Fisheries Research 106 (2010) 239–247

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Nautilus pompilius fishing and population decline in the Philippines: A comparison with an unexploited Australian *Nautilus* population

A. Dunstan[a,*], O. Alanis[b], J. Marshall[c]

[a] Queensland Brain Institute, University of Queensland, Brisbane, Qld 4072, Australia
[b] C. Castro Road, Brgy. San Pedro, Puerto Princesa City 5300, Palawan, Philippines
[c] School of Biomedical Sciences, University of Queensland, Brisbane, Qld 4072, Australia

ARTICLE INFO

Article history:
Received 18 March 2010
Received in revised form 24 June 2010
Accepted 24 June 2010

Keywords:
Nautilus
Fisheries
CITES
Sustainability
Osprey Reef

ABSTRACT

Baseline capture and mark-and-release studies of *Nautilus pompilius* conducted at Osprey Reef, Coral Sea, Australia reveal that this unexploited population is stable from a catch per unit effort (CPUE) basis over 12 years. In contrast, data from a detailed interview questionnaire of *N. pompilius* fishers and traders in Palawan, Philippines highlight a fishery that is unsustainable. The results from the Philippines show up to 80% declines in reported CPUE from 1980 to the present, fewer than three *Nautilus* generations, which can be attributed to fishing pressure. This is evidence for *N. pompilius* (and by ecological association, other *Nautilus* species) to be assessed as 'endangered' in the IUCN (International Union for Conservation of Nature) Red List. Questionnaire responses suggested there is no cultural or historical relevance of *Nautilus* fishing to local communities and the fishery only provides approximately 10–20 years of economic return before becoming non-viable. Identification of new *Nautilus* fishing sites and training of locals by buyers from distant depleted fishing areas illustrate how the value and demand for *Nautilus* shells generates fishing pressure.

1. Introduction

This paper investigates the changes in catch per unit effort in *Nautilus* fishery regions in comparison to an unexploited *Nautilus* population. Aspects of local culture related to the fishery as well as life history and ecology of *Nautilus* are incorporated to identify future conservation requirements to ensure long term survival of *Nautilus* populations. Nautiloids and their extinct predecessors have been a feature of the earth's oceans for over 500 million years and survived almost unchanged through five major mass extinction events (Hanlon and Messenger, 1996; Strugnell and Lindgren, 2007; Ward, 1980). Now only two to five species of *Nautilus* (taxonomy remains uncertain) (Bonnaud et al., 2004; Saunders, 1981b; Saunders and Landman, 2010; Sinclair et al., 2007; Wray et al., 1995) and one separate genus, *Allonautilus* (Ward and Saunders, 1997) represent the nautiloids in a distribution restricted to deep-water tropical habitats of the Indo-Pacific. Their k-selected life history traits of low fecundity, late maturity and long life span (Cochran et al., 1981; Saunders, 1983; Shigeno et al., 2008; Uchiyama and Tanabe, 1996; Westermann et al., 2004) lead to the vulnerability of *Nautilus* to overfishing, which is a major threat to their continued survival. They are facing similar threats to other k-selected iconic species targeted by fishing, including many shark species, maori wrasse and sea turtles whose numbers have seriously declined (Wilkinson, 2008).

At present, *Nautilus pompilius* and other *Nautilus* species are not included within the IUCN Red List (IUCN, 2009). Population demographics are poorly known and sustainable fishing levels have not been addressed in the *Nautilus* fisheries of the Indo-Pacific. There is a strong argument that demand from the ornamental shell trade worldwide and restricted habitat preferences are contributing to their rapid decline. This paper documents overfishing and related changes to *Nautilus* populations in the Philippines as compared to an unexploited population in at Osprey Reef, Coral Sea, Australia.

2. Materials and methods

2.1. *N. pompilius* population study – Osprey Reef, Coral Sea, Australia

Baseline capture, mark and release studies of *N. pompilius* conducted at Osprey Reef examine the stability and CPUE of an unexploited population over 12 years. A barrel shaped trap (90 cm × 77 cm) constructed from wire mesh (7.5 cm × 9 cm mesh size), baited with chicken and set to 300 m depth, was used to

* Corresponding author. Tel.: +61 040965071; fax: +61 07 33654522.
E-mail addresses: andy.dunstan@gmail.com (A. Dunstan), omeralanis@yahoo.com (O. Alanis), justin.marshall@uq.edu.au (J. Marshall).

0165-7836/$ – see front matter
doi:10.1016/j.fishres.2010.06.015

Table 1
Nautilus trapping, captures and recaptures at Osprey Reef.

Year	# samples	Captures				# recaptures
		Total	Mean	Median	SEM	
1997	11	38	3.5	1.0	1.04	1
1998	19	122	6.4	3.0	1.47	2
1999	36	249	6.9	4.0	1.15	17
2000	50	234	4.7	4.0	0.66	22
2001	59	426	7.2	4.0	0.94	39
2002	44	241	5.5	4.0	0.83	43
2003	45	174	3.9	4.0	0.58	27
2004	33	276	8.4	4.0	1.46	22
2005	53	350	6.6	4.0	0.91	37
2006	24	200	8.3	4.0	1.70	9
2007	27	264	9.8	5.0	1.88	20
2008	16	99	6.2	5.5	1.55	13
Total	417	2673	6.4	5.0	0.31	252

trap *Nautilus*. Sampling was conducted between 1997 and 2006 throughout the year (with the exception of February only having one sample) with a total of 417 traps set and retrieved (Tables 1 and 2). Sample sites were around the entire circumference of Osprey Reef but with 92% of sampling undertaken at the Entrance site (Fig. 1). Traps were deployed for 12 h; set at dusk and retrieved vertically at dawn at 15 m/min with *Nautilus* immediately placed in a dedicated, dark refrigerated tank to contain the animals during the tagging process at temperatures between 16 and 19 °C.

All *Nautilus* individuals were engraved on the shell with a unique tag number, photographed, measured for diameter and aperture width, and maturity and sex were recorded. Recaptured animals were re-photographed, measured and sexed before release. Tags were always visible but identity of each recapture was checked during later analysis using the unique 'fingerprint' of each individual shell pattern (Fig. 2). To reduce the chance of predation by visual predators upon release, *Nautilus* were kept on board for 13 h prior to release after dark. Animals were checked for neutral buoyancy and normal swimming and descent behaviour during release by scuba at 30 m at the capture location.

2.2. *Nautilus* fishery study – Philippines

A 30-point questionnaire was conducted with 26 fishers and 7 shell buyers from the nine main *Nautilus* fishing locations in Palawan (Fig. 3). The survey addresses the history and cultural relevance of *Nautilus* fishing in the Philippines, trade demand, and local *Nautilus* fishery revenue as well as fishing methods and changes in

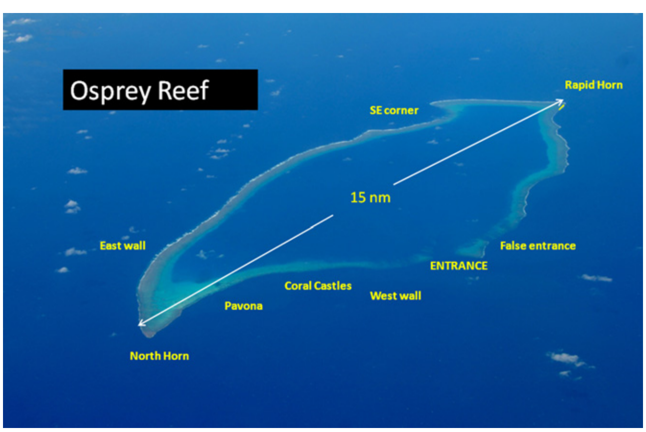

Fig. 1. Osprey Reef *Nautilus* sampling sites.

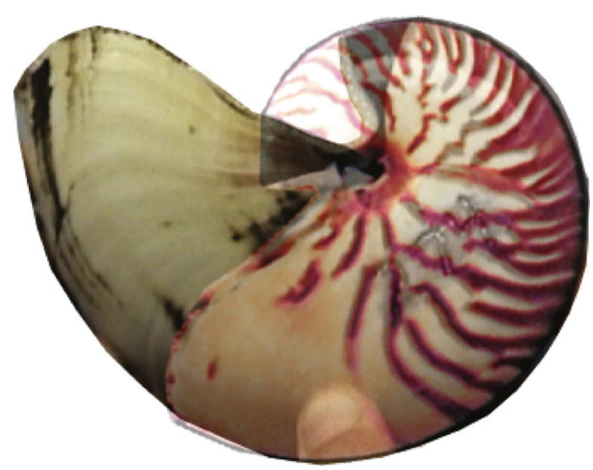

Fig. 2. *Nautilus* #274 is shown with initial capture image overlaid with final capture image to calculate circumference increase and growth rate.

Table 2
Capture and recapture data from Osprey Reef sampling sites.

Location	Distance from entrance (nm)	# samples	# captures	# recaptures	% recaptures
Entrance	0	382	2466	226	9.2
False entrance	1	5	17	3	17.6
West wall	2.1	1	7	1	14.3
Castles	2.5	13	69	7	10.1
North Horn	5.3	3	9	3	33.3
Pavona	4.3	6	60	8	13.3
Osprey east wall	8.3	1	11	2	18.2
Rapid Horn	12	2	8	0	0.0
SE corner	18	4	26	2	7.7
Total		417	2673	252	9.4

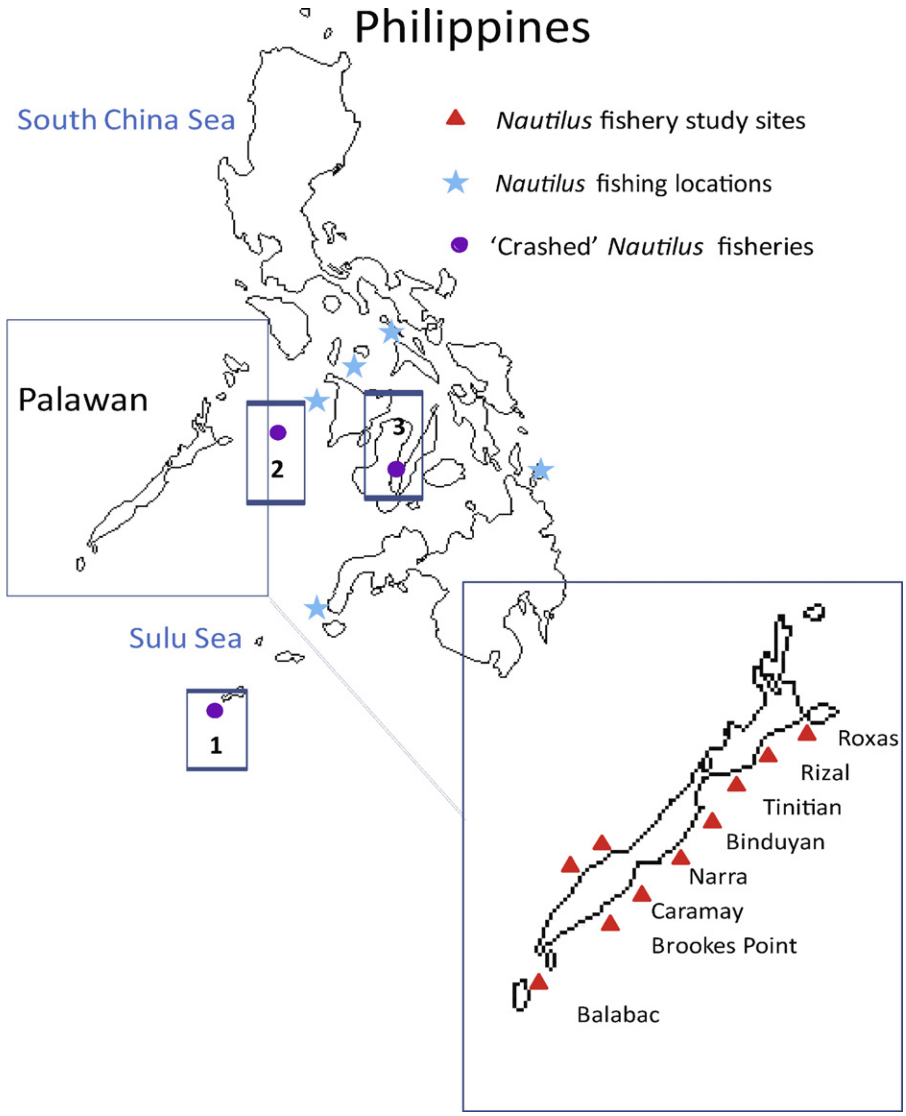

Fig. 3. *Nautilus* fishing locations in the Philippines as identified by study respondents including 'crashed fisheries at Tawi Tawi (1), Cayangacillo (2) and Tanon Straits/Cebu (3). Inset shows the Palawan region and the locations of *Nautilus* fisheries and interviews with fishers and traders.

catch per unit effort (CPUE). Identities of fishers remain confidential. The recruitment of a local research assistant with contacts and relationships in the Palawan community and extensive local coastal and marine knowledge allowed access to, and cooperation from, the *Nautilus* fishing communities. Mark and recapture studies would greatly benefit this dataset but logistics and funding precluded this at the time of publication.

Economic and cultural relevance to the community were considered a vital component of the study to ensure future management plans are sensitive to the needs of the local people.

Questions (see Table 3) addressed five main areas of interest:

- history of *Nautilus* fishing in the area
- fishing methods
- changes in catch per unit (CPU) effort
- cultural relevance of *Nautilus* to the community
- trade demand levels and origin and *Nautilus* prices paid to fishers

Research was conducted under permit from the Australian Fisheries Management Authority and with ethics approval from the University of Queensland Animal Ethics Committee.

Catch per unit effort (CPUE) was derived as

$$\text{CPUE} = \text{daily catch rate}/\#\ \text{traps}.$$

Total catch rates were derived as:

$$\text{Total annual catch} = \text{daily catch rate} \times \text{estimated number of fishing days per year}$$

Data from three sites in Quezon – Caramay, Narra and Quezon two sites in North Palawan – Roxas and Rizal and two sites in Central Palawan – Binduyan and Tinitian are combined due to their close proximity (Fig. 3) and lack of data to analyse each as separate sites.

Income from *Nautilus* fishing was derived from an average price of $2 USD per shell at current exchange rates. Current catch rate and fishing effort were used to derive total catch and total income.

Statistical analysis of CPUE changes over time for both the Osprey Reef and Philippines *Nautilus* populations was conducted using R package (R Development Core Team, 2009). Osprey Reef CPUE data was investigated for change over time using regression analysis. Philippines CPUE data were analysed using one way ANOVA comparing CPUE at start of fishing and final fish-

Table 3
Questionnaire survey of *Nautilus* fishers and traders of Palawan.

Questions	Total # responses
1. Do you trap especially for nautilus?	27
2. When did you start fishing for nautilus	24
3. When did you stop fishing for nautilus	24
4. What are your trapping methods, bait used?	26
5. How many nautiluses would you catch at a time?	22
6. How many times a month would you go out to trap nautilus?	23
7. Do you do this whole year long? Or is there a special season for trapping?	22
8. How many traps are used?	26
9. Are they harder to catch now?	26
10. Catch rate at first?	12
11. Catch rate now?	20
12. Do you think that if you go on catching them they will soon disappear?	21
13. When did the demand for nautilus start? And has it increased?	26
14. Are the nautilus shells valuable?	11
15. To whom do you sell them?	25
16. Were they valuable to your culture before you started selling them?	10
17. Do ever eat them?	15
18. How did you learn this?	26
19. Do you know other people in other areas doing this?	24
20. What is the history of nautilus prices to fishers	15
21. Is Nautilus fishing important to you	26

ing CPUE. One way ANOVA was also performed to compare key fishery sites of mainland Palawan and the separate Balabac region.

Methods used to integrate data within IUCN redlist requirements relate to calculation of *Nautilus* generation time and population size reduction. Generation time was calculated as the time taken for most (>50%) individuals to reach maximum reproductive output (IUCN, 2008). Population size reduction is estimated from the Philippines data for regional levels of decline according to IUCN principles for vulnerable species A4(d); "An observed, estimated, inferred, projected or suspected population size reduction of ≥50% over any 10-year or three generation period, whichever is longer (up to a maximum of 100 years in the future), where the time period must include both the past and the future, and where the reduction or its causes may not have ceased" (IUCN, 2001).

3. Results

3.1. *N. pompilius* population study – Osprey Reef, Coral Sea, Australia

Studies conducted at Osprey Reef over a 12-year period with capture, mark-and-recapture methods for *N. pompilius* have shown a stable CPUE (# *Nautilus*/trap) (Table 2, Fig. 4). A mean CPUE of 6.8 *N. pompilius* per trap with fluctuations between mean CPUE of 3.5/trap in 2003 and of 9.8/trap in 2007 demonstrate the stability of this unfished population.

Regression analysis of these data demonstrates a slight increase of 28% over the 12 years of the study, although this increase is not significant ($p = 0.0638$; $F_{1,10} = 4.339$; Fig. 4).

9.4% of marked individuals were recaptured. All recaptures were *Nautilus* which were initially captured and released at the Entrance site. The percentage recapture rate of Entrance individuals at other sites around Osprey Reef is very similar to the recapture rate at the Entrance (Table 2). Maximum time between capture and recapture of an already mature animal with no recorded growth is 5.3 years with a mean recapture period of 48 weeks. For details of recapture times see Fig. 5.

The growth rates observed in recaptured sub-mature *N. pompilius* at Osprey Reef (Fig. 6) show a mean shell circumference increase of 0.053 mm/day (using linear regression; mean 0.046, median 0.045, SD 0.026).

3.2. *Nautilus* fishery study – Philippines

3.2.1. Summary

Four of the five sites (including sites amalgamated from the initial nine survey sites) have a reported decline by fishers and traders in CPUE of 80% from a mean of 0.99 to 0.21 *Nautilus*/trap/day over periods from 1980 to the present (Table 4, Fig. 7). 81% of respondents stated that *Nautilus* are harder to catch now, although 88%

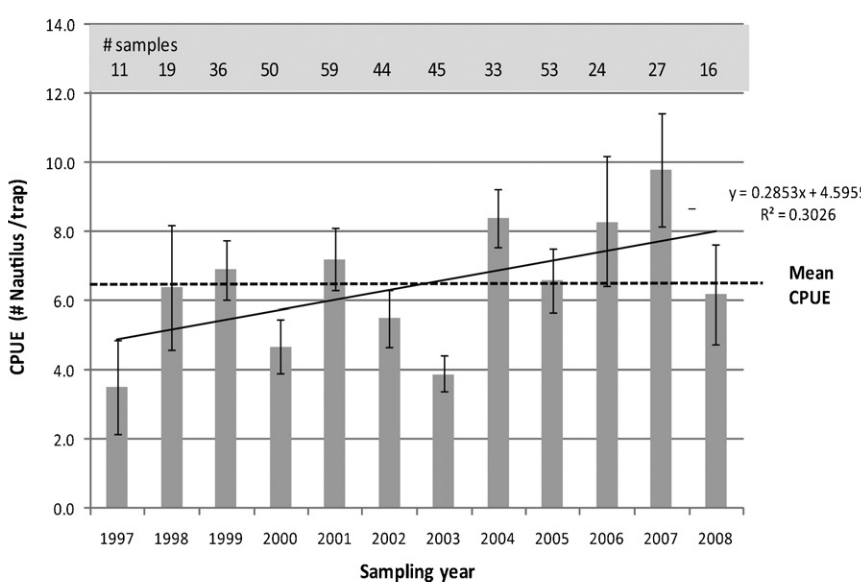

Fig. 4. Mean annual catch rates for *Nautilus pompilius* at Osprey Reef. Catch per unit effort (CPUE) rates for *Nautilus* trapping at Osprey Reef from 1997 to 2008 (error bars are SEM) showing mean CPUE and regression line of best fit.

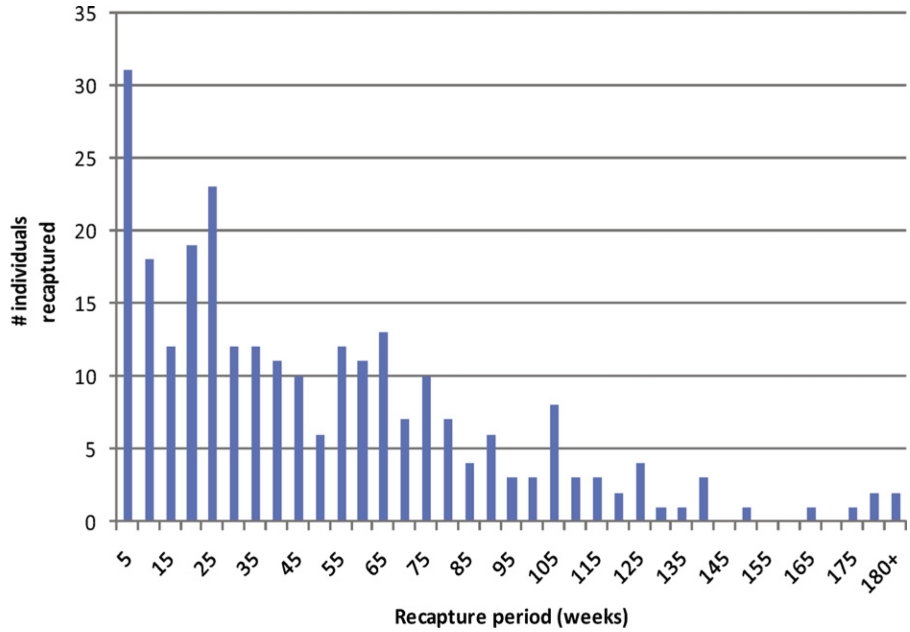

Fig. 5. Osprey Reef *Nautilus* periods between initial capture and recapture in weeks.

thought there was no risk of *Nautilus* 'disappearing' if they continued to fish (Table 5).

Nautilus fishing has no cultural or historical relevance to the Palawan community and the impetus to initiate *Nautilus* fishing in Palawan and the fishing techniques came from buyers from distant depleted *Nautilus* fishing areas. Demand for supply of *Nautilus* shells is always greater than the supply and the price per shell paid to fishers has increased from $0.50 USD in 1980 to $3.40 USD for the best quality and largest shells (Table 5).

Interviews with fishers and traders identified a range of *Nautilus* fishing locations throughout the Philippines. Locations at Tawi Tawi (1), Cagayancillo (2), and Tanon Straits/Cebu (3) (Fig. 3) were identified as being greatly depleted in *Nautilus* and where *Nautilus* fishing was no longer viable and had been discontinued.

3.2.2. Changes in CPUE for Nautilus fishery

Over a period of between 6 and 23 years the catch per unit effort has decreased by around 80% in four of the five fishery locations surveyed in Palawan. Balabac is the only site showing no decline in catch rates however two respondents reported declines in catch rates without providing catch data (Table 4, Fig. 7)

The ANOVA showed highly significant changes in CPUE over time for all locations except Balabac, both for individual (statistics not shown) and pooled results ($p = 0.0011$; $F_{1,11} = 19.033$). Balabac showed no change in CPUE over time.

Analysis of differences in CPUE between locations showed Balabac to be highly significantly different in CPUE changes over time when compared to the other four locations ($p < 0.001$; $F_{4,7} = 55.91$).

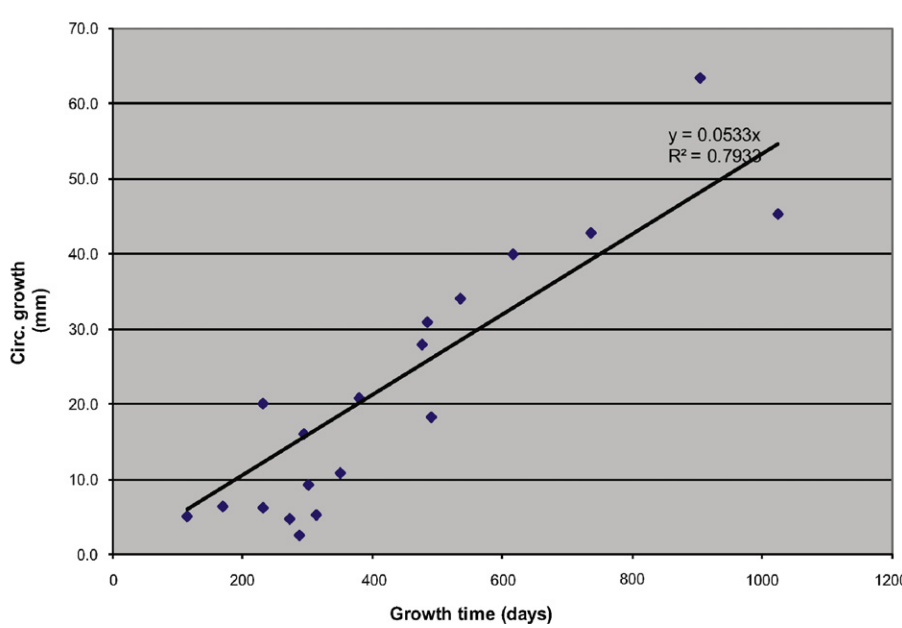

Fig. 6. Osprey Reef *Nautilus pompilius* growth rates (mm/day).

Table 4
Catch and fishing effort data from the Palawan *Nautilus* fishery.

	Municipality of Quezon		Municipality of Brookes Point			Municipality of Binduyan		Municipality of Roxas		Municipality of Balabac		
Trapper ID number	1	2	3	4	5	6	7	8	9	10	11	12
Start *Nautilus* fishing	1990	1988	1988	1987	1990	1980s	1986	1980	1986	2000	2007	2006
Start *Nautilus* catch rate (# *Nautilus*/day)	150	12.5	250	120	180	20	100	33	40	200	80	50
Stop *Nautilus* fishing	2007	2005	2006	No	2000	No	No	1986	2003	2008	No	No
Final *Nautilus* catch rate (# *Nautilus*/day)	15	2.5	75	20	10	5	15	10	10	200	80	50
Number of traps	245	10	150	250	200	80	60	72	40	220	100	86
Days/year fishing	240	240	240	240	240	270	270	64	100	210	50	80
Catch/year – start	36,000	3000	60,000	28,800	42,440	21,600	27,000	2112	4000	42,000	4000	4000
Catch/year – final	3600	600	18,000	4800	2400	5400	4050	640	1000	42,000	4000	4000
Initial CPUE (# *Nautilus*/day/trap)	0.61	1.00	1.67	0.48	0.88	1.00	1.70	0.46	1.14	0.91	0.80	0.58
Final CPUE (# *Nautilus*/day/trap)	0.06	0.25	0.50	0.08	0.05	0.25	0.25	0.14	0.29	0.91	0.80	0.58
% CPUE decline	90%	80%	70%	83.3%	94.3%	75%	85%	70%	75%	0%	0%	0%
Time period for decline (years)	18	17	18	24	10	22	22	6	17	8	1	2

3.2.3. Fishing methods and economic return

Trapping is conducted from small outrigger 'bancas' with an average of around 120 traps per vessel. Traps are small (approximately 0.6 m × 0.4 m × 0.3 m mesh design) and run out on a line ('bandera') along the bottom, with around 30 traps per bandera. Fishing is weather dependent rather than dependent on *Nautilus* behaviour and is conducted generally for between 7 and 10 months of the year for as many dusk to dawn trapping opportunities weather conditions allow. The income from *Nautilus* fishing is derived from an average price of $2 USD per shell at current rates and from current catch rate and fishing effort (Table 6). Each fisher represents a number of employees to help run the vessel and trapping operation (generally 3–4). These figures represent an average return of around $12,000 USD per fishing team. This is most likely an overestimate as total catch is based on total fishing days which are weather affected and likely to be less than reported.

3.2.4. Historical, cultural and community aspects of Nautilus fishing

The summary of responses to questions about the value of *Nautilus*, cultural history and general observations on the future of *Nautilus* are summarized (Table 5). Examples of common responses or relevant quotes from respondents are included.

4. Discussion

We find strong evidence for *N. pompilius* (and by ecological association, other *Nautilus* species) to be assessed as 'endangered' in the IUCN (International Union for Conservation of Nature) Red List and provide impetus for CITES (Convention on International Trade in Endangered Species) listing.

The data from Osprey Reef support the life history of slow growth and longevity of individual *Nautilus* while capture rates over 12 years indicate a population that is stable and not fluctuating during at least this time period. A slight increase in CPUE over the time of the study could be due to either an increase in the population or due to natural fluctuations but this trend was not significant.

This is in stark contrast to the *Nautilus* populations in active fishing areas of the Philippines. The data from both Osprey Reef and the Philippines studies show CPUE and changes over time. Although data from Osprey Reef were based on mark–recapture work, and the Philippines data were based on interviews, both datasets rely on overall catch per unit effort (CPUE) from traps.

The Philippines study demonstrates an 80% decline in CPUE over less than 30 years. Growth rates from Osprey Reef (this study) equate closely with previous observations of growth rates in the wild (Saunders, 1984) and aquarium studies which estimate growth to maturity to take between 8 and 10 years (Okubo et al., 1995; Westermann et al., 2004). Recaptures of mature individuals after 3–5 years at Osprey Reef provides an estimate of at least 13–15 years maximum life span for *N. pompilius*. Following IUCN guidelines this gives *N. pompilius* a generation time of approximately 10 years (IUCN, 2008). Hence the declines in CPUE in the Philippine study occurred over fewer than three *Nautilus* generations and notably between only one or two generation periods. This decline is from a relatively low level of and technologically poor fishing effort of three to four fishers per area with small weather-dependent vessels and an average of 20,000 small trap days per year per vessel.

Past studies show *Nautilus* to be a series of genetically different populations which are separated geographically by ocean depths >800 m (Bonnaud et al., 2004; Saunders and Landman, 2010; Sinclair et al., 2007; Strugnell et al., 2006; Wray et al., 1995). The Palawan area affords a contiguous habitat for a single *Nautilus*

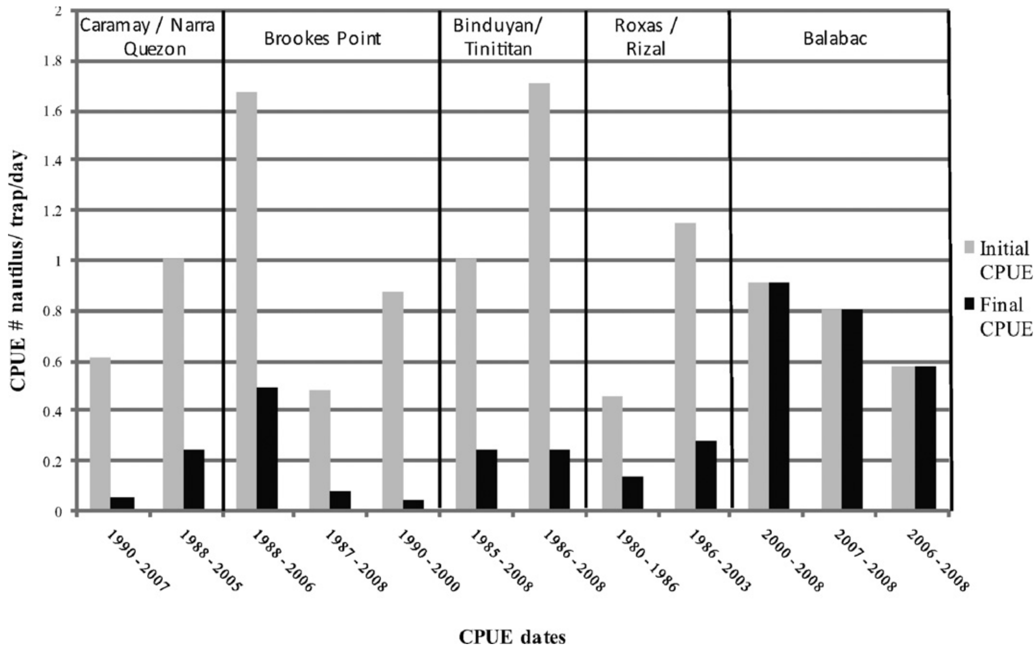

Fig. 7. Changes in catch per unit effort (CPU) over time for Palawan *Nautilus* fishery. CPUE changes from fisher reports between the start of fishing efforts to either current or last recorded (if fishing was discontinued) CPUE for *Nautilus* in the Palawan and Balabac regions of the Philippines.

population and shows the expected similar catch declines over all fishing locations around the island. Balabac is the only site where catch reports indicate no decline with fishing effort but with anecdotal reports of reduction in catch. This area could be a separate population of *Nautilus* due to current and depth effects of the trench separating this from the main Palawan island. The fishery in this region has been active for less time (<8 years) and with fewer fishers, so total catch may not have yet reached a point where

Table 5
Key Palawan *Nautilus* fisher responses to questionnaire.

Questions	Yes	No	Key comments
Is *Nautilus* fishing important for you?	100%	0	Really important. It is where I get the sustenance for my family. It is really important. I have 12 children. This is where I get most of our daily expenses. Some of my children graduated college because of *Nautilus* shell.
The only importance of *Nautilus* fishing to the people of Palawan is money. The economic importance of *Nautilus* fishing to the fishers and flow-on to the community is evident. The length of time for this economic reliance is short term due to demonstrated limited time of fishing before it is abandoned due to reduced catch and economic viability.			
Were they valuable to your culture before you started selling them?	0	100%	No. We only need money out of them.
The overwhelming response to this question indicates the lack of cultural or historic importance of *Nautilus* fishing to the Palawan people.			
Are they harder to catch now?	81%	19%	3 of 5 negative respondents had only been fishing for previous 3 years or less.
Nearly all respondents, including the trader and one fisher from Balabac area noted the decline in catch rates. Most of the respondents indicating no decline had been fishing for only a short period of 3 years or less.			
If you go on catching them will they disappear?	12%	88%	They may lessen in numbers but they cannot be disappear because the sea is big. No, almost every nautilus that we catch has eggs. Whenever the catch is decreasing, we transfer to another sites for catching until the former site has recovered. No, we also make sure that our traps only catch the mature ones and not the juveniles.
The responses to this question indicate the lack of knowledge of sustainable fishing practices to protect breeding populations and to understand the biology of the target organism. There was one indication of knowledge of site rotation to allow replenishment of the population but this practice was not observed in reports of actual fishing effort at any locations.			
When did the demand for *Nautilus* start? Has it increased?			Earliest reported buying demand in 1975 in Cagayancillo. All respondents reported 'always plenty of buyers for all shells'.
The response to this question from all participants was that *Nautilus* shell demand always outweighs the supply.			
To whom do you sell them?			Local buyers – Quezon, Caramay, Puerto Princessa, Roxas, Brookes Point, Garay, Zamboanga, Balabac and Cebu. International buyers – United States, China, Hong Kong, Hawaii, Taiwan, Australia and Europe.
Demand for *Nautilus* shells is world-wide and comes from many of the countries which also initiate the demand for shark fin and beche de mer.			
How did you learn *Nautilus* fishing?			From Cagayancillo, Cebu, Brookes Point, Rizal, Roxas and Tawi Tawi.
The people of Palawan had no history of *Nautilus* fishing. They were introduced to it by traders and fishers from other locations where the *Nautilus* fisheries had already crashed. The demand for the shells prompted the initiation of new fisheries at these Palawan sites.			
What bait is used			Dolphin, chicken, stingray, eel, fish, shark, dog, monitor lizard, triggerfish, pig, chicken, turtle, frog, toad and snake.
Bait is a real economic issue with many of the fishers noting that this was one expense or shortage of supply which could restrict their fishing efforts. Some of the bait used is also on the protected species lists such as dolphin and turtle, while other baits may also adversely impact local fauna.			

Table 6
Summary of fishing effort, catch and income for Palawan *Nautilus* fisheries.

	Binduyan/Tinitian	Caramay/Narra/Quezon	Rizal	Brookes Point	Balabac
# fishers	4	4	5	7	3
Trapping effort (traps/year)	103,800	85,600	60,428	157,460	58,080
# *Nautilus*/year	16,022	13,000	10,376	26,700	50,000
Income ($USD/year)	$40,305	$32,500	$25,940	$66,750	$125,000

population crashes occur or are evident in catch rates as typified by animals with k-selected life histories (Gärdenfors et al., 2001). Other regions of the Philippines, Tawi Tawi, Cayagancillo and Tanon Straits/Cebu, which are geographically separated, show population crashes consistent with separate populations.

The responses of fishers and traders show that while *Nautilus* fishing is important as an income source there is no cultural or historical relevance to local communities, and the fishery will only provide approximately 10–20 years of economic return before becoming non-viable. There is limited understanding of, or appreciation for, sustainable fishing practices for *Nautilus* which extends to the impact this fishery may have on vulnerable species used as bait for *Nautilus* traps.

Income figures of around $290K USD are considerable but possibly inflated by the estimation method of using maximal reported catch rates and fishing days. This income is however only short term and may provide a new expectation and lifestyle for the local fishers, which like the *Nautilus* fishery, is unsustainable.

We find strong evidence that if the IUCN criteria were applied to information for *N. pompilius* off the Philippines using the guidelines for regional application of the criteria (IUCN, 2003), it would be placed in the endangered category.

Extrapolating this to the global level, the Indo-Pacific region in the case of *Nautilus* distribution, is beyond the scope of this data. It is however, within the IUCN guidelines for global assessment to extrapolate future demand, fishing effort, and decline of *Nautilus* through analogous experiences (IUCN, 2001). The international trade demand for shark fin and beche de mer provides this analogous experience and within these same regions has resulted in massive declines of these species (Wilkinson, 2008). Identification of new *Nautilus* fishing sites and training of locals by buyers from distant depleted fishing areas in the Philippines demonstrates the value and demand *Nautilus* shells have to generate introduced fishing effort and international market forces may well drive future development of *Nautilus* fisheries to encompass the overall distribution of *N. pompilius* throughout the Indo-Pacific. The international demand for *Nautilus* shells, the ease with which local Indo-Pacific communities have adopted unsustainable fishing practices introduced by foreign parties, and the ecology and life history of the animal provide strong arguments towards IUCN globally endangered Red List categorization.

The geographical isolation of genetically distinct *Nautilus* populations (Sinclair et al., 2007; Woodruff et al., 1983; Wray et al., 1995) precludes, or drastically slows, recolonisation of depleted sub-populations and supports a strong argument for protection of all *Nautilus* stocks to maintain the genetic diversity necessary to allow survival of this living fossil. Close similarities in biology and ecology of other *Nautilus* species (Saunders, 1981b; Saunders and Landman, 2010; Sinclair et al., 2007; Strugnell et al., 2006; Ward and Saunders, 1997; Wray et al., 1995) argues for the inclusion of all members of this group in any management decisions. All current evidence suggests the life history of slow growth, long life, low fecundity and restricted dispersal and recruitment are features of all *Nautilus* and *Allonautilus* species (Saunders, 1981a; Saunders et al., 1989; Saunders and Spinosa, 1979; Saunders and Ward, 1987; Sinclair et al., 2007; Tanabe et al., 1990; Ward, 2008; Ward and Saunders, 1997). The shells of *N. pompilius*, *N. macromphalus* and *A. scrobiculatus* are all marketed and sold by the international shell trade. While *N. pompilius* is the most exploited and comprises by far the largest segment of the *Nautilus* shell market, the other species are also at risk of overfishing if fisheries are initiated in their population locations such as Papua New Guinea or Palau.

Protection of *Nautilus* through CITES listing would have minimal long-term impact on local cultures or economies. Limiting catch rates to "sustainable levels" would create economic challenges of reduced income but may be viable if fishing effort and therefore costs are reduced while other income options are developed for non-*Nautilus*-fishing periods. The marine knowledge of the fishers could provide opportunities for sustainable income in fields such as ecotourism and marine research support. Incentive payment initiatives allowing funding for education and alternative livelihood development to Nautilus fishers in return for reducing or ceasing fishing efforts could follow the successful implementation of such programs in sea turtle conservation (Ferraro and Gjertsen, 2009). Collaboration with social scientists and marine resource managers would be required to instigate such plans in a culturally sensitive manner using an approach similar to that of dugong fishery management (Kwan et al., 2006).

The value of raising public awareness about life in the deep ocean is a key component in *Nautilus* exhibits in world-wide public aquaria. Using minimal take of wild *Nautilus* for sustainable aquarium populations and scientific research marine laboratories may convincingly argue for their continued use to further the knowledge of this remarkable living fossil and the biology, paleobiology and evolution of organisms in the deep seas (Crook and Basil, 2008; Crook et al., 2009; Shigeno et al., 2008; Staples and Boutilier, 2005; Wani, 2007; Westermann and Beuerlein, 2005).

Acknowledgements

This work was funded by The Australian Research Council Linkage Grant – Deep Ocean Australia, University of Queensland and Undersea Explorer who had no role in the study design, data collection, writing or direction for publication of this paper. The work of Jurgen and Stella Freund to identify *Nautilus* fishing locations and bring Omer Alanis into the project is greatly appreciated. The work and reporting efforts of Joern auf dem Kampe from European Geo magazine were also of great assistance to this study.

References

Bonnaud, L., Ozouf-Costaz, C., Boucher-Rodoni, R., 2004. A molecular and karyological approach to the taxonomy of *Nautilus*. C. R. Biol. 327, 133–138.
Cochran, J.K., Rye, D.M., Landman, N.H., 1981. Growth-rate and habitat of *Nautilus pompilius* inferred from radioactive and stable isotope studies. Paleobiology 7, 469–480.
Crook, R., Basil, J., 2008. A biphasic memory curve in the chambered *Nautilus*, *Nautilus pompilius* L. (Cephalopoda: Nautiloidea). J. Exp. Biol. 211, 1992–1998.
Crook, R.J., Hanlon, R.T., Basil, J.A., 2009. Memory of visual and topographical features suggests spatial learning in *Nautilus* (*Nautilus pompilius* L.). J. Comp. Psychol. 123, 264–274.
Ferraro, P.J., Gjertsen, H., 2009. A global review of incentive payments for sea turtle conservation. Chelonian Conserv. Biol. 8, 48–56.
Gärdenfors, U., Hilton-Taylor, C., Mace, G., Rodríguez, J.P., 2001. The application of IUCN Red List Criteria at regional levels. Conserv. Biol. 15, 1206–1212.
Hanlon, R.T., Messenger, J.B., 1996. Cephalopod Behaviour. Cambridge University Press, Cambridge, Cambridge.

IUCN, 2001. IUCN Red List Categories and Criteria (Version 3.1). www.iucnredlist.org. Downloaded on 29 October 2009.

IUCN, 2003. Guidelines for Application of IUCN Criteria at Regional Levels. Version 3.0. IUCN Species Survival Commission, IUCN, Gland, Switzerland and Cambridge, UK, ii+26 pp.

IUCN, 2008. Guidelines for Using the IUCN Red List Categories and Criteria (Version 7.0). www.iucnredlist.org. Downloaded on 29 October 2009.

IUCN, 2009. IUCN Red List of Threatened Species. Version 2009.1. www.iucnredlist.org. Downloaded on 29 October 2009.

Kwan, D., Marsh, H., Delean, S., 2006. Factors influencing the sustainability of customary dugong hunting by a remote indigenous community. Environ. Conserv. 33, 164–171.

Okubo, S., Tsujii, T., Watabe, N., Williams, D.F., 1995. Hatching of Nautilus belauensis Saunders, 1981, in captivity—culture, growth and stable-isotope compositions of shells, and hisatology and immunochemistry of the mantle epithelium of the juveniles. Veliger 38, 192–202.

R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL http://www.R-project.org.

Saunders, W.B., 1981a. A new species of *Nautilus* from Palau. Veliger 24, 1.

Saunders, W.B., 1981b. The species of living *Nautilus* and their distribution. Veliger 24, 8.

Saunders, W.B., 1983. Natural rates of growth and longevity of *Nautilus belauensis*. Paleobiology 9, 280–288.

Saunders, W.B., 1984. *Nautilus* growth and longevity—evidence from marked and recaptured animals. Science 224, 990–992.

Saunders, W.B., Bond, P.N., Hastie, L.C., Itano, D., 1989. On the distribution of *Nautilus pompilius* in the Samoas, Fiji and Tonga. Nautilus 103, 99–104.

Saunders, W.B., Landman, N.H. (Eds.), 2010. *Nautilus*: The Biology and Paleobiology of a Living Fossil, Reprint with Additions (Topics in Geobiology). Springer, New York.

Saunders, W.B., Spinosa, C., 1979. *Nautilus* movement and distribution in Palau, Western-Caroline-Islands. Science 204, 1199–1201.

Saunders, W.B., Ward, P.D., 1987. Sympatric occurrence of living *Nautilus* (*N. pompilius* and *N. stenomphalus*) on the Great Barrier Reef, Australia. Nautilus 101, 188–193.

Shigeno, S., Sasaki, T., Moritaki, T., Kasugai, T., Vecchione, M., Agata, K., 2008. Evolution of the cephalopod head complex by assembly of multiple molluscan body parts: evidence from *Nautilus* embryonic development. J. Morphol. 269, 1–17.

Sinclair, B., Briskey, L., Aspden, W., Pegg, G., 2007. Genetic diversity of isolated populations of *Nautilus pompilius* (Mollusca, Cephalopoda) in the Great Barrier Reef and Coral Sea. Hobart, Australia. Rev. Fish Biol. Fisher. 17, 223–235.

Staples, J.F., Boutilier, R.G., 2005. Hypoxia tolerance in the chambered *Nautilus*. Comp. Biochem. Phys. A 141, S176–S1176.

Strugnell, J., Jackson, J., Drummond, A.J., Cooper, A., 2006. Divergence time estimates for major cephalopod groups: evidence from multiple genes. Cladistics 22, 89–96.

Strugnell, J.M., Lindgren, A.R., 2007. A barcode of life database for the Cephalopoda? Considerations and concerns. Rev. Fish Biol. Fisher. 17, 337–344.

Tanabe, K., Tsukahara, J., Hayasaka, S., 1990. Comparative morphology of living *Nautilus* (Cephalopoda) from the Philippines, Fiji and Palau. Malacologia 31, 297–312.

Uchiyama, K., Tanabe, K., 1996. Hatching of *Nautilus macromphalus* in the Toba Aquarium, Japan. In: Oloriz, F., RodriguezTovar, F.J. (Eds.), Granada, Spain, pp. 13–16.

Wani, R., 2007. How to recognize in situ fossil cephalopods: evidence from experiments with modern *Nautilus*. Lethaia 40, 305–311.

Ward, P., 2008. Chambers of secrets. New Sci. 198, 40–43.

Ward, P.D., 1980. Restructuring the chambered *Nautilus*. Paleobiology 6, 247–249.

Ward, P.D., Saunders, W.B., 1997. *Allonautilus*: a new genus of living Nautiloid cephalopod and its bearing on phylogeny of the Nautilida. J. Paleontol. 71, 1054–1064.

Westermann, B., Beck-Schildwachter, I., Beuerlein, K., Kaleta, E.F., Schipp, R., 2004. Shell growth and chamber formation of aquarium-reared *Nautilus pompilius* (Mollusca, Cephalopoda) by X-ray analysis. J. Exp. Zool. Part A 301A, 930–937.

Westermann, B., Beuerlein, K., 2005. Y-maze experiments on the chemotactic behaviour of the tetrabranchiate cephalopod *Nautilus pompilius* (Mollusca). Mar. Biol. 147, 145–151.

Wilkinson, C. (Ed.), 2008. Status of Coral Reefs of the World: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, Australia, 296 pp.

Woodruff, D.S., Mulvey, M., Saunders, W.B., Carpenter, M.P., 1983. Genetic-variation in the cephalopod *Nautilus belauensis*. Proc. Acad. Nat. Sci. Phila. 135, 147–153.

Wray, C.G., Landman, N.H., Bonacum, J., 1995. Genetic-divergence and geographic diversification in *Nautilus*. Paleobiology 21, 220–228.