps were set and 114 *N. pompilius* were captured (Blanc 1988). Those shells that were in good condition (approximately two-thirds of the total) were sold locally for around 300 to 500 VUV each (\$2.89 to \$4.81 U.S. dollars based on 1987 conversion rate) (Blanc 1988). It was noted in the report that the capture of nautilus can be a good supplementary source of income (Blanc 1988).

Vietnam

Nautilus shells are available from sellers in Vietnam. An interview with a Vietnamese seller revealed that his nautilus shells come from islands in Vietnam and that 1,000 shells a month are able to be acquired (of 5 to 7 inches in size; 127 to 178 mm) (Freitas and Krishnasamy 2016). However, the species was not identified, nor was it clear whether the origin of the shells was from Vietnam (indicating potential harvest) or if the islands simply serve as transit points for the trade.

No Known Commercial Harvest

American Samoa

There is no known local utilization or commercial harvest of chambered nautilus (CITES 2016).

Australia

There is no known local utilization of chambered nautilus (CITES 2016). Additionally, nautilus are not currently harvested in Australia's commercial fisheries (Department of the Environment and Energy 2016).

Fiji

Carlson (2014) reported on surveys conducted throughout Fiji from 1972 to 1975, which yielded no living nautilus; however, successful trapping methods were unknown at this time. While interviews with locals indicate that no one has ever seen a living nautilus (Carlson 2014), surveys conducted in Suva and Beqa passage in the 1980s and 2000s have successfully trapped living *N. pompilius* individuals (Zann 1984; Saunders et al. 1989; Tanabe et al. 1990; Barord et al. 2014), verifying the presence of *N. pompilius* in these waters.

Excerpt from CITES (2016):

There is no known local utilization of this species and there have been no known commercial fisheries. Drift shells have been incidentally collected for use in making jewelry and wood inlays that may be sold to tourists (Carlson pers. comm. 2009). LEMIS (2016) reports recent U.S. imports from Fiji (during 2011-2014). In the absence of commercial fisheries, exports from Fiji may be supplied by incidental collection (Carlson pers. comm. 2009; HSUS & HSI 2008).

Specifically, the Law Enforcement Management Information System (LEMIS) data mentioned above showed that the United States imported over 3,000 nautilus products from Fiji over the years 2011 to 2014.

Solomon Islands

There are no known commercial fisheries for nautilus. The jewelry and inlays in woodcarvings that are sold to tourists are obtained solely from drift shells (Carlson 2014).

Western Samoa

There is no known local utilization or commercial harvest of chambered nautilus (CITES 2016). Additionally, despite trapping efforts, the presence of chambered nautilus within these waters has not been confirmed, indicating that Western Samoa may not be part of the *N. pompilius* range (Saunders et al. 2017a; Saunders et al. 1989).

It is important to highlight that in those areas where the species is not subject to commercial harvest, populations appear stable (with the exception of Fiji; however, the threat in this case was not identified as overutilization—see **Present or Threatened**

Destruction, Modification, or Curtailment of Habitat or Range section). Given that the species exists as geographically isolated populations, it is unlikely that these local, unfished populations will see significant declines as a result of overutilization in other portions of its range. However, overall, out of the 10 nations in which *N. pompilius* is known to occur, potentially half historically or currently have targeted nautilus fisheries. Given that this harvest is largely unregulated, and has led to the serial depletion and extirpation of local *N. pompilius* populations, with no evidence of a decline in fishing effort or demand for the species, the best available information indicates that overutilization of *N. pompilius* is likely the most significant threat to the species throughout its range.

Trade Data

As mentioned previously, the commercial harvest of the chambered nautilus is primarily demand-driven for the international shell trade. The Philippines and Indonesia appear to supply the majority of the nautilus products in the trade. In Indonesia, most of the networks that aid in the illegal trade of marine mollusks originate in Java and Bali, with the United States, China, and New Caledonia as main destinations (Figure 6) (Nijman et al. 2015). While the extent of export from these two countries is unknown, data collected from Indonesia over the past 10 years suggest the amounts are likely substantial. For example, based on seizure data from 2005 to 2013, over 42,000 marine mollusk shells protected under Indonesian law, including over 3,000 chambered nautilus, were confiscated by Indonesian authorities (Nijman et al. 2015). At least two-thirds of the shells were meant to enter the international trade, with the largest volumes destined for China and the United States (Nijman et al. 2015). Between 2007 and 2010, De Angelis (2012), citing a personal communication, estimated that around 25,000 nautilus specimens were exported from Indonesia to China for the Asian meat market.

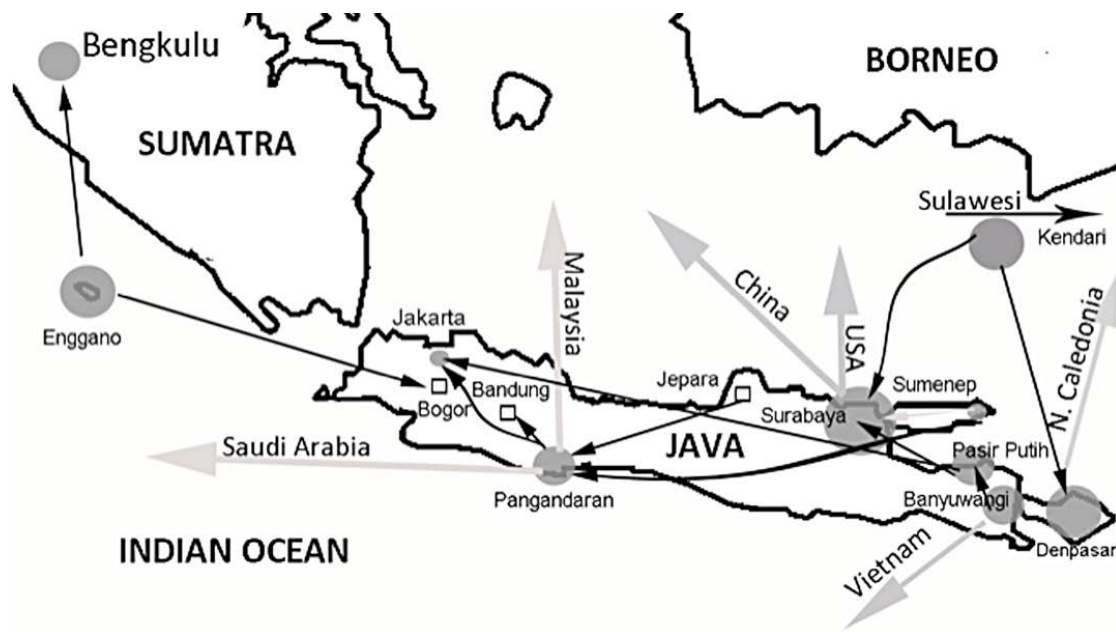


Figure 6. Known networks for the illegal trade of protected marine mollusks within Indonesia. Arrows point to destinations and the size of circles correspond to the volume of trade. Small circles = tens of traded shells, medium circles = hundreds of shells, large circles = thousands of shells, very large circles = shells traded in the ten thousands. Source: Nijman et al. (2015).

In addition to the United States and China, other major consumer destinations for nautilus commodities include Europe, the Middle East, and Australia, with suspected markets in South Africa, South America (Argentina), and Israel (Figure 7) (Freitas and Krishnasamy 2016).

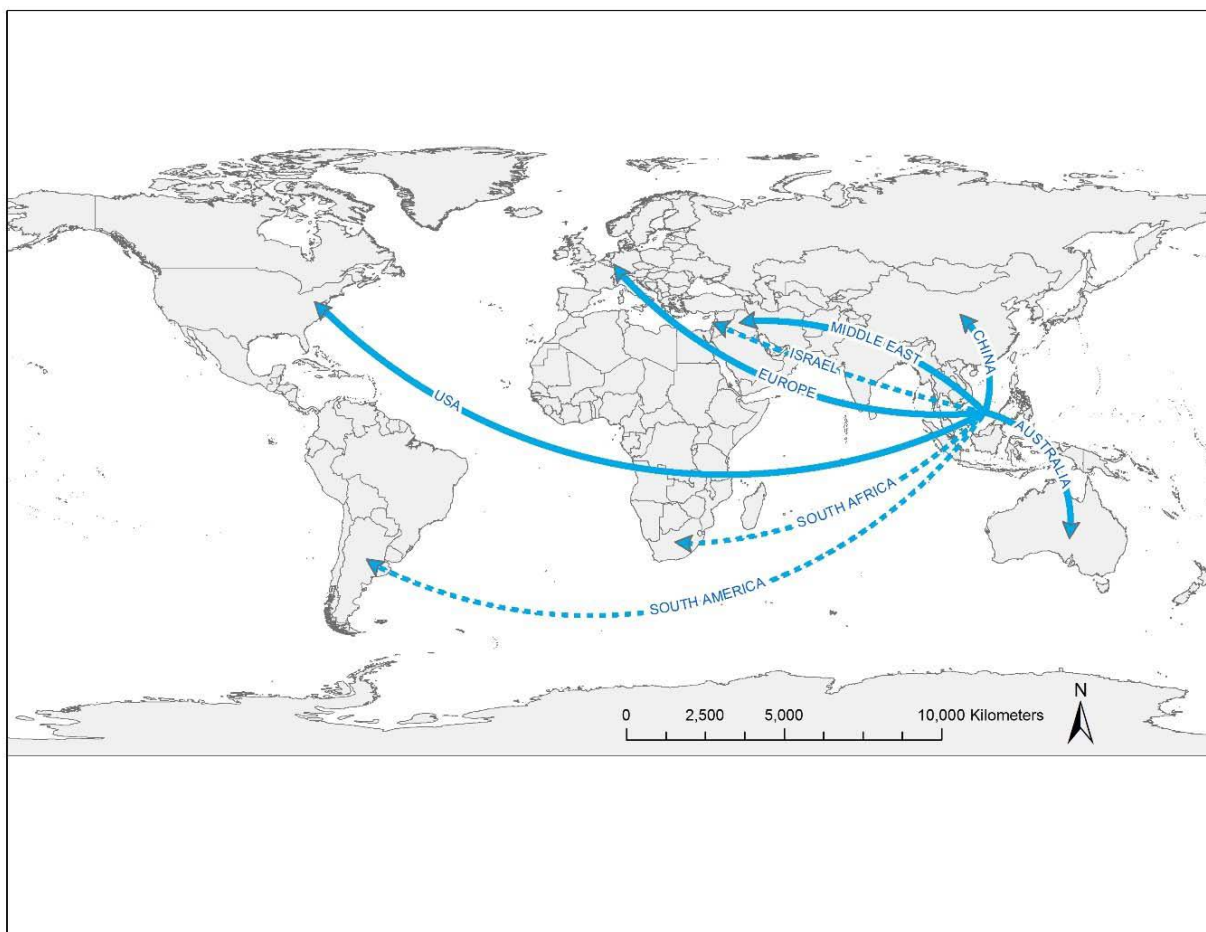


Figure 7. Global trade in nautilus. Known consumer markets identified through solid blue lines and suspected consumer markets identified through dotted blue lines. Source: Freitas and Krishnasamy (2016).

In Europe, Freitas and Krishnasamy (2016) indicate that the trade and sale of nautilus occurs at fairly low levels and mainly involves whole nautilus shells. Internet research and consultations indicate that the majority of websites selling nautilus products are located in France, Germany and the United Kingdom; however, details regarding the product, including species and origin of the nautilus, are often not provided (Freitas and Krishnasamy 2016). Based on interviews with trade experts and online sellers, the Philippines is the main source of nautilus shells for the European trade (Freitas and Krishnasamy 2016). Some German online sellers indicate that the wholesalers also receive imports from Thailand (Freitas and Krishnasamy 2016).

In the United States, the most recent 5 years of available trade data (2010 to 2014) reveal that around 6 percent of the imported commodities were whole shells ($n=9,076$) and less than 1 percent were live animals ($n=142$), with the remaining products primarily

comprised of jewelry, shell products, and trim pieces (CITES 2016). Based on trade data from 2010-2013 and using rough approximations of individual nautilus counts for different commodity labels, Freitas and Krishnasamy (2016) estimated that between 20,000 and 100,000 nautilus individuals comprised the commodities being imported into the United States, representing between 6,000 and 33,000 individuals annually. However, it is important to note that even these figures likely underestimate the actual trade volumes in the United States, as additional nautilus imports could have also been lumped under a more general category, such as “mollusks” (De Angelis 2012). This is likely true for other countries, as specific custom codes are lacking for nautilus products (with nautilus commodities frequently lumped as “coral and similar materials” and worked or unworked shell products) (Freitas and Krishnasamy 2016). Therefore, estimating the global number of nautilus individuals traded annually remains extremely challenging. Despite these unknowns, based on the available trade data from the United States, and data garnered from seizures and research, it is clear that nautilus commodities are in high demand and nautilus products are likely globally traded in the hundreds of thousands (De Angelis 2012), with this demand considered a significant threat driving the commercial harvest and overutilization of *N. pompilius* throughout most of its range.

Disease or Predation

Diseases in nautilus are not well known, nor is there information to indicate that disease is contributing to population declines of the species. However, shells of *N. pompilius*, like other mollusks, are subject to marine fouling from a variety of epizoans and may also be hosts to parasites. In an examination of 631 *N. pompilius* shells from the Philippines (n=350) and Papua New Guinea (n=281), Landman et al. (2010) found the incidence of encrustation by epizoans varied by site. In the *N. pompilius* shells from the Philippines, 12 percent were encrusted whereas 49 percent of the shells from the Papua New Guinea sample showed signs of encrustation. However, the encrusted area only averaged around 0.5 percent of the shell surface, with the maximum encrustation at 2.2 percent (Landman et al. 2010). Additionally, the authors note that the encrusted surface comprised less than 1 percent of the total shell weight in air, which they deemed “a negligible factor in the overall buoyancy of the animal” (Landman et al. 2010). As such, it is likely that the species has some other defense against epizoan settlement, with encrustation not likely a significant threat to the survival of *N. pompilius* individuals. In terms of parasites, Carlson (2010) notes that newly collected nautilus individuals are usually heavily infested with the copepod *Anchicaligus nautili*; however, no information on the effect of these infestations on the nautilus animal is available. Therefore, based on the available data, marine fouling and parasitism do not appear to be significant threats to the biological status of the species.

Excerpt from CITES (2016):

Predation limits chambered nautilus' movements within their habitat (Jereb & Roper 2005; Saunders pers. comm. 2009, 2016; Saunders et al. 2010; Ward 1987). Chambered nautilus show little defense or escape response, beyond retreating inside the chamber and closing their mantle (Daw & Barord 2007; Saunders & Landman 2010; Saunders et al. 2010). However, they exhibit certain behaviours that appear to be favourable to predator avoidance (Jereb & Roper 2005). Chambered nautilus avoid swimming in the open water column, where they are more vulnerable to predation (Saunders 1984b, 1990). Chambered nautilus migrate vertically within their habitat, with individuals moving into shallow water at night (up to about 100 m) and migrating back into deep-water at dawn (Saunders 1984b, 1990), which appears to coincide with reduced activity of teleosts in the shallows (Saunders et al. 2010; Saunders pers. comm. 2009, 2016; Ward 1987). While all chambered nautilus seem to exhibit these vertical movements, the frequency and extent of such migrations differ, probably depending on habitat, food availability, and predator conditions (Dunstan et al. 2011b; Saunders & Ward 1987; Ward & Martin 1980).

Excerpt from CITES (2016):

Natural predators of chambered nautilus include teleost fish, octopuses, and sharks (Saunders 1984b; Saunders & Ward 2010; Saunders et al. 1989, 1991; Ward 1987, 1988) (See Figure 2). Predation is evident on drift shells and as "shell wounds" on living animals (Arnold 1985; Saunders et al. 1989, 1991; Ward 1987, 1988). Predation pressure varies across their range. For example, research in Papua New Guinea indicated that more than 50 percent of drift shells showed evidence of bore hole predation by octopus species, and that 2–8 percent of live-caught animals showed evidence of octopus drilling (Saunders et al. 1991), while predation rates in Fiji appeared to be lower (Ward 1987).

In an investigation of two populations from Indonesia (Ambon and Sumbawa), Saunders et al. (2017b) found octopus predation rates that were similar to those in the live-caught animals from Papua New Guinea. Specifically, the authors found evidence of octopod drill holes in 4.5 percent of the Ambon population and 11 percent in the Sumbawa population (Saunders et al. 2017b). Elsewhere, octopod predation rates on live animals have been estimated at 1.1 percent in the Philippines, 5 percent (n=39) in American Samoa, and 3.2 percent (n=31) on Australia's Great Barrier Reef, indicating that predation by octopuses likely occurs throughout the entire species' range (Saunders et al. 1991).

Recently, Ward (2014) analyzed the prevalence of shell breaks in nautilus as an indicator of predation and found that those nautilus populations subject to fishing had a statistically significant higher number of major shell breaks compared to unfished populations. Specifically, Ward (2014) found that over 80 percent of mature *N. pompilius* shells had

major shell breaks in the fished Bohol, Philippines population (in 2012 and 2013) and calculated an over 40 percent rate in the fished New Caledonia *N. macromphalus* population in 1984. In contrast, only 30 percent of mature shells had major shell breaks in the unfished nautilus populations on the Great Barrier Reef (based on 2012 data) (Ward 2014). In the unfished Osprey Reef population, this rate was around 20 percent (based on 2002 to 2006 data), and in Papua New Guinea and Vanuatu in the 1980s, this rate was less than 20 percent (Ward 2014).

Predation is clearly evident in all sampled nautilus populations. However, it appears that predation rates may be substantially higher in those populations compromised from other threats (such as overutilization). This, in turn, exacerbates the risk that predation poses to those already vulnerable chambered nautilus populations, contributing significantly to their likelihood of decline and to the species' overall risk of extinction.

Inadequacy of Existing Regulatory Mechanisms

Based on the available data, *N. pompilius* appears most at risk of overutilization in those range states supplying the large majority of nautilus shells for the international trade. Substantial commercial harvest of the species in Indonesia, Philippines, India and potentially Papua New Guinea has led to observed declines in the local *N. pompilius* populations. Despite national protections, poor enforcement and illegal fishing demonstrate that the existing regulatory mechanisms inadequate to achieve their purpose of protecting the chambered nautilus from harvest and trade.

In Indonesia, *N. pompilius* was provided full protection in the nation's waters in 1999 (Government Regulation 7/1999). While the species was first added to Indonesia's protected species list in 1987 (SK MenHut No 12 Kptd/II/1987), the implementing legislation in 1999 made it illegal to harvest, transport, kill, or trade live or dead specimens of *N. pompilius* (CITES 2016). Despite this prohibition, the commercial harvest and trade in the species continues (see ***Overutilization for commercial, recreational, scientific, or educational purposes***). For example, in a survey of 343 shops within 6 Provinces in Indonesia, Freitas and Krishnasamy (2016) found that 10 percent were selling nautilus products, with the majority located in East Java. Interviews with local suppliers of nautilus shells revealed that many are aware of the prohibition and therefore have found ways to conduct business covertly, such as selling more products online and purposely mislabeling *N. pompilius* shells as *A. perforatus* (which are not protected) (Freitas and Krishnasamy 2016). Nijman et al. (2015) observed the sale of chambered nautilus shells in two of Indonesia's largest open markets (Pangandaran and Pasir Putih, both on Java) and remarked that the shells were prominently displayed. In interviews with the traders, none mentioned the protected status of the species (Nijman et al. 2015). Additionally, nautilus shells and products (such as furniture) are often on display by government officials and

offered for sale in airports, indicating that enforcement of the Indonesian regulation protecting the species is very weak. Therefore, given the apparent disregard of the prohibition, with substantial evidence of illegal harvest and trade in the species, and issues with enforcement, existing regulatory mechanisms are inadequate to protect the species from further declines in Indonesia from overutilization.

In the Philippines, shelled mollusks are protected from collection without a permit under Fisheries Administrative Order no. 168; however, it is unclear how this is implemented or enforced for particular species (CITES 2016). In Palawan Province, a permit is also required to harvest or trade the chambered nautilus as it is listed as “Vulnerable” under Palawan Council for Sustainable Development Resolution No. 15-521 (CITES 2016). Freitas and Krishnasamy (2016) report that some municipalities in Cebu Province and the Panay Islands have local ordinances that prohibit the trade and harvest of *N. pompilius*; however, even in these Provinces, there is evidence of harvest and trade in the species. For example, in a survey of 66 shops in Cebu, the Western Visayas region, and Palawan, 83 percent of the shops sold nautilus products. As recently as March 2017, shell exporters on Mactan Island (the major export hub for shells from Philippine waters) had a few hundred specimens of nautilus shells in stock and ready for sale (Dr. Karsten Schroeder personal communication, 2017).

Under Section 102 (b) of the Philippine Fisheries Code of 1998 (RA 8550 as amended by RA 10654), it is unlawful to fish, take, catch, gather, sell, purchase, possess, transport, export, forward or ship out aquatic species listed under Appendix II and III of CITES. In October 2016, the chambered nautilus was listed on Appendix II of CITES (see below) and the Philippine prohibition became effective on January 2, 2017. However, the export of government-inventoried chambered nautilus Pre-Convention specimens used in the shell craft industry of Cebu, Philippines is allowed until 2018. Given that this prohibition only recently went into effect, the enforcement of this regulation and subsequent adequacy in reducing the threat of overutilization to the species in the Philippines is highly uncertain.

Overall, based on the available information suggesting that enforcement of current regulations may be lacking or highly uncertain, with prior harvest and trade of nautilus that was essentially unregulated throughout the Philippines (Freitas and Krishnasamy 2016), and evidence of significant declines in the *N. pompilius* populations throughout this portion of the species’ range, existing regulations to protect *N. pompilius* from overutilization throughout the Philippines are inadequate.

In India, *N. pompilius* has been protected from harvest and trade since 2000 when it was listed under Schedule I of the Indian Wildlife (Protection) Act of 1972 (John et al. 2012). However, as noted in the ***Overutilization for commercial, recreational, scientific, or educational purposes*** section, *N. pompilius* shells were being collected in Indian waters

and sold in major coastal tourist curio markets as recently as 2007. Interviews with retail vendors (n=180) indicated that a large majority were aware of the Indian Wildlife Protection Act and legal ramifications of selling protected species yet continued to sell large quantities of protected marine mollusks and corals in the curio shops (John et al. 2012). Because there is no official licensing system for these shops, the annual quantities sold remains largely unrecorded and unknown (John et al. 2012). The high demand for nautilus shells and profits from this illegal curio trade, coupled with the lack of enforcement of existing laws, indicates that overutilization of *N. pompilius* will continue to threaten populations within Indian waters.

In China, *N. pompilius* is listed as a “Class I” species under the national Law of the People’s Republic of China on the Protection of Wildlife, which means that harvest is allowed (under Article 16) but only with special permission (i.e. for purposes of scientific research, ranching, breeding, exhibition, or “other”). Unfortunately, enforcement of this law has proven difficult as many nautilus products for sale have unknown origin or claim origin from the Philippines (Freitas and Krishnasamy 2016). While the extent of harvest in East Asia remains unclear based on the available data, the fact that trade is allowed, and the difficulties associated with enforcement and identifying *N. pompilius* products and origin in the trade, indicate that existing regulatory measures are likely inadequate to prevent the harvest of the species within Chinese waters.

In areas where trade of *N. pompilius* is prohibited, available data suggest smugglers are using other locations as transit points for the trafficking and trade of the species to circumvent prohibitions and evade customs (Freitas and Krishnasamy 2016). For example, New Caledonia, where only *N. macromphalus* is protected, has become a stop-over destination for smuggling nautilus shells to Europe (CITES 2016; Freitas and Krishnasamy 2016). In 2008, officials confiscated at least 213 *N. pompilius* shells that were being smuggled into New Caledonia from Bali, Indonesia (Freitas and Krishnasamy 2016). At this time, the extent of the illegal trade, including transit points for smugglers, remains largely unknown; however, the impact of this illegal trade on the species contributes further to its overutilization.

Overall, given the ongoing demand for chambered nautilus products, the apparent disregard of current prohibition regulations by collectors and traders, lack of enforcement, and the observed declining trends in *N. pompilius* populations and crashing of associated fisheries, the available information suggests that existing regulatory mechanisms are inadequate to control the harvest and overutilization of *N. pompilius* throughout most of its range, significantly contributing to the species’ risk of extinction.

As the international trade is the clear driving force of the intense exploitation of nautilus, in October 2016, the member nations to CITES agreed to add all nautilus species to

Appendix II of CITES (effective January 2017). This listing means increased protection for *N. pompilius* and the other nautilus species, but still allows for some legal and sustainable trade. Export of nautilus products now requires CITES permits or re-export certificates that ensure the products were legally acquired and that the Scientific Authority of the State of export has advised that such export will not be detrimental to the survival of that species (i.e., a “non-detriment finding”). Given that the international trade is the main driver of the threat to the species (i.e., overutilization), this listing should provide *N. pompilius* with some safeguards against future depletion of populations and potential extinction of the species. However, given the limited information on the present abundance of the species throughout its range, it is likely going to be difficult for State Authorities to determine what level of trade is sustainable. As the FAO panel notes, based on previous cases for species listed under Appendix II with similar circumstances, the following outcomes are likely to occur: 1) international trade ceases; 2) international trade continues but without proper CITES documentation (“illegal trade”); and/or 3) international trade continues with inadequate non-detriment findings (FAO 2016). Because this listing only recently went into effect (January 2017), it is too soon to know which outcome(s) will dominate, and, thus, the adequacy of the CITES listing is uncertain at reducing the threat of overutilization to the point where the species may no longer be at risk of declines throughout its range.

Other Natural or Manmade Factors Affecting its Continued Existence

Ecotourism

Excerpt from CITES (2016):

There are reports of ecotourism operations in Palau which trap chambered nautilus [*N. belauensis*] for use in photographs with customers of dive tour operations; the chambered nautilus are subsequently released into shallow waters. Although not as intensive as a commercial export fishery, chambered nautilus are especially vulnerable to predation from shallow water predators in the daytime. This has been noted by researchers conducting capture-release studies, where teleost fish attack the chambered nautilus as they are released in waters as shallow as 20 m (NMFS 2014; Saunders *et al.* 2010; Ward 1987). As seen in recent video footage, when animals are released in a consistent location, it essentially becomes a feeding station for triggerfish (Carlson & Awai 2015; <https://www.youtube.com/watch?v=dM9TFKUxnYc>). In addition, captured chambered nautilus can overheat and die before they are returned to the deep (Aguiar 2000); *Allonautilus* die quickly if pulled out of the water (NMFS 2014); and chambered nautilus may develop air bubbles upon descent which inhibits their ability to quickly return to the safety of their deep-water habitat zone (NMFS 2014). Thus, ecotourism may increase the predation threat to the animals upon their release. Given this tendency toward higher daytime predation in shallow waters,

researchers have modified their techniques to release animals in deeper waters following capture-release studies (Carlson & Awai 2015; Dunstan *et al.* 2011c).

Given that the above information on ecotourism is derived primarily from other nautilus species (*N. belauensis*), it is unclear if there are dive tour operators within the *N. pompilius* range who also practice the same behavior (i.e., taking photographs and releasing the species in shallow waters). In terms of researcher handling techniques, as the above excerpt notes, these have been modified to ensure nautilus are released in deeper waters to minimize the negative physiological responses to handling and potential predation risk of the species. As such, the best available information does not indicate that ecotourism is likely a significant threat to the species.

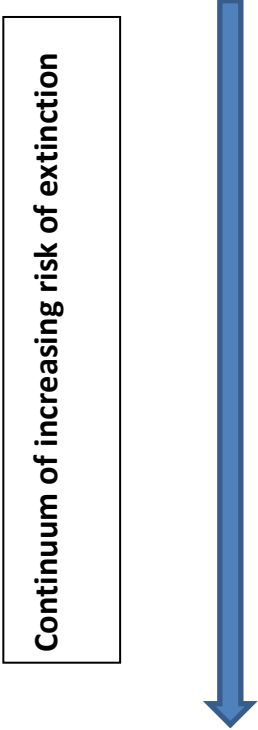
Natural Behavior

Because of their keen sense of smell (Basil *et al.* 2000), chambered nautilus are easily attracted to baited traps. Additionally, field studies indicate that nautilus may also habituate to baited sites. For example, in a tag and release study conducted in Palau, the proportion of previously tagged animals over the trapping period increased in the baited traps, reaching around 58 percent in the last trap deployed (Saunders *et al.* 2017a). Given this behavior, nautilus populations, including *N. pompilius*, are likely highly susceptible to being successfully caught by fisheries. For isolated and small populations, this could result in rapid depletions of these populations in a short amount of time, potentially just months (Saunders *et al.* 2017a). However, Saunders *et al.* (2017a) note that this vulnerability to depletion from overfishing is likely lower in those populations where barriers to movement do not exist, such as Papua New Guinea and Indonesia. These sites both have large swaths of habitat (thousands of km) within the optimal nautilus depth range that are parallel to coastal areas and could serve as natural refugia but also allow for the restocking of depleted populations (Saunders *et al.* 2017a). Therefore, the best available information suggests that these aspects of the species' natural behavior (i.e., attraction and habituation to baited trap sites) are likely significant threats to those *N. pompilius* populations that are already subject to other threats (e.g., overutilization) or demographic risks (e.g., spatially isolated, small populations).

EXTINCTION RISK ANALYSIS

In determining the extinction risk of a species, it is important to consider both the demographic risks facing the species as well as current and potential threats that may affect the species' status. To this end, a demographic analysis was conducted for the chambered nautilus and considered alongside the information presented on threats to the species in the first section of this status review report. A demographic risk analysis is an assessment of the manifestation of past threats that have contributed to the species'

current status and informs the consideration of the biological response of the species to present and future threats. This analysis evaluated the population viability characteristics and trends available for the chambered nautilus, such as abundance, growth rate/productivity, spatial structure and connectivity, and diversity, to determine the potential risks these demographic factors pose to the species. The information from this demographic risk analysis in conjunction with the available information on threats (summarized in a separate threats assessment section below) was interpreted to determine an overall risk of extinction for *N. pompilius*. Because species-specific information is sporadic and hindered by many uncertainties, qualitative 'reference levels' of extinction risk were used to describe the assessment of extinction risk. The definitions of the qualitative 'reference levels' of extinction risk are provided below:

Qualitative 'Reference Levels' of Extinction Risk	
	<p><u>Low Risk:</u> A species is at low risk of extinction if it is not at moderate or high level of extinction risk (see “Moderate risk” and “High risk” below). A species may be at low risk of extinction if it is not facing threats that result in declining trends in abundance, productivity, spatial structure, or diversity. A species at low risk of extinction is likely to show stable or increasing trends in abundance and productivity with connected, diverse populations.</p>
	<p><u>Moderate Risk:</u> A species is at moderate risk of extinction if it is on a trajectory that puts it at a high level of extinction risk in the foreseeable future (see description of “High risk” below). A species may be at moderate risk of extinction because of projected threats or declining trends in abundance, productivity, spatial structure, or diversity. *</p>
	<p><u>High Risk:</u> A species with a high risk of extinction is at or near a level of abundance, productivity, spatial structure, and/or diversity that places its continued persistence in question. The demographics of a species at such a high level of risk may be highly uncertain and strongly influenced by stochastic or compensatory processes. Similarly, a species may be at high risk of extinction if it faces clear and present threats (e.g., confinement to a small geographic area; imminent destruction, modification, or curtailment of its habitat; or disease epidemic) that are likely to create imminent and substantial demographic risks.</p>

* The appropriate time horizon for evaluating whether a species is more likely than not at high risk in the “foreseeable future” depends on various case- and species-specific factors. For example, the time horizon may reflect certain life history characteristics (e.g., long generation time or late age-at-maturity) and may also reflect the time frame or rate over which identified threats are likely to impact the biological status of the species (e.g., the

rate of disease spread). The appropriate time horizon is co-extensive with the period of time over which reliable projections can be made as to the specific threats facing the species as well as the species' response, but it is not limited to the period that status can be quantitatively modeled or predicted within predetermined limits of statistical confidence. Reliable projections may be qualitative in nature.

With these caveats in mind, the "foreseeable future" for this extinction risk analysis was considered to extend out several decades (>40 years). Given the species' life history traits, with longevity estimated to be at least 20 years, maturity ranges from 10 to 17 years, with very low fecundity (potentially 10-20 eggs per year with a 1-year incubation period), it would likely take more than a few decades (i.e., multiple generations) for any recent management actions to be realized and reflected in population abundance indices. Similarly, the impact of present threats to the species could be realized in the form of noticeable population declines within this timeframe, as demonstrated in the available survey and fisheries data (see Table 4). As the main potential operative threat to the species is overutilization by fisheries, this timeframe would allow for reliable predictions regarding the impact of current levels of fishery-related mortality on the biological status of the species. Additionally, this timeframe allows for consideration of the previously discussed impacts on chambered nautilus habitat from climate change and the potential effects on the status of this species.

Demographic Risk Analysis

Threats to a species' long-term persistence, such as those evaluated in the **Analysis of the ESA Section 4(A)(1) Factors** section of this review, are manifested demographically as risks to its abundance, productivity, spatial structure and connectivity, and genetic and ecological diversity. These demographic risks thus provide the most direct indices or proxies of extinction risk. In this section, the current status of each of these risks is assessed in turn by responding to a set of questions adapted from McElhany et al. (2000) and incorporated into the NMFS *Guidance on Responding to Petitions and Conducting Status Reviews under the Endangered Species Act* (NMFS 2016). These questions are based on general conservation biology principles applicable to a wide variety of species. These questions were used as a guide to the types of considerations that are important to each of the broader demographic risk categories of abundance, productivity, spatial structure, and diversity.

Below, we provide a discussion of the demographic risks for the species.

Abundance

- *Is the species' abundance so low that it is at risk of extinction because of environmental variation or anthropogenic perturbations (of the patterns and magnitudes observed in the past and expected in the foreseeable future)?*
- *Is the species' abundance so low, or variability in abundance so high, that it is at risk of extinction because of depensatory processes?*
- *Is the species' abundance so low that its genetic diversity is at risk because of inbreeding depression, loss of genetic variants, or fixation of deleterious mutations?*
- *Is the species' abundance so low that it is at risk of extinction because of its inability to provide important ecological functions throughout its lifecycle?*
- *Is the species' abundance so low that it is at risk because of demographic stochasticity?*

The global abundance of the chambered nautilus is unknown, with no available historical baseline population data. The species likely exists as small, isolated populations distributed throughout its range. However, abundance estimates of these fragmented populations are largely unavailable as the species is difficult to survey. Currently, population size has been estimated for *N. pompilius* off Osprey Reef in Australia using baited trap techniques (n = 844 to 4,467 individuals) and for the Palawan region, Philippines and Western Australia populations using genetic markers (median population size for Western Australia = 2.6 million individuals; for Philippines = 3.2 million individuals). Population density estimates (individuals / km²) are also available from Osprey Reef (13.6 to 77.4), the Great Barrier Reef (0.34), American Samoa (0.16), Fiji (0.21) and the Panglao region, Philippines (0.03). While there may be some sampling bias in the baited trap technique, we find that the population size and density estimates from these studies may provide a good representation of the current abundance of the species because they rely on the best available field data.

If a population is critically small in size, chance variations in the annual number of births and deaths can put the population at added risk of extinction. Demographic stochasticity refers to the variability of annual population change arising from random birth and death events at the individual level. When populations are very small, chance demographic events can have a large impact on the population. However, the threshold for depensation in the chambered nautilus is unknown.

Populations of *N. pompilius* are assumed to be naturally small, and, when not faced with outside threats, appear stable (e.g., Osprey Reef population increased by 28 percent over the course of a decade). However, those populations in areas where nautilus fishing occurs have experienced significant declines in less than a generation time for the species, indicating a greater risk of extirpation because of depensatory processes. Saunders et al. (2017a) suggest that trapping data that result in <1 to 2 nautilus per trap likely reflect a minimally viable population level. In other words, further removal of individuals from

those populations would likely result in population crashes and potential extirpation. Based on the available abundance trend data (see Table 4), many of the populations surveyed in Indonesia and the Philippines currently reflect this minimally viable level, indicating that abundance of these particular populations may be close to levels that place them at immediate risks of inbreeding depression and demographic stochasticity, particularly given their reproductive isolation. Extirpations of these populations would inherently increase the risk of extinction for the entire species.

While overall abundance is highly uncertain, the evidence that the species exists as small and isolated populations throughout its range, making them inherently vulnerable to exploitation and depletion, with data to suggest that many of these populations are in decline and may be extirpated in the foreseeable future, indicates that *N. pompilius* is likely at an increased risk of extinction from environmental variation or anthropogenic perturbations.

Productivity

- *Is the species' average productivity below replacement and such that it is at risk of satisfying the abundance conditions described above?*
- *Is the species' average productivity below replacement and such that it is unable to exploit requisite habitats/niches/etc. or at risk because of compensatory processes during any life history stage?*
- *Does the species exhibit trends or shifts in demographic or reproductive traits that portend declines in per capita growth rate which pose a risk of satisfying any of the preceding conditions?*

The current net productivity of *N. pompilius* is unknown because of the imprecision or lack of available abundance estimates or indices. Fecundity, however, is assumed to be low (no egg-laying has been observed in the wild). Based on estimates from other captive Nautilus species (i.e., *N. macromphalus* and *N. belauensis*), they may lay up to 10 to 20 eggs per year, with a long incubation period (10 to 12 months). Given that the species is a slow-growing and late-maturing species (with maturity estimated between 10 and 17 years, and longevity at least 20 years), the species has likely very low productivity and, thus, is extremely susceptible to decreases in its abundance.

In terms of demographic traits, Saunders et al. (2017a) suggest that a population at equilibrium would have a higher percentage of male (75 percent) and mature (74 percent) animals. Ratios that are significantly lower than these estimates suggest the population is in “disequilibrium” and may likely portend declines in per capita growth rate. Saunders et al. (2017a) further provides evidence that fished nautilus populations tend to show significant demographic differences in relative age class (i.e., predominance of immature

individuals) and sex ratios (i.e, no longer male-biased) compared to unfished populations. Under the current assumption that males are the critical sex for population growth, the significant change in the population demographics for these fished populations may portend further declines and potential extirpations of these populations, inherently increasing the risk of extinction for the entire species in the foreseeable future. However, with the exception of the Osprey Reef (Australia), Lizard Island (Great Barrier Reef; Australia), and Sumbawa Island (Indonesia) populations, which showed male percentages of 82 to 91 percent and mature percentages of 58 to 91 percent based on data from the past decade (Saunders et al. 2017a), we have no available recent data to assess the demographic traits of current *N. pompilius* populations throughout the rest of the species' range.

Spatial Structure

- *Are habitat patches being destroyed faster than they are naturally created such that the species is at risk of extinction because of environmental and anthropogenic perturbations or catastrophic events?*
- *Are natural rates of dispersal among populations, meta-populations, or habitat patches so low that the species is at risk of extinction because of insufficient genetic exchange among populations, or an inability to find or exploit available resource patches?*
- *Is the species at risk of extinction because of the loss of critical source populations, subpopulations, or habitat patches?*

Chambered nautilus populations are extreme habitat specialists. The species is closely associated with steeply-sloped forereefs and muddy bottoms and is found in depths typically between 200 and 500 m. Both temperature and depth are barriers to movement for *N. pompilius*, which cannot physiologically withstand temperatures above around 25°C or depths greater than 800 m. Chambered nautilus are bottom-dwelling scavengers and do not swim in the open water column. While larger-scale migrations have occurred (across shallow, warm waters and/or depths >1000m), these events are assumed to be extremely rare, with gene flow thought to be inversely related to the geographic distance between populations (Swan and Saunders 2010). As such, current chambered nautilus populations, particularly those separated by large geographic distances, are assumed to be largely isolated, with a limited ability to find or exploit available resources in the case of habitat destruction. Collectively, this information suggests that gene flow is likely limited among populations of *N. pompilius*, with available data specifically indicating the isolation between populations in the Fiji and Western Australia and those in the Philippines.

In terms of the destruction of habitat patches, while anthropogenic threats, such as climate change and destructive fishing practices, have been identified as potential sources that could contribute to habitat modification for the chambered nautilus, there is no evidence

that habitat patches used by *N. pompilius* are being destroyed faster than they are naturally created such that the species is at risk of extinction. Additionally, there is no information to indicate that *N. pompilius* is composed of conspicuous source-sink populations where loss of one critical population or subpopulation would pose a risk of extinction to the entire species.

Diversity

- *Is the species at risk because of a substantial change or loss of variation in life history traits, population demography, morphology, behavior, or genetic characteristics?*
- *Is the species at risk because natural processes of dispersal and gene flow among populations have been significantly altered?*
- *Is the species at risk because natural processes that cause ecological variation have been significantly altered?*

As noted above, *N. pompilius* likely exists as isolated populations with low rates of dispersal and little gene flow among populations, particularly those that are separated by large geographic distances and deep ocean expanses. Given the physiological constraints and limited mobility of the species, coupled with the selective targeting of mature males in the fisheries, connectivity among breeding populations may be disrupted. Additionally, while it is unknown whether genetic variability within the species is sufficient to permit adaptation to environmental changes, the available information suggest that genetic variability has likely been reduced due to bottleneck events and genetic drift in the small and isolated *N. pompilius* populations throughout its range. Because higher levels of genetic diversity increase the likelihood of a species' persistence, the current, presumably reduced level among chambered nautilus may pose a risk to the species.

Threats Assessment

According to section 4 of the ESA and NMFS' implementing regulations, the Secretary (of Commerce or the Interior) determines whether a species is threatened or endangered as a result of any one or a combination of the following section 4(a)(1) factors: (A) destruction or modification of habitat, (B) overutilization, (C) disease or predation, (D) inadequacy of existing regulatory mechanisms, or (E) other natural or man-made factors. Collectively, we simply refer to these factors as "threats." The first part of this status review provides a detailed description and analysis of the likely impact of the above threats on the status of the species. Below, we have summarized the impact of each threat identified in terms of its contribution to the extinction risk of the species using the following qualitative risk definitions:

- Very low or low risk

- It is unlikely that this threat contributes significantly to the species' extinction risk.
- Moderate risk
 - This threat contributes significantly to long-term risk of extinction (through the foreseeable future), but does not in itself presently constitute a danger of extinction.
- High risk
 - This threat contributes significantly to long-term risk of extinction (through the foreseeable future) and is likely to significantly contribute to short-term risk of extinction.

Uncertainty

A confidence rating (CR) was given to the impact of each threat based on the available information. Below are the definitions of the confidence rating scores (adapted from the confidence ratings in Lack et al. (2014)):

- ✦ 0 (no confidence) = No information.
- ✦ 1 (low confidence) = Very limited information.
- ✦ 2 (medium confidence) = Some reliable information available, but reasonable inference and extrapolation required.
- ✦ 3 (high confidence) = Reliable information with little to no extrapolation or inference required.

Those threats where little to no information was available on the impact on the status of the species (where CR = 0 to 1), indicating significant uncertainty regarding the risk to the species, are highlighted in gray.

ESA 4(a)(1) Factor	Identified Threats	Risk to <i>N. pompilius</i>	CR
(A) Destruction or modification of habitat	Unselective/destructive fishing techniques	Medium	0
	Pollution/Sedimentation	Low	1
	Climate change/Ocean Acidification	Low – Medium	1
(B) Overutilization	Commercial Harvest	Medium	2
	Trade	Medium – High	2
(C) Disease or Predation	Disease	Low	1
	Predation*	Medium	2

ESA 4(a)(1) Factor	Identified Threats	Risk to <i>N. pompilius</i>	CR
(D) Inadequacy of Existing Regulatory Mechanisms	Addressing Commercial Harvest	Medium	2
	Addressing Trade	Low – Medium	0-1
(E) Other natural or human factors	Ecotourism	Low	1
	Natural Behavior*	Medium	3

*Alone, these threats may not significantly contribute to the extinction risk of the species. But, in combination with other threats that, for example, decrease the abundance of the species (e.g., overutilization) or potentially affect important life history functions, these threats may exacerbate the impact of the other threats on the status of the species.

The most significant and certain threat to the chambered nautilus is overutilization through commercial harvest to meet the demand for the international nautilus shell trade. Out of the 10 nations where *N. pompilius* is known to occur, potentially half historically or currently have targeted nautilus fisheries. These waters comprise roughly three-quarters of the species' known range, with only the most eastern portion (e.g., eastern Australia, American Samoa, Fiji) afforded effective protection from harvest. Fishing for nautilus is fairly inexpensive and easy, and the attraction of *N. pompilius* to baited traps further increases the likely success of these fisheries (compounding the severity of this threat on the species). The estimated level of harvest from many of these nautilus fisheries in the Philippines (where harvest data are available) have historically led to extirpations of local *N. pompilius* populations. Given the evidence of declines (of 70 to 94 percent) in the CPUE from these Philippine nautilus fisheries, and the fact that fished populations tend to experience higher predation rates (another compounding factor that further increases the negative impact of fishing on the species), these Philippine populations are likely on the same trend toward local extinction. Serial depletion of populations based on anecdotal trapping reports is also evident throughout nautilus fishing sites in Indonesia, with reported declines of 70 to 97 percent. In India, the predominance of immature shells for sale in the curio markets suggests potential overfishing of these local populations as well. Commercial harvest of the species is also thought to occur in Papua New Guinea, East Asia, Thailand, Vanuatu, and Vietnam. Efforts to address overutilization of the species through regulatory measures appear inadequate, with evidence of targeted fishing of and trade in the species, particularly in Indonesia, Philippines, and China, despite prohibitions.

As fishing for the species appears to have no cultural or historical relevance, trade appears to be the sole driving force behind the commercial harvest and subsequent decline in *N. pompilius* populations, with significant consumer markets in the United States, China,

Europe (Italy, France, Portugal, United Kingdom), the Middle East, and Australia. If international trade can be successfully managed to ensure sustainable harvest of *N. pompilius*, then it could essentially stop the serial decline of local populations and allow partially depleted populations time to recover, preventing extinction of the species through the foreseeable future. The CITES Appendix II listing aims to achieve these conservation outcomes; however, given that the listing only recently went into effect (i.e., January 2017), it is too soon to evaluate the ability and capacity of the affected countries (who are parties to CITES) to implement the required measures and ensure the sustainability of their trade. Of concern is the illegal selling and trade of the species that already exists despite domestic prohibitions. Therefore, it is unclear whether and how the new CITES requirements will be adequately implemented and enforced in those countries that are presently unable to prevent the overutilization of the species despite prohibitions (e.g., Indonesia, Philippines, China). We note that the United States appears to be a significant importer of nautilus products and, therefore, this CITES listing could potentially cut-off a large market (and associated demand) for the species if adequate non-detriment findings are not issued by the exporting countries. However, the evidence of illegal trade routes (see Figure 7) and difficulty with tracking the amount and origin of nautilus products suggests that it may take some time before the extent of the “ins and outs” of the nautilus trade are fully understood. Therefore, we find that the adequacy of the CITES Appendix II listing in reducing the threat of overutilization (through ensuring sustainable trade) is highly uncertain at this time.

Additional threats to *N. pompilius* that were identified as potentially contributing to long-term risk of the species include unselective and destructive fishing techniques (e.g., blast fishing and cyanide poisoning) and ocean warming and acidification as a result of climate change effects; however, because of the significant data gaps (such as the effects on nautilus habitat and the species’ physiological responses), the impact of these threats on the status of the species is highly uncertain.

Overall Risk of Extinction

Given the species’ low reproductive output and overall productivity and existence as small and isolated populations, it is inherently vulnerable to threats that would deplete its abundance, with a very low likelihood of recovery or repopulation. While there is considerable uncertainty regarding the species’ overall current abundance, the best available information indicates that the species has experienced population declines of potentially significant magnitude, including evidence of extirpations, throughout most of its range, primarily because of fisheries-related mortality. While stable populations of the species likely exist in those waters not subject to nautilus fishing (e.g., Osprey Reef, Australia and American Samoa), only a few populations have actually been found and studied. These populations appear small (particularly when compared to trade figures) and

genetically and geographically isolated, and, therefore, if subject to environmental variation or anthropogenic perturbations in the foreseeable future (such as through illegal fishing or climate change), may not be able to recover.

Currently, the best available information, though not free from uncertainties, does not indicate that the species is at such a high risk of extinction that its persistence is in question or that it currently faces imminent and substantial demographic risks. The species is still traded in substantial amounts (upwards of thousands to hundreds of thousands annually), with evidence of new sites being established for nautilus fishing (e.g., in Indonesia, Philippines, Papua New Guinea), and areas of stable, unfished populations (e.g., eastern Australia, American Samoa), indicating that current overall abundance throughout its range is not so low that the species' viability is at risk. However, the continued harvesting of the species for the international nautilus shell trade and the subsequent serial depletion of populations are placing the species on a trajectory to be at a high risk of extinction within the foreseeable future, likely within the next couple of decades. The species' current demographic risks, including small and isolated populations, low productivity, habitat specificity, and physiological limitations that restrict large-scale migrations, means that as populations are depleted and extirpated, recovery of those populations and/or repopulation is unlikely. Many of the observed populations of the species are already on this path, with data indicating significant declines in abundance and even local extinctions. Further exacerbating these declines is the evidence of increased predation on fished nautilus populations and the disruption of population demographics (through the attraction of predominantly males and mature individuals to baited traps). As the unsustainable harvesting of nautilus continues, with fisheries that follow a boom-bust cycle, and fishing efforts that serially exploit populations and then move on to new sites as the populations become depleted (particularly evident in the Philippines and Indonesia), this trend is unlikely to reverse in the foreseeable future. In fact, despite current domestic prohibitions on the harvest and trade of the species throughout most of the species' range (and particularly in the large exporting range states), these regulatory measures are ineffective because they are largely ignored or circumvented through illegal trade networks. Further, although the species was recently listed on CITES Appendix II, there is as of yet no basis to conclude whether that listing will be effective at decreasing the threat of overutilization to the species through the foreseeable future.

Given the best available information, we find that *N. pompilius* is at a moderate risk of extinction. Without adequate measures controlling the overutilization of the species, *N. pompilius* is on a trajectory where its overall abundance will likely see significant declines to the point where the species will be at a high risk of extinction throughout its range in the foreseeable future.

CONSERVATION EFFORTS

In terms of conservation efforts, we identified a non-profit website devoted to raising the awareness of threats to the chambered nautilus (e.g., <http://savethenautilus.com/about-us/>), including raising funds to support research on the species. Additionally, we note that chambered nautilus are found in a number of aquariums worldwide where additional research is being conducted on the reproductive activity of the species. However, survival of the species in captivity is relatively low compared to its natural longevity. Based on a 2014 survey of 102 U.S. aquariums with nautilus species (with 52 responses), Carlson (2014) reported that survival rates for captive *N. pompilius* of more than 5 years was only 20 percent. The rates of survival for less than 5 years were as follows: 0 to 1 year = 33.3 percent, 1-2 years 6.7 percent; 2 to 3 years = 20.0 percent, 3 to 5 years = 20.0 percent. While some of these aquariums have successfully bred nautilus species (e.g., Waikiki Aquarium (U.S.), Birch Aquarium at Scripps (U.S.), Toba Aquarium (Japan), Farglory Ocean Park (Taiwan) (Tai-lang 2012; Blazenhoff 2013; Carlson 2014), based on the results from these efforts, it is unlikely that aquaculture or artificial propagation programs could substantially improve the conservation status of the species in the wild. On average, survival rate after hatching is less than 1 in 1,000 (Tai-lang 2012) and to date, none of the captive-bred nautilus have obtained sexual maturity (NMFS 2014). The process is also costly and time-consuming (given the year-long incubation period of eggs). Therefore, captive breeding would not be a feasible alternative to help satisfy the trade industry or restore wild populations (NMFS 2014). Additionally, it should be noted that the shells of nautilus in captivity tend to be smaller and irregular, with black lines that mar the outside of the shells (Moini et al. 2014). Therefore, these shells would likely not work as suitable alternatives to wild-caught shells in the trade, given the preference for large, unblemished nautilus shells in the market.

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