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Nautilus: biology, systematics, and paleobiology as viewed from 2015

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Abstract The natural history of the nautilid genus *Nautilus*, composed of a controversial number of extinct and extant species, has been the subject of scientific scrutiny for centuries. While a great research effort lasting from the mid-1970s to 1990s contributed vast amounts of new information concerning the evolutionary history, current diversity, mode of life, and ecological position in its habitats took place, since that time there has been far less concentrated research, and most of that has concerned the diversity and genetic distance of isolated populations using genetic techniques. In spite of the reprinting of one of the two 1987 books examining aspects of *Nautilus* biology, the only new field-based work on *Nautilus* until recently has been the important, Ph.D. thesis conducted by Andrew Dunstan on the isolated, seamount inhabiting nautilus living on Osprey Reef, Australia. In this contribution we attempt to integrate Dunstan's important new work with other, post-2010 research so as to update our current understanding of the evolutionary history (based on fossil as well as modern genetic work), characteristic habitats, mode of life, and physiology so as to give a 2015 perspective on those aspects of the natural history of *Nautilus* that are of paleobiological relevance.

Keywords *Nautilus* · Conservation · Cephalopod · Paleobiology · Coral reef · Genetics

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Introduction

The most important scientific questions about the anatomy, physiology, evolution and natural history of the genus *Nautilus* (Cephalopoda; Figs. 1, 2, 3) have centered more on its value in deciphering the overall evolution of various extinct Cephalopoda than on understanding its position in modern ecosystems (i.e., [Shigeno et al. 2008](#)). Only recently has there been much concern with understanding the role of extant nautilus in their current habitats, and this research has been spurred by indications that local extinctions of local populations of various *Nautilus* species might be threatened with extinction ([del Norte-Campos 2005](#); [Dunstan et al. 2011a](#); [De Angelis 2012](#); [Barord et al. 2014](#)). With regard to anatomy, and then ecology, the questions have been whether the primitive eyes (i.e., [Hurley et al. 1978](#)), nervous system (i.e., [Young 1965](#)), numerous tentacles among other anatomical aspects (i.e., [Kier 2010](#)), and ecology (i.e., [Saunders and Ward 1987a, b](#)) are actually windows into the past, or conversely, are more recent adaptations of a once shallow water organism to deeper water habitats of at least 300 m. In such depths, excellent chemosensory reception would be far more advantageous than vision. In addition, if mode of life changed from active predation (as is assumed to be the case for mode of life of externally shelled, extinct cephalopods) to strict scavenging of low-quality food sources by the extant nautilus, a lowering of growth rate, daily energy expenditures, and even abundance might be expected. Living fossil, or new and superbly adapted animal for existence in the deep sea?

Much of the currently accepted information about extant nautilus remains little changed from 1987, when two summary books ([Ward 1987](#); [Saunders and Landman 1987](#)) were published. Five research areas have been undertaken

Fig. 1 *Nautilus pompilius*, Vanuatu. This population swims to near surface depths. It is recognized by having the highest percent pigmentation of *N. pompilius*. Of all nautiluses, only *N. macromphalus* has the same degree of pigmentation on shell (as a percentage of shell area when viewed from the side). Like the Vanuatu population, *N. macromphalus* comes to near-surface depths. All deeper water nautiluses show less pigmentation. The only difference between *N. pompilius* and *N. macromphalus* is the absence of an umbilical plug and a slightly higher D shell-coiling statistic. Photo P.D. Ward



Fig. 2 *Nautilus pompilius* from American Samoa. This population is recognized by the very distinctive zig-zag shell color patterning. Photo P.D. Ward

since 1987 of great note: (1) the field work of Andy Dunstan and colleagues at Osprey Reef, Australia, who trapped thousands of *Nautilus*, affixed permanent markings, and then re-trapped them to analyze for growth (Dunstan et al. 2011b); (2) the use of new generation ultrasonic transmitters (Dunstan et al. 2011c) far better than those used in the past (with original data from Palau in Carlson et al. 1984; Ward et al. 1984; Ward 1987; O'Dor et al. 1993); (3) the use of Baited Remote Underwater



Fig. 3 *Nautilus pompilius*, Central Philippines. Compared to the two previous populations, the amount of shell color is less. It also has a mean diameter of about 190 mm compared to 170 mm for the two previous populations. Photo P.D. Ward

Video Systems (BRUVS) (Dunstan et al. 2011a; Barord et al. 2014); (4) the use of advanced genetic analyses by multiple groups to test various hypotheses about the genetic distances and gene flow rates of separated island populations (Wray et al. 1995; Bonnaud et al. 2004; Sinclair et al. 2011; Bonacum et al. 2011; Vandepas et al. in review) and (5) the investigations into the learning and memory capabilities of nautiluses (Crook and Basil 2008; Basil et al. 2011).

The goal of this paper is to summarize the new knowledge in these five areas, and supplement it with new data to arrive at an up to date summary of *Nautilus* biology in this

early part of the twenty-first century. Specifically, the contribution here seeks to summarize results important in understanding the ancient nautilids: (1) How many are there on a given area of their habitat? (2) How long do they live after reaching full growth? (3) What is the ecological role of *Nautilus* in its habitat, and what in fact are its depths of habitat? (4) How many species are there, and what is their range? (5) How has habitat and ecological role shaped the navigational abilities of nautiluses?

Methods

While the brunt of this paper is review, we provide new information coming from analyzing rates of growth from data kindly supplied by Andy Dunstan [Queensland, Australia] from Osprey Reef, as well using both photography and Scanning Electron Microscopy to illustrate morphology of the so-called “Black Bands” on the apertures of mature specimens. We also provide new data obtained from the Philippine Islands, as well as Efate Island, Vanuatu, of daily behavior coming from the use of ultrasonic transmitters. For cohesiveness and understanding, we also describe the methodology of two unique surveying tools: baited remote underwater video systems and the use of ultrasonic transmitters.

Baited remote underwater video systems (BRUVS) were used to record nautilus abundance. To date, BRUVS have been deployed at six geographic locations in the Indo-Pacific: Australia, Philippines, Fiji, American Samoa, Vanuatu, and Papua New Guinea. Each BRUVS unit is comprised of one–two HD camcorders in an underwater housing and one LED light source in an underwater housing mounted to a steel frame (1 m × 1 m × 1 m). A bait stick extends from the frame out 1.5 m in view of the camera. The primary bait used is raw chicken, although tuna and mackerel have also been used. The frame is attached to a surface buoy with polyethylene fishing line (8–12 mm). The BRUVS are deployed each night at dusk to depths between 250 and 350 m and retrieved the following morning at dawn, resulting in a total deployment or ‘soak-time’ of 12 h. After retrieval, the video data are downloaded and the unit is readied for deployment again.

We fitted three individual specimens of *Nautilus pompilius* in the central Philippines (in August, 2013) with VEMCO ultrasonic transmitters, and then again, in April, 2014, fitted two more specimens with a newer generation transmitter (VEMCO) which was both smaller in volume as well as in water weight, and provided constant depth and temperature data. In November through mid-December 2014, two more *N. pompilius* were also thus “tagged” and tracked off Efate Island, Vanuatu. The transmitters were attached to the shells using incompressible saddles made

up of fiberglass resin impregnated with 3-M silicon microspherules so as to provide neutral buoyancy for the transmitters, which, without buoyancy compensation, would make the nautiluses dense enough in seawater to affect swimming. After ensuring the transmitters are securely attached, the nautiluses are dived down to approximately 10–15 m to ensure the nautiluses jet down safely to deep water. Nautilus tracking is ‘active tracking’ and requires a surface vessel with a receiver and hydrophone to follow the nautiluses around 24 h a day, for up to 2 weeks.

Finally, we combine new morphological data with both COI and 16S genetic information coming from Vandepas et al. (in review) to make an assessment of the species concept in *Nautilus*, as well as our interpretation of the currently valid, extant nautilids, as well as summarizing two new published papers on nautilid genetics (Groth et al. 2015; Williams et al. 2012). Non-lethal genetic tissue samples were collected from nautiluses caught with baited traps at multiple locales. A small (2 cm) tentacle snip or hood sample was collected for later genetic analyses.

Results

Population sizes

The impression given by nautilus fishing is that there are vast numbers of them living in front of Indo-Pacific coral reefs, with publicized cases from Palau where as many as sixty have been taken by a single trap, and a photograph in the color photo section of Saunders and Landman (1987) shows such a rich capture. However, from 40 years of experience trapping in New Caledonia, Fiji, Samoa, Vanuatu, the Philippines, Australia, and New Guinea at various sites, most single traps yield from none to less than five. What is clear is that nautiluses are drawn to any kind of dead or decaying meat, be it chicken or crustacean or fish, and it appears that their superb chemoreception ability, as recently documented through an ingenious, recent study (Basil et al. 2005), causes what we now know to be low population numbers accumulating quickly in traps.

A further and almost unlikely source of population numbers comes from the only published estimate of nautilus material having been imported into the United States (De Angelis 2012), of the staggering total of more than 500,000 shells or parts of shells. Since the only known source of nautilus shells commercially fished is the Philippine Islands, there remains the possibility that more than half million nautiluses have come from the Philippine Islands, and perhaps most from the two known sites of fishing, the Tanon Straits, and the sea between Cebu and Bohol, with perhaps additional animals being caught and exported from Palawan (Dunstan et al. 2010). On the other

hand, it might be that even before fishing there was not a half million nautilus in all of the vast Philippine archipelago, let alone from but three sites.

The first quantitative attempt to measure a population size is from Dunstan et al. (2011a), from Osprey Reef, Australia. In this study the novel use of BRUVS (baited remote underwater video systems) by Dunstan and colleagues resulted in a quantitative estimate that there are around 2200 nautilus for the entire seamount. Because nautilus are known to live and swim just above the sea bottom, an estimate of the number of nautilus per square kilometer of fore reef slope benthos was made. The area measured for the Osprey reef fore reef slope from 100 to 700 m, the depths of habitation there (Dunstan et al. 2011a) yield a population density figure of about 13–14/km².

Dunstan et al. (2011b) also gave data on the ratio of males to females, and immature to mature specimens; these data, however, came from trapping studies, not BRUVS results. The sex of the nautilus observed in BRUVS videos cannot be determined. There is information on the ratio of immature to mature from BRUVS, although this is somewhat compromised by the inability to see whether any given specimen has the one to several millimeter black edge of the aperture that fully mature nautilus possess. However, the presence or absence of an ocular sinus can be seen on BRUVS, and this does give some information about this particular aspect of demographics. Previously it has been shown that *Nautilus* populations in other areas are composed of a majority of males (Saunders and Spinosa 1978; Dunstan et al. 2011b), and a majority of both males and females were mature specimens. However, it was not known if these results were caused by the methods by which these data were obtained: trapping in baited cages; it was considered possible that males and mature animals more readily found or entered traps, and that trapping was thus not representative of populations as a whole. For instance, perhaps juvenile *Nautilus* are not attracted to the bait used in the traps, or perhaps they do not live in the same places where trapping traditionally is undertaken.

Osprey Reef is an atypical habitat for nautilus, in that it is an isolated seamount far from the nearest land; in most cases the areas inhabited by nautilus are fore reef slopes hundreds of kilometers long, producing thousands of square kilometers of habitable area for them. But perhaps more importantly, *Nautilus* habitats are normally close to rich sources of tropical vegetation that brings copious amounts of carbon into the fore reef slope muds, making these areas rich in nutrients, and hence life. But Osprey Reef is small, and so far from mainland Australia as well as being steep sided that its benthic habitats are not the organic-rich muds common to most areas where *Nautilus* are found. Perhaps for these reasons—both a small habitat as judged by area, as well as one with far lower nutrients—

it has one of the smallest of all variants of *N. pompilius*, in a manner perhaps equivalent to the dwarfing of various ice-aged mammals (Roth 1992; Lister 1996, 2004) that were isolated on small islands by Pleistocene sea level rise. Osprey is steep sided, and there is no source of organic rich mud found closer to land, mud that gets most of its organics from land-based vegetation being swept out to sea. It is on such mud-rich bottoms of far larger surface area that appear to be the more typical habitat for nautilus, such as the quite large, gently sloping fore reef slope depths in front of Palau, all of the larger Philippine islands, much of Indonesia, Papua New Guinea and the Admiralty Islands, the larger Solomon Islands, New Caledonia, Fiji, American Samoa (and probably Western Samoa) and both Western Australia and the Great Barrier reef of Eastern Australia.

Because of its difference from other *Nautilus* habitats, it can be argued that what appears to be almost rarity of nautilus per square kilometer off Osprey is related to its very smallness. To test this, BRUVS have now been deployed off the Great Barrier Reef, Fiji, American Samoa, the central Philippines (Barord et al. 2014), and most recently Vanuatu. In fact, the Osprey estimates are quite representative of even the far larger habitats. In unscientific terms, nautilus are rare.

As to the number of mature to immature specimens, our BRUVS results to date validate the data coming from trapping that there are far more mature to immature specimens in all but one place: our work off Bohol Island, in the traditional *Nautilus* fishing grounds, in both trapping results (Fig. 4) and BRUVS found more immature than matures. A comparison of trapping results with our new Philippine data is shown in Fig. 5. It is certainly no coincidence that this unique aspect of the Philippine population takes place at the area with one of the longest known and highest yield *Nautilus* fisheries still taking place. Coinciding with the maturity results at fished and unfished areas, nautilus shell breaks (Fig. 6) also tend to occur more in areas with more fishing pressure (Fig. 7). It is possible that nautilus fishing has unintended consequences of altering the predator/prey landscape in the deep sea. This could explain a shift in shell breaks observed in fished areas. Perhaps nautilus fishing is also removing a normal predator of nautilus. Without that predator, a new predator has emerged to prey on nautilus, and may be responsible for the discrepancies in shell breaks in fished and unfished areas.

Growth rates

The trapping results of Saunders (1983, 1984), Dunstan et al. (2011b) demonstrated that nautilus are far slower growing in the wild than in aquaria, where full size could

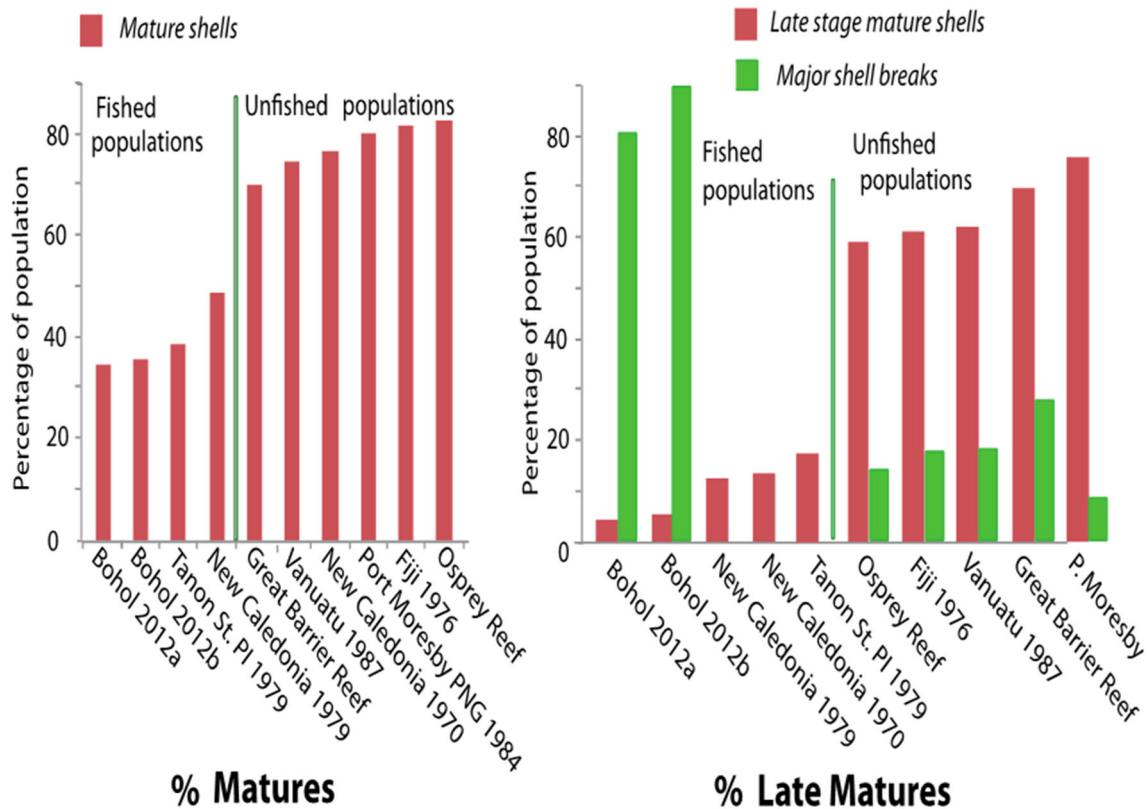


Fig. 4 Comparison of demographics of mature versus immature *N. pompilius* and *N. macromphalus*. Unfished populations show a far higher percentage of immature to mature specimens

be reached in several years at most. Instead, the recapture of still growing specimens in Palau demonstrated a growth rate to maturity of 12–15 years, and the indirect geochemical methods of Jacobs and Landman (1993) corroborated this for other populations. Saunders (1984) also made the highly significant discovery that at least among the Palau population, uniquely among known cephalopods; nautilus do not die after reaching maturity (and presumably breeding once). This highly important finding has more recently been corroborated by Dunstan et al. (2011b) who added immensely to our understanding of this animal by recapturing nautilus that had been tagged as much as 5 years previously.

Yet if living at least 5 years after reaching maturity (and thereby having from 17 to 22 years of age at minimum), to date there has been no way to actually age a mature shell. All that is known is that the width of the black band present on matures is variable, and that the black layer on the shell above the head also contains thickened layers as well as what looks like an extended space of growth lines that seems related to the thickness of the black band. However, the novel use by Cochran et al. (1981) of looking for pre-atomic age shell chemistry could solve this problem of the ultimate age of nautilus, using this method on early

growth stages of specimens caught in the 1960s and 1970s. It is not known if a maximum width is reached (the widest we have observed comes from shells in Palau (which is also the second largest *Nautilus* at maturity) is 7 mm wide, but can also be up to 2 mm high, and can be seen to be composed of numerous lamellae piled upon one another (Figs. 8, 9).

Migration studies with new generation transmitters

Attaching the sound emitting, and cross-sectional shape changing transmitters to the shells of mature nautilus should justifiably be critically evaluated with regard to behavior: we are assuming that even with this change in swimming cross section (even if neutrally buoyant, the resistance from the cross-sectional shape would surely affect the tagged nautilus in some way), as well as the constant emission of the ultrasonic transmissions inevitably leads to the following question: will daily behavior be affected, and to what degree? In these experiments, three unforeseen events subsequent to starting these experiments are notable.

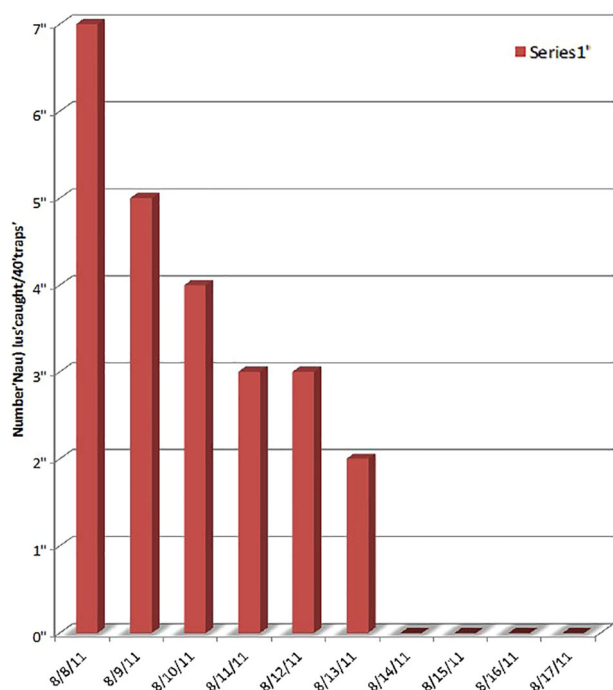


Fig. 5 Graph showing the catch using 40 traps in Central Philippines over a 2-week period. Nautilus are easily fished out, and our new information shows that at least this population, off Panglao, Bohol Island, is territorial and remains in the same place for many months or years, based on transmitter results

While there have been several studies to date of nautilus fitted with ultrasonic transmitters (Carlson et al. 1984; Ward et al. 1984; Dunstan et al. 2011c), in no case could it be ascertained whether the animal subsequently tracked was indeed the nautilus to which the transmitter was attached to, or (as we trackers, living in small boats in all-weather day and night, would tell ourselves), possibly a larger predator ingesting the transmitters. While such a possibility would seem unlikely, it could never be excluded. If a tagged nautilus were eaten by a larger predator, perhaps a deep-water shark or grouper (as evidenced from recent BRUVS in Australia), the transmitter would still continue to function for several weeks. New evidence, in fact, gives credence to the functionality of this kind of research.

First, two of the three Philippine (Panglao) *N. pompilius* fitted with transmitters in August of 2013 were later recaptured by fishermen at virtually the same place where they had first been captured, and the transmitters returned to us (the shells of the nautilus they were attached to, both quite alive when recaptured, were immediately sold, unfortunately). The recaptures were 3 and 5 months, respectively, from the time we began these experiments. This shows that, for a minimum of 3 months, the tagged nautilus not only were *not* killed soon after, or even weeks after having the transmitter attached, but that they

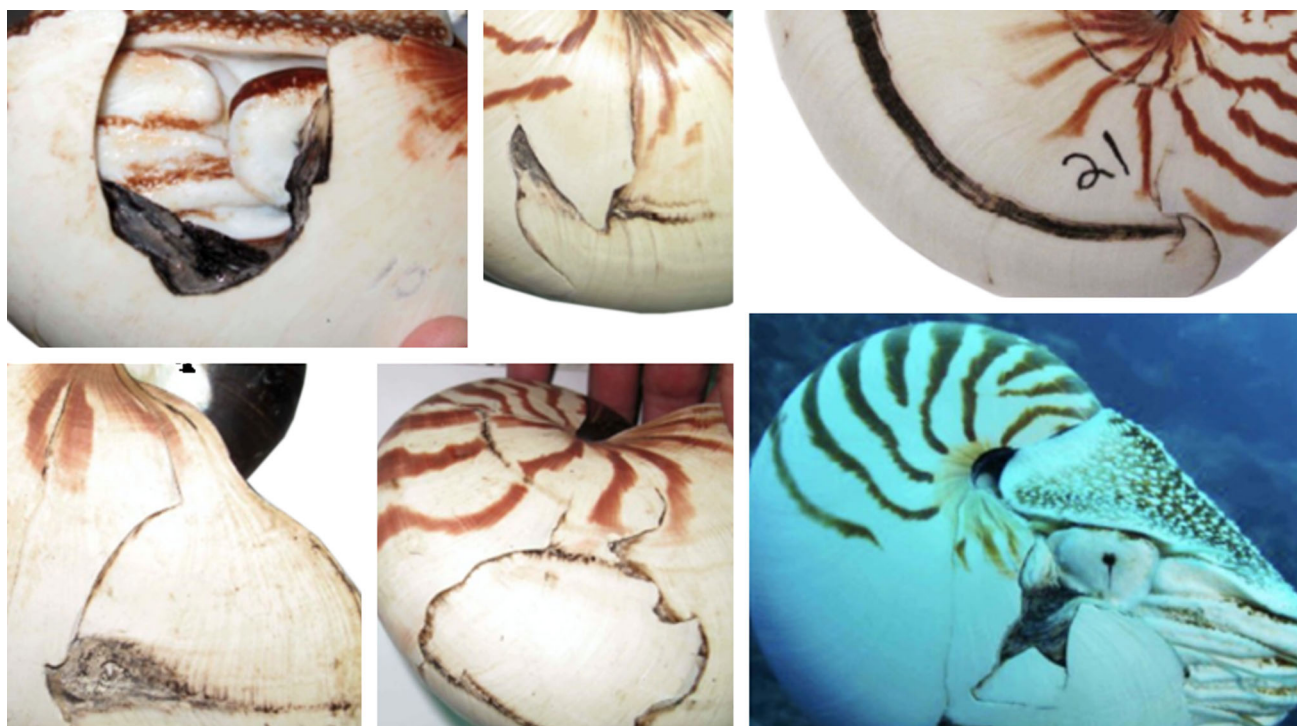


Fig. 6 Types of shell break on *Nautilus pompilius* at Panglao. The large, U-shaped break and shell removal was seen on four other specimens, and such a shell break has never been observed in other *Nautilus* shells from elsewhere

Fig. 7 Bar graph showing percentage of nautilus shells with “major” shell breaks, which can be defined as running a least a quarter of the apertural perimeter, or the removal of about 10 g of shell followed by re-healing. This graph demonstrates the very high level of breakage in the Panglao population, which is also heavily fished

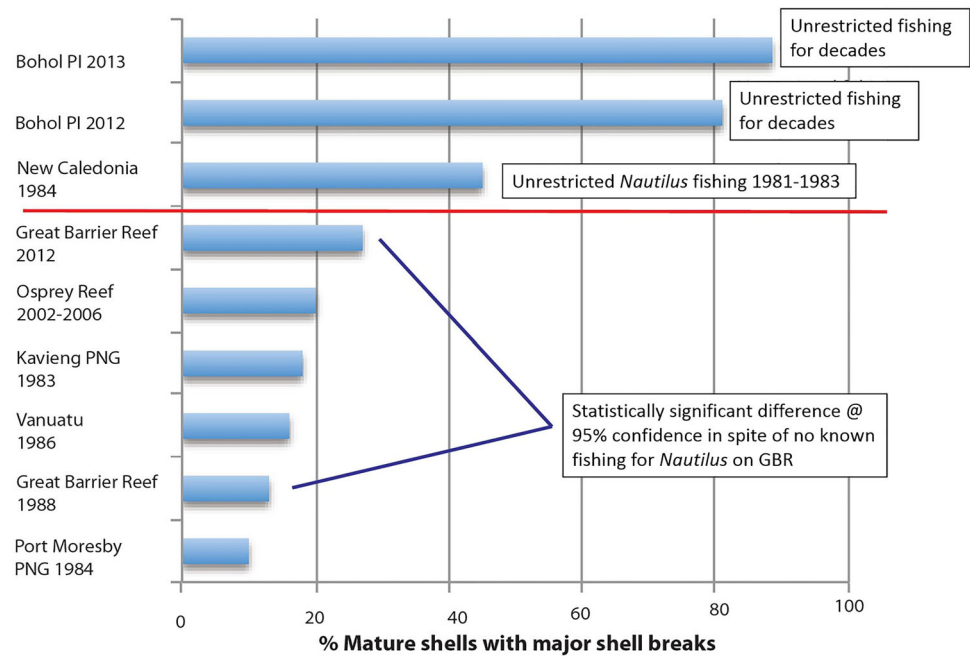


Fig. 8 Photograph of black band region in mature *N. pompilius* from Vanuatu



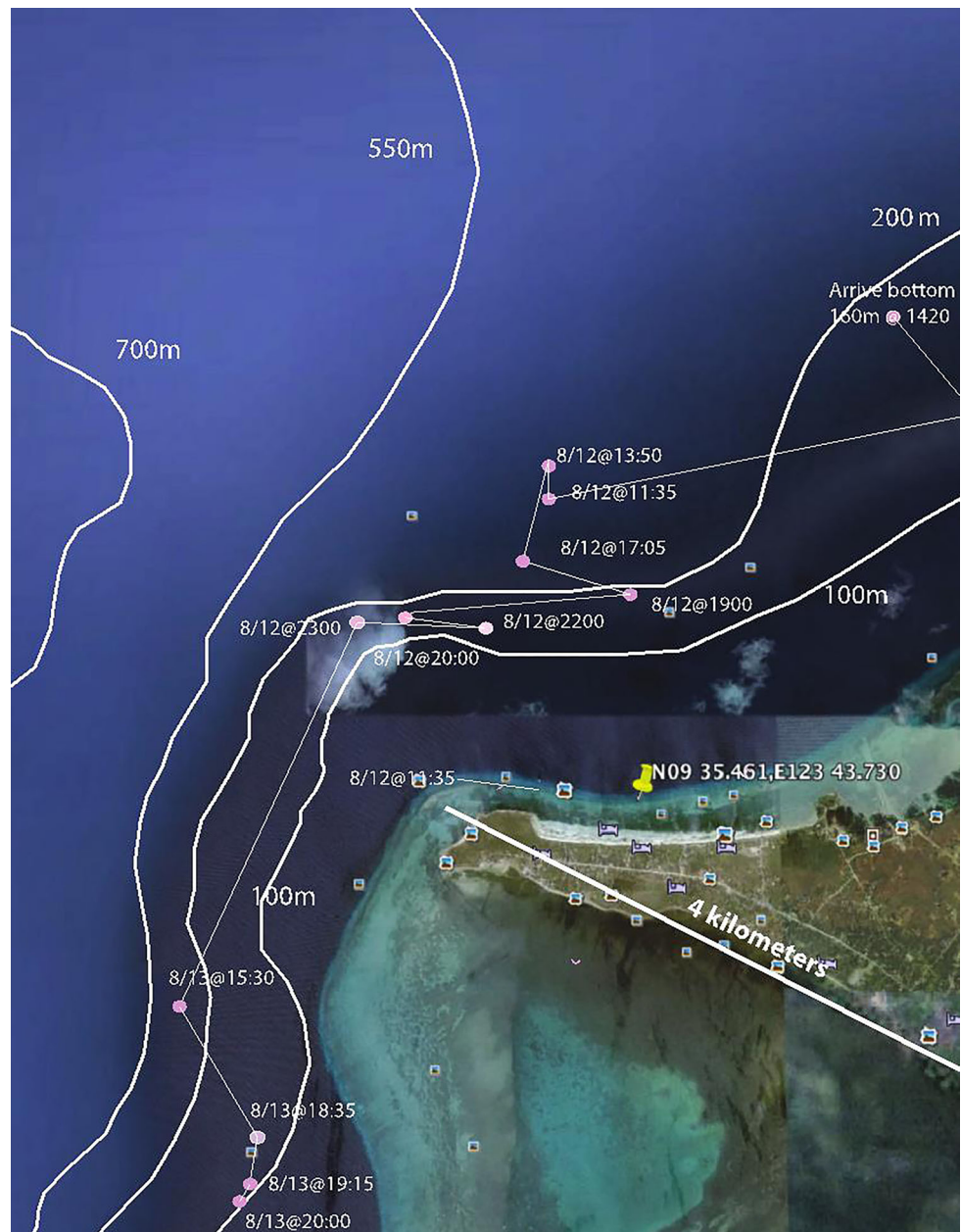
Fig. 9 Photograph of corresponding black layers deposited beneath the hood region on an inner whorl of the nautilus shown in Fig. 6. The number of layers shown here are the same as layers that can be counted in the apertural black band

remained active, alive, and living in the same region that they were first trapped in. Most interestingly, as noted above, both animals were recaptured within a kilometer of where we caught them in the first place. Both animals were first captured in early August 2013; one was recaptured in November, the other in December of 2013. The subsequent capture of these nautilus supports our initial tracking data of their horizontal movements in August (Fig. 10). Our tracking data of their depth profiles are unique in that the nautilus were tracked to different depth profiles which appeared to be correlated with the habitat type (Fig. 11). The *Nautilus* habitat in Bohol Sea off of Panglao is

significantly different in only a kilometer of movement. Part of their habitat is characterized by deep sloping sandy bottoms with little to no structure. The other part of their habitat is characterized by sharp, steep reef slopes with varying depth changes. Thus, the nautilus depth movement was more gradual and consistent when on the sandy bottom and varied when migrating through rocky bottoms and reef walls. Habitat, then, may be the primary factor in determining how nautilus migrate in other areas.

Secondly, one of the specimens of *N. pompilius* captured, and fitted with a transmitter in November 2014

Fig. 10 Acoustic transmitter results of horizontal movement of *Nautilus pompilius* in Panglao, Philippines, August 2013



(Fig. 12), in Vanuatu, was attracted to a baited trap 4 days after its initial capture, some 10 km from its initial capture. While this specimen was not recaptured, the BRUVS camera system and its bait, that the transmitter-fitted animal was drawn to, captured on video the swimming and behavior of this animal (Fig. 13). For more than 3 h it hovered and swam around the baited camera system. In no way did its swimming or behavior appear any different from that of other nautilus attracted to bait that night. We found that in aggregate, tagged nautilus moved several kilometers every day. We also have evidence that they stay in one general area, and that they are fully capable of living what appears to be a normal life even carrying a transmitter

(since the transmitter is attached to the shell via a saddle of epoxy and silicon micro balloons of density low enough to produce neutral buoyancy). Two of our nautilus tagged in August, 2013, were recaptured 3, and 5 months later by Philippine fishermen. Both animals were captured alive, the transmitters (with batteries long since dead) still in place. The importance of these recaptures beyond showing that nautilus so tagged are not immediately doomed was that both animals were captured in precisely the same geographic position where they were first captured months earlier. The nautilus tracked in Vanuatu also show that not all nautilus migrations are created equal. As in the Philippines, the Vanuatu nautilus migrations were less

Fig. 11 Acoustic transmitter results of *Nautilus pompilius* in Panglao, Philippines August 2013

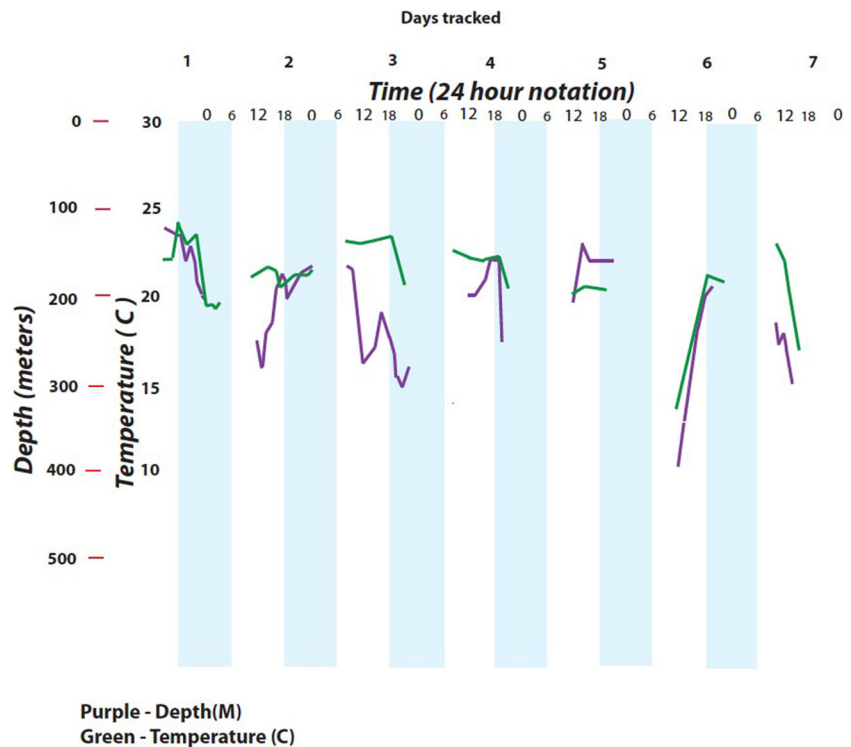


Fig. 12 Photographs of Vanuatu animals mounted with new generation Vemco transmitters capable of constant depth and temperature readouts

consistent and the nautilus migrated shallower than nautilus tracked in Palau (Fig. 14). The water temperature in Vanuatu is cooler at shallower depths which would

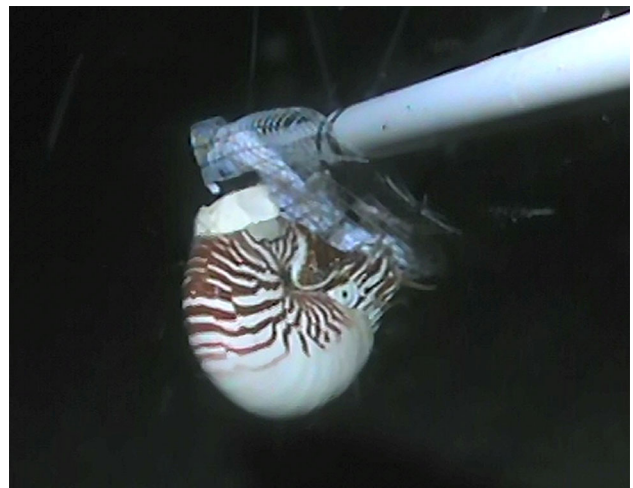


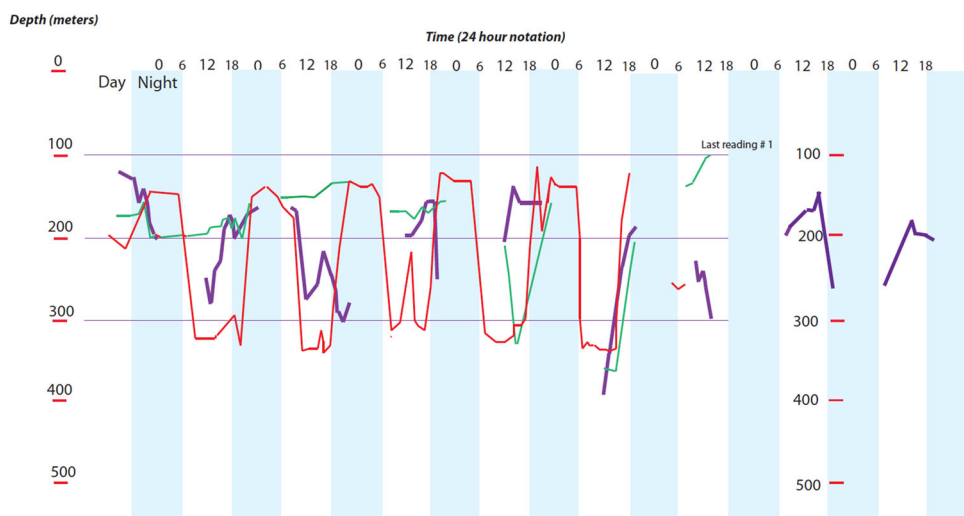
Fig. 13 Snapshot of BRUVS footage showing a tagged nautilus was still alive and behaving normally. In this case, the nautilus was attracted to our BRUVS and bait

explain why nautilus migrate shallower here. Still, the different overall patterns of migrations between locales suggest that there are other factors at play.

Ecological role in habitat

There has long been speculation about the role of *Nautilus* in its fore reef slope environment: are they predators, scavengers, or an opportunistic mix of the two? To date the

Fig. 14 Acoustic transmitter results from Vanuatu, November–December 2014, Efate, and Palau July 1983. Two very different kinds of daily behavior are apparent. The Palau animals never came shallower than 100 m at night, and were highly regular with movement up at sunset and movement down at dawn. In contrast, the Vanuatu animals were less regular, and also moved into much shallower water



only known information came from Ward and Wickstein (1980), on hand-caught specimens of *N. macromphalus* from New Caledonia where gut contents were removed and in many cases identified, even to species. All gut material was found to be crustacean.

While other gut contents from trapped specimens have been available, these are always suspect, in that the confined space of a nautilus cage, which often also trap tens to hundreds of deep-sea shrimp (mainly *Heterocarpus* sp.) as well as other kinds of crustaceans and isopods, might allow trapped nautilus to prey on living crustaceans, or might be consuming crustaceans killed within the traps.

There have been many investigators who have kept nautilus in aquaria, and there has been some effort to see if nautilus can be observed to eat live prey. There is no such observation that has been published, or that we have heard about; negative results rarely do get published, and this is a problem with all of science, not just ours, yet in fact it is often negative results that are the most important in discriminating between hypotheses.

Some information about the possibility that nautilus eat the shrimp that they co-inhabit with in all known nautilus habitats is available from BRUVS observations. Although the same bait drawing nautilus to the video cameras also brings in a large diversity of meat eaters, from arthropods to echinoderms to other mollusks to fish, in none of the hundreds of hours of video can nautilus be seen to eat or be attracted to anything but the bait. In fact, in some videos, large shrimp can be seen riding atop nautilus that are swimming around the bait. In a specific case, a juvenile nautilus simply touches a hermit crab with its tentacles and immediately jets away from the much smaller crab.

We suggest the information to date indicates that nautilus are exclusively opportunistic scavengers, and

readily and commonly eat arthropod molts, which all contain surprising amount of organic integuments holding the calcareous or chitinous parts together. We have also observed nautilus to swim slowly forward with one or more tentacles gently trawling through the upper millimeters of soft mud bottom. Unpublished aquarium results (Ward, Unpub.) and recently published work (Barord 2015) have shown that nautilus will excavate meat from sediment that is buried up to 25 mm below the surface: it blows sediment away with exhalation of the hyponome while inserting tentacles into the sediment down to the bait.

Just as little is known about the predators of the nautilus in their natural habitat; the single reliable observation comes from Hayasaka et al. (1987), in their finding of a set of nautilus jaws in a deep-sea shark. All other observations on predation, summarized in Saunders et al. (1989), come from artificial situations where nautilus are placed in shallow water during daytime hours, something that never happens in nature.

The BRUVS observations do allow one additional detail. On separate occasions, the BRUVS videos from 300 m off the Great Barrier Reef some 60 km south of Lizard Island, large grouper can be seen attacking and ingesting a nautilus. In one case it was a mature, in the other one of the smallest immature we have observed on video. In both cases the nautilus were fully engulfed in the mouth, and then expelled. Both nautilus swam away. In either case, however, the powerful jaws could surely have caused shell breaks that are commonly seen on Nautilus shells.

Genetics of *Nautilus* populations: species validity

The number of valid species of the genus *Nautilus* has been debated for more than a century; Saunders (1981) lists the

many named species, most based on variants of what is now accepted to be *N. pompilius*. All of these identifications and species (and in some cases subspecies) identifications were based on hard parts only. The most significant change was the splitting of what was *N. scrobiculatus* Solander out of *Nautilus*, which was motivated by not only hard part differences (shell shape and ornament, which had long been known), but from the magnificent achievement of Bruce Saunders in being the first scientist to trap living specimens, in 1984. It was quite apparent from the first trapping that not only hard parts, but also a thick gelatinous periostracum atypical of *Nautilus* were observed for the first time. The first dissection of soft parts, however, was not made until 1996, and it was the discovery of soft part as well as hard part differences that stimulated our taxonomic decision.

Since then, a half dozen studies using DNA have been published, the first being by Wray et al. (1995), followed by Bonnaud et al. (2004), Sinclair et al. (2007), Bonacum et al. (2011), and more recently Sinclair et al. (2011). Most of these studies have been based on comparing a single gene (COI), and have generated trees based on genetic differences of this gene. No hard part characters have been included in any of the analyses. All have concluded that nautilus found on island or continental regions separated from other such areas by deep water have nautilus populations that are genetically distinct.

There has also been a strong geographic component to these findings, with populations found close to the edges of the total range (such as *N. pompilius* from Fiji and Samoa) being more distinct from populations closer to the center of the range (the so-called Coral Triangle). Those studies including *Allonautilus scrobiculatus* found it to be significantly distinct from all other taxa included in *Nautilus* (which at this time are generally considered to be *N. pompilius*, *N. macromphalus*, *N. stenomphalus*, and *N. belauensis*).

We have supervised a study of samples taken by recent, non-lethal sampling in the central Philippines, Great Barrier Reef, Fiji, American Samoa, and Vanuatu; both COI, 16 s, and more recently, whole gene approaches were used. Although these results are still preliminary (Vandepas et al. in review), we believe they validate the prior conclusions about separate genetic identities on separate island groups. However, by including hard part differences, and using genetic results in larger sample numbers from individual localities, we have arrived at two conclusions concerning the valid number of species. We believe that the combined genetic and morphological results are sufficient to invalidate both *N. stenomphalus* and *N. belauensis*, and that they are both more parsimoniously placed in *N. pompilius*.

One of the most striking differences of *A. scrobiculatus* from other extant nautilids is its hood ornament. While *N.*

pompilius and *N. macromphalus* have identical hoods, orange in color with white, low papillae, with a double row of raised white flush down the middle (Fig. 15), *A. scrobiculatus* has numerous, raised papillae longer than the low protuberances of *N. pompilius* and *N. macromphalus*, and no double row. At the time of defining *Allonautilus*, the only other extant nautilid with such hood ornament was *N. stenomphalus*, which was first seen alive only in the late 1980s (Saunders and Ward 1987a, b). The first captured living specimens of *N. stenomphalus* showed to also have raised papillae, no double line, and also differs from *N. pompilius* in having no umbilical callus, and a color pattern different from that of most or all *N. pompilius* and *N. macromphalus* in having the characteristic vertical stripes crossing the shell center, but terminating well before the umbilical region, thus leaving a large white, un-pigmented patch in the middle of the shell centered on the umbilicus. Yet the trapping of *N. stenomphalus*, made off Lizard Island of the great Barrier reef, resulted in a few specimens typical of *N. pompilius* elsewhere, but dominated by specimens showing a mix of umbilical morphology, color patterns, hood tubercular ornament, and the double white hood lines. Saunders and Ward (1987a, b) concluded that while valid, at least in the study site, *N. stenomphalus* hybridizing with *N. pompilius* indicated that one or the other had only relatively recently arrived at this part of the Great Barrier Reef, and that the genetic separation of the two was insufficient to stop successful interbreeding. By one of the most fundamental biological definitions of a species (successful interbreeding), if true, this meant that *N. stenomphalus* was not distinct from *N. pompilius*. Subsequently, detailed dissections of specimens with the *N. stenomphalus* shells (open umbilicus; shell color stripes only along venter, thus leaving a white patch around umbilical shell region without pigment) show no differences in the ctenidia and reproductive structures, both shown to be different from *Nautilus* in *Allonautilus* (Ward and Saunders 1997).

A cruise in 2012 allowed us to collect 30 nautilus on a transect along the Great Barrier Reef. We have coded four morphological characters as being one of three states: *N. pompilius*, *N. stenomphalus*, or in between. These characters were the morphology of the umbilicus, the color pattern, the hood papillae morphology, and the double white stripes. Each of these specimens was then analyzed for the COI and 16 s gene, and then compared to other *Nautilus* populations. These results (Figs. 16, 17) show that while morphologically distinguishable, the end members most “*N. pompilius*—like” and most “*N. stenomphalus*—like” cannot be discriminated by genetics. We conclude that the Great Barrier Reef nautilus population shows the widest morphological variation of any yet studied, but that these differences are phenotypic, not genotypic. *Nautilus*



Fig. 15 Soft part comparisons of two *Nautilus pompilius* from Great Barrier Reef, near Lizard Island. The upper photos come from what has traditionally been identified as *Nautilus stenomphalus*. However, as noted by Saunders and Ward (1987a, b) this taxon is an end member of intergrading forms to traditional *N. pompilius*. Saunders

stenomphalus should be considered a junior synonym of *N. pompilius*.

The definition of *Nautilus belauensis* Saunders as a separate species is more easily invalidated. Even the first genetic work (Wray et al. 1995) showed *N. belauensis* to have little support in generated trees, and additional, subsequent work only emphasized this. In hard parts as well, there is little that differentiates *N. belauensis* from *N. pompilius*, the major difference being a faint longitudinal set of striae on the shell, and what we have observed to be a slightly thicker, gelatinous “periostracum” on the outer shell. While it is larger in mean size than most other extant *Nautilus*, the population that it is closest to it (using the genetic studies) is the large specimens of *N. pompilius* off Western Australia that were originally defined as *Nautilus*

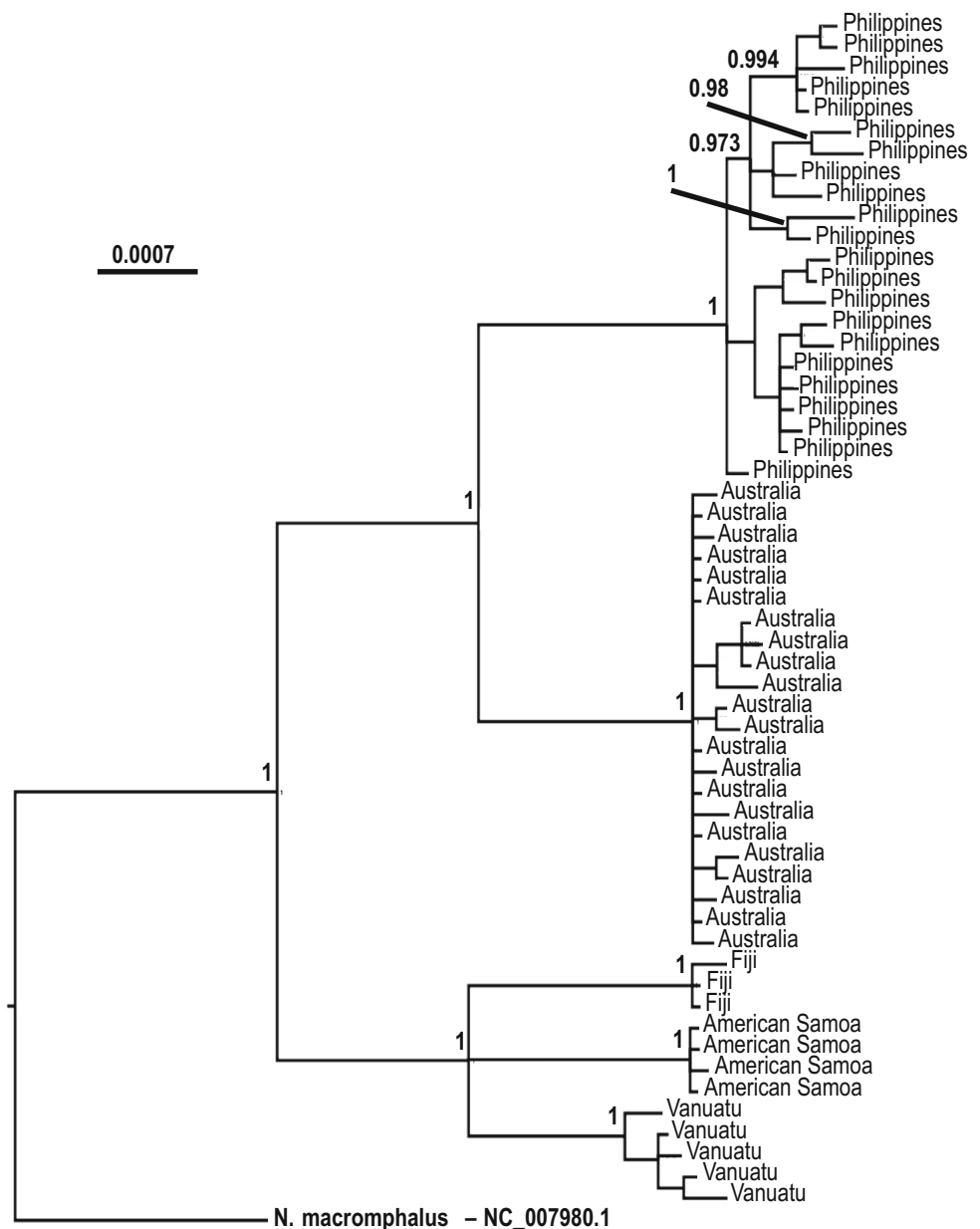
and Ward (1987a, b) suggested that there was hybridization between the two. But the new genetic findings, above, show no differences in the two different trees among these taxa. They appear to be genetically identical, but arrive at different phenotypes during ontogeny

repertus Iredale. Compared to the nautilus of Palau, these are larger yet in mean diameter of mature males and females than those from Palau. During Pleistocene low stands there was probably a ready, migrational corridor. To date, no detailed analysis of the soft part morphology of *N. belauensis* has been carried out.

Implications for paleobiology and biology

Nautilus have long been viewed as a living fossil for most of its geological range. In fact, that conclusion was one of the great misnomers of Paleontology. While supposedly a living fossil (a taxon of long geological range, but one producing few new species or showing little

Fig. 16 Bayesian inference tree based on *cytochrome oxidase subunit 1 (CO1)* sequences of *Nautilus macromphalus* (Genbank accession: NC_007980.1) and *N. pompilius* from our study. Posterior probabilities below 0.95 are not shown. From Vandepas et al. (in review)



significant evolutionary change itself), the taxonomists most versed in nautilids, including Miller (1947), Kummel (1956), and Stenzel (1957), concluded that *Nautilus* had no fossil record at all. The first specialist to publish on a nautilid fossil included in *Nautilus* was Shimansky (1957), in describing *N. praepompilius* from the Eocene of Russia. Saunders et al. (1989) later published more information on this, and specimens collected subsequent to the original Shimansky publication. Later, Squires (1988) described Eocene specimens that he placed in *Nautilus*. We have now found specimens that can be placed in *Nautilus* from late Early Cretaceous of Australia, the Late Cretaceous of California and British Columbia, the Paleocene of

Australia, and the Eocene of Great Britain (see Fig. 18). Others are undoubtedly present in many museums, and identified as *Cimomia*, *Eutrephoceras*, or not identified at all.

An example of how fossil *Nautilus* has been overlooked was our discovery of well-preserved *Nautilus praepompilius* in the collections of the Australian Museum in Sydney, Australia. In spite of its age, this specimen was curated into the collection of modern shells. In morphology it is similar to extant *Nautilus* with the exception of having less sutural complexity, previously noted in this species by Saunders et al. (1996).

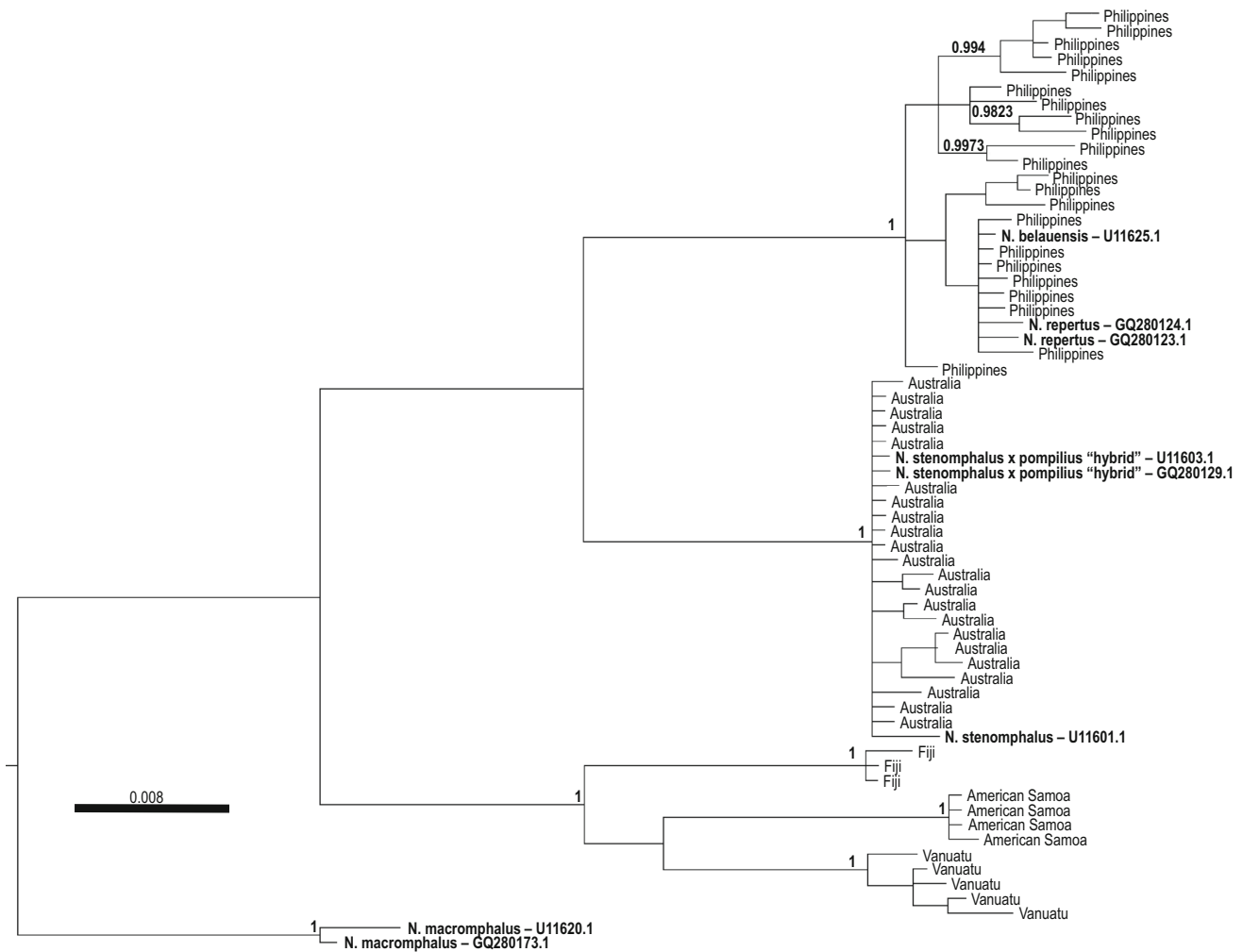


Fig. 17 Bayesian inference tree of *16S* rDNA sequences of *N. pompilius* sequences from our study, and sequences of other *Nautilus* species from GenBank. Posterior probabilities below 0.95 are not

shown. *N. belauensis*, *N. stenomphalus*, *N. repertus*, and *N. pompilius* do not fall into discrete clades

Based on the genetic work, [Bonacum et al. \(2011\)](#) and [Sinclair et al. \(2011\)](#) made the same suggestion that perhaps each separate and genetically distinct nautilus population was a separate species, and that the radiation of many new species took place either immediately before, or during the Pleistocene; the Coral Triangle being the origin of the modern radiation. Our own conclusion is that *Nautilus* originated possibly as early as the Middle Jurassic, but more probably in the Early Cretaceous, and that its maximum diversity was during the Late Cretaceous; there appear to be three separate species in the Nanaimo Group alone, from the Santonian through the Campanian stage.

Both ribbed and un-ribbed *Nautilus* species appear by the Late Cretaceous; one of these is *Nautilus campbelli* from Campanian deposits of Nanaimo Group of Vancouver; and earlier, unnamed ribbed *Nautilus* comes from Santonian aged strata there. Currently, all ribbed

Cretaceous nautilids are dumped into the genus *Cymatoceras*. In fact, *Cymatoceras* is composed of both ribbed *Nautilus*, ribbed *Eutrephoceras*, and perhaps other taxa, united simply because of ornament but ignoring all other characters. Specimens of *N. praepompilius* are also known from Turonian strata in the Chico Formation, the Maastrichtian of the Moreno Formation of California as well as in Cenozoic strata of many continents ([Squires 1988](#); [Saunders et al. 1996](#)). The transition from *N. praepompilius* of the Paleogene to *Nautilus* of the modern day may have simply been by long-term phyletic evolution producing a more compressed shell, but gradually over time. What is apparent is that this taxon is phenotypically variable, but apparently relatively immune to forming new species, even when genetically isolated. All evidence to date indicates that Cretaceous and Paleogene nautilids were shallow water, and are not associated with reef faces. Because the



Fig. 18 *Nautilus praepompilius* from Paleocene strata of South Australia

deep sea is less likely to leave any sort of fossil record, it may be that there were ancient, as well as extant nautilids living in the 100–700 m range. But our own view is that this is a taxon driven into ever deeper habitats by the continued expansion of shell breaking predators, perhaps, for nautilids, exclusively teleost fishes, themselves colonizing ever deeper, darker habitats.

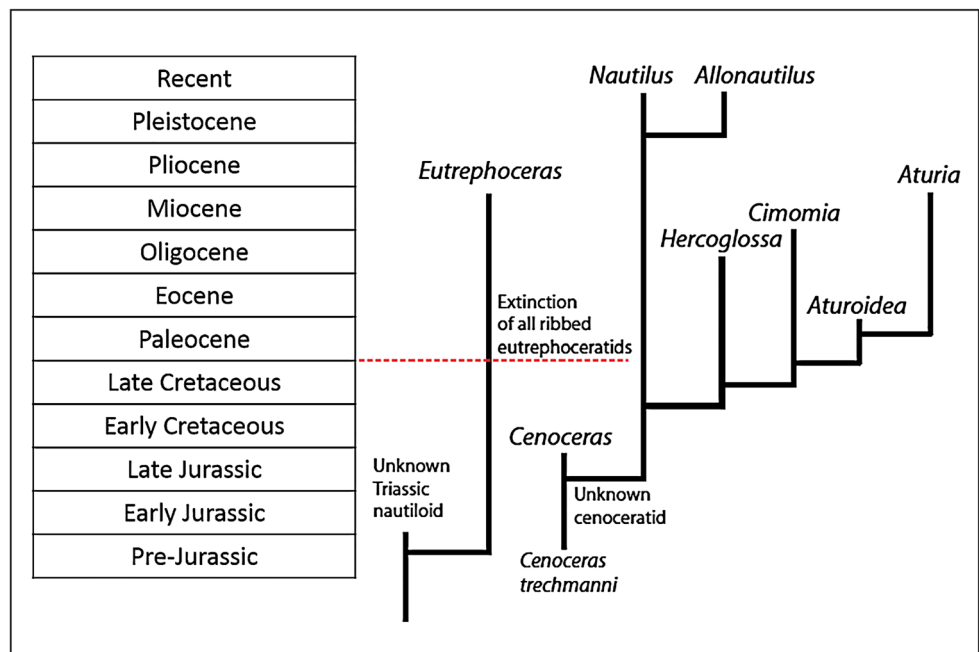
If true, nautilus must be up against a final environmental barrier. Its very slow growth has to be from the difficulty of new chamber formation at depth, caused by the problems of osmotically removing cameral liquid through the siphuncle against pressure gradients up to 70 atm. That nautilus can grow to maturity three times faster than at their common depths suggest that they now live in a place far less than optimal for their construction. The predation pressure may be pressing nautiluses up against their implosion depth.

Evolution of the genera *Nautilus* and *Allonautilus*

Based on time of occurrence combined with morphological attributes, we propose a tentative phylogeny of some of the post-Jurassic Nautilida as shown in Fig. 19. *Nautilus* evolved from some *Cenoceras* ancestor either in the Late Jurassic or Early Cretaceous, and becomes common during the Cretaceous.

The evolution of *Allonautilus* is puzzling. The new genetic data suggest that it first appeared either in the Pliocene or Pleistocene. However, many aspects of its shell appear primitive, including the large umbilicus. The hood

Fig. 19 Hypothesized phylogeny of some post-Jurassic nautilida



soft parts are also quite different from the extant *Nautilus* species. In shell form, *A. scrobiculatus* is a perfect homeomorph of *Cenoceras orbigny* (Prinz), right down to the cross-hatched shell ornament. The sole difference is in the initial coiling that is present in the shell produced while in the egg: the earliest shell of *Cenoceras* spp. is almost orthoconic for the first two chambers, than coils. *Nautilus* and *Allonautilus* species now extant show far earlier coiling in the earliest shell.

Conclusions

The future survival of nautilus is in a race not against time, but against a world-wide demand for their ornamental shell. Although nautilus fisheries have been around for decades, the lack of any management or surveying data has left nautilus in a precarious situation as we head into the coming decades. Today, their continued existence is closely intertwined to the continued research into many of their basic natural history questions still unanswered and misunderstood. The call to save nautilus is loud. However, questions still remain concerning the validity and number of extant species of nautilus, their navigational tactics, population size in un-surveyed areas, their reproductive strategies, and their overall role and impact in a deep-sea ecosystem that is even less studied than nautilus. Recent efforts into these areas have significantly increased our overall understanding of extant nautilus. Continuing to address these aspects will continue to inform our understanding of ancient nautilus while also providing pertinent information to ensure that nautilus do not continue to decline to extinction.

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