
Article:
Williams, R.C., Jackson, B.C., Duvaux, L. et al. (3 more authors) (2015) The genetic structure of Nautilus pompilius populations surrounding Australia and the Philippines. Molecular Ecology. Published Online 1 June 2015.

https://doi.org/10.1111/mec.13255

Received Date : 18-Feb-2015
Revised Date : 21-May-2015
Accepted Date : 27-May-2015
Article type : Original Article

The genetic structure of *Nautilus pompilius* populations surrounding Australia and the Philippines

Rachel C. Williams*[1,2], Benjamin C. Jackson[3†], Ludovic Duvaux[3†], Deborah A. Dawson[2], Terry Burke[2], William Sinclair[1]

[1] Centre for Wildlife Conservation, University of Cumbria, Ambleside LA22 9BJ, UK

[2] NERC Biomolecular Analysis Facility, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

[3] Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

* Rachel Williams, Centre for Wildlife Conservation, University of Cumbria, Ambleside LA22 9BJ, UK. Email: Williams.RachelC@gmail.com

[†] These authors contributed equally

Key words:

Approximate Bayesian computation, cephalopod, marine conservation, microsatellite, population structure

Running title:

Population structure of *Nautilus pompilius*

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/mec.13255

Abstract

Understanding the distribution of genetic diversity in exploited species is fundamental to successful conservation. Genetic structure and the degree of gene flow among populations must be assessed to design appropriate strategies to prevent the loss of distinct populations. The cephalopod *Nautilus pompilius* is fished unsustainably in the Philippines for the ornamental shell trade and has limited legislative protection, despite the species' recent dramatic decline in the region. Here, we use 14 microsatellite markers to evaluate the population structure of *N. pompilius* around Australia and the Philippines. Despite their relative geographical proximity, Great Barrier Reef individuals are genetically isolated from Osprey Reef and Shark Reef in the Coral Sea (F_{ST}=0.312, 0.229, respectively). Conversely, despite the larger geographical distances between the Philippines and west Australian reefs, samples display a small degree of genetic structure (F_{ST}=0.015). Demographic scenarios modelled using approximate Bayesian computation analysis indicate that this limited divergence is not due to contemporary gene flow between the Philippines and west Australia. Instead, present-day genetic similarity can be explained by very limited genetic drift that has occurred due to large average effective population sizes that persisted at both locations following their separation. The lack of connectivity among populations suggests that immigrants from west Australia would not facilitate natural recolonization if Philippine populations were fished to extinction. These data help to rectify the paucity of information on the species' biology currently inhibiting their conservation classification. Understanding population structure can allow us to facilitate sustainable harvesting, thereby preserving the diversity of genetically distinct stocks.

Introduction

Throughout the world, many commercial marine species are experiencing significant population declines (Hutchings 2000; Worm *et al.* 2006; Neubauer *et al.* 2013; Watson *et al.* 2013). The harvesting of marine animals began 42,000 years ago (O'Connor *et al.* 2011), up to 50,000 years after the anthropogenically triggered extinctions of large mammals seen on land (Koch & Barnosky 2006). Human access to the marine environment is no longer technologically inhibited, and defaunation of

the oceans is now occurring (McCauley *et al.* 2015). Present extinction rates are probably a thousand times higher than extinction rates in the absence of human actions (Pimm *et al.* 2014). Identifying species with a high risk of extinction (Davidson *et al.* 2012) can facilitate policy changes and prevent declines. An international agreement between governments that was developed to regulate declines is the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). CITES aims to ensure that the survival of species is not threatened by international trade, and the convention is reliant on biological data to construct a specific framework for participating countries to implement (CITES 2015). Unfortunately, the absence of biological information and global industrial data can prevent qualification for CITES protection (De Angelis 2012).

Population connectivity data can be used by CITES to design effective conservation strategies for marine resources. Contemporary movement and migration among marine populations have been monitored using tracking devices, but success has been variable (see Semmens *et al.* 2007). Movement among populations can be estimated using population genetic analyses (Pearse & Crandall 2004). Although specific individuals cannot always be tracked, molecular techniques do allow the detection of gene flow among populations through patterns of shared genetic variation (Levin 2006; Cowen & Sponaugle 2009). For vulnerable species, knowledge of the genetic structure of populations can be used to inform sustainable harvesting practices, prevent local extinctions and preserve the diversity of genetically distinct stocks (Carvalho & Hauser 1994). Oceans are considered to present few physical barriers to gene flow so that widely separated areas can remain connected, making absolute vicariance rare in a marine environment (Palumbi 1994; Mirams *et al.* 2011). Population structure and speciation have, however, been attributed to oceanic features, such as salinity (Rocha 2003; Lessios *et al.* 2003), depth and temperature (Zardi *et al.* 2007). Ocean fronts (Galarza *et al.* 2009) and currents (White *et al.* 2010) have also been shown to represent major barriers to gene flow, suggesting that marine environments may contain more barriers to dispersal than is generally appreciated.

Oceanic features with the potential to act as a barrier to movement can result in genetic structure that ranges from panmixia (Lessios *et al.* 2003) to complete separation (Baums *et al.* 2012). The inference of demographic history over long time scales can answer questions regarding long-term gene flow between, and distribution of genetic diversity among, populations (Semmens *et al.* 2007). This ability to infer a species' movements can be used in various areas of conservation, for example, to evaluate whether marine protected areas are appropriate (i.e. to assess that species movement does not extend beyond protected boundaries; Grüss *et al.* 2011), to trace the origins of a catch (Hobson 1999), or to ensure that illegal catches are not being missold to the consumer (Griffiths *et al.* 2013).

Despite the technology and conservation strategies available, population declines continue in most species (Neubauer *et al.* 2013). The poor success of attempts to aid the recovery of commercial marine species (Hutchings 2000) suggests that anthropogenic pressure is too high and that there are gaps in scientific knowledge that must be resolved to enable effective conservation (Sale *et al.* 2005). A key example of a species currently lacking biological and population connectivity data is the shelled cephalopod, *Nautilus pompilius.* Nautiloids (*Nautilus* spp. Linnaeus and *Allonautilus* spp. Ward and Saunders) are heavily overfished for the ornamental shell trade. The long-term effects of fishing on populations, or their ability to recover, are unknown (De Angelis 2012). An 80% decline in catch per unit effort for *N. pompilius* during 1980–2010 has been reported from Philippine fisheries (Dunstan *et al.* 2010). The current deficiency of data on the species' biology has inhibited the development of appropriate legislative mechanisms to prevent the species' overexploitation and decline. Understanding migration and its effect on population dynamics is important when deciding on appropriate protection measures for populations through *in-situ* means, such as marine protected areas (Grüss *et al.* 2011).

Cephalopod migration, however, is poorly understood, and this is exacerbated by the difficulties associated with tracking them (Stark *et al.* 2005; Semmens *et al.* 2007). In coleoids (octopus, cuttlefish, squid), juveniles are often too small to be tagged, tag placement in adults can be difficult,

and capture rates fluctuate and are often reliant on fishermen reporting catches (Sauer *et al.* 2000). Improvements in technology, with concomitant decreases in device size and cost, will aid progress in this area.

Historical movement of *N. pompilius* populations has been investigated using molecular approaches; hypothesised differentiation of *N. pompilius* populations was confirmed by comparing variation at *cytochrome c oxidase subunit I* (*COI*). Populations separated into three geographically distinct monophyletic clades, which comprise a west Australian/Indonesian clade, an east Australian/Papua New Guinean clade and a west Pacific clade (Wray *et al.* 1995; Sinclair *et al.* 2007, 2011; Bonacum *et al.* 2011; Williams *et al.* 2012). The observed population structure was proposed to be the result of dispersal from an ancestral population in the Philippines (Wray *et al.* 1995). Historical expansions of nautiloid distribution will have been restricted by at least three biogeographical barriers (Crick 1993): water depth, distance between adjacent shelf seas and sea temperature. These constraints are also relevant to modern *Nautilus* and *Allonautilus,* whose movements are limited to some extent by their morphology. Nautiloids are typically found between depths of 130 and 700 m (Dunstan *et al.* 2011), remaining close to the reef for protection from predators. The internal arrangement of the *Nautilus* shell means that their deepest position in the water column is limited by their risk of shell implosion. As a consequence, the maximum depth at which an individual would be encountered is considered to be approximately 800 m (Saunders & Wehman 1977; Kanie *et al.* 1980). These limitations create a dispersive barrier and, despite small geographical distances, genetic differentiation has occurred (Sinclair *et al.* 2007), furthered by the absence of a juvenile larval stage that might aid dispersal (Saunders & Landman 2010). Understanding gene flow between current populations can help to inform sustainable fishing and aid the design of specific genetic management, and yet nothing has been known about the current connectivity of *N. pompilius* populations. Understanding population connectivity will help to establish the impact that fishing is having across their distribution following *N. pompilius* population declines in the Philippines (Barord *et al.* 2014).

Here, we use molecular techniques and statistical analyses to assess the connectivity of *N. pompilius* populations surrounding Australia and the Philippines. These data will contribute towards rectifying the information deficiency that currently inhibits the legal classification of *N. pompilius* as an endangered species, and our findings can be used to assess the species' qualification for CITES listing. Approximate Bayesian computation (ABC) analysis has enabled a powerful assessment of the species' genetic diversity and made it apparent that, despite the persistence of high levels of variability that are usually associated with large populations, there is limited gene flow into shrinking contemporary populations. This implies that overfishing currently threatens some populations with extinction.

Materials and Methods

Sample collection

Australian samples were collected from seven reefs in the Indo-Pacific Ocean (Fig. 1) under an Australian Fisheries Management Authority Scientific Permit (number 1002548). West Australian (WA) samples were taken from four reefs: Clerke Reef, Imperieuse Reef, Ashmore Reef and Scott Reef. East Australian (EA) samples consisted of Osprey Reef and Shark Reef in the Coral Sea, and the Far North Great Barrier Reef. Samples from the Philippines (PH) were collected from three locations: Tinitian, Roxas and Palawan. Collections were made under a Gratuitous Permit from the Department of Agriculture in the Republic of the Philippines.

N. pompilius was caught using traps positioned on the reefs at a depth of ~200 m (Sinclair *et al.* 2011) baited with ~1 kg of uncooked chicken (*Gallus gallus*), set at dusk and collected at dawn. Tissue collection was non-lethal: a 1–2 cm-long labial tentacle sample was collected before each individual was released. Tentacles were immediately placed into a 20% DMSO (dimethylsulfoxide), 100 mM EDTA pH 8, saturated $NaCl_2$ solution and stored at 4°C in the field. Samples were later washed in TE buffer (1 M Tris-HCl pH 7.5; 0.5 M EDTA pH 8.0; Sambrook *et al.* 1989) and placed into 1 ml absolute ethanol in the laboratory for storage at room temperature (Sinclair *et al.* 2011).

Microsatellite Genotyping and Validity

Genomic DNA was extracted using Qiagen DNeasy tissue kits (QIAGEN Ltd, Manchester, UK). DNA concentration was quantified using a fluorometer (Fluostar Optima) and its quality assessed with electrophoresis on a 1% agarose gel. Fourteen polymorphic *N. pompilius* microsatellite loci (Williams *et al.* 2015) were selected based on satisfactory results from quality checks, and used to genotype all 215 individuals sampled. PCR amplification was performed in 2-µl PCR reactions, including 10 ng air-dried DNA, 0.2 µM reverse primer, 0.2 µM forward fluorescent primer (6FAM, HEX, VIC or PET labelled) and 1 µl Qiagen Multiplex Master mix. Multiplexes were amplified under the following profile: 95°C for 15 min, followed by 44 cycles of 94°C for 30 s, 56°C for 90 s, 72°C for 90 s and finally 72°C for 10 min. PCR products were analysed on an ABI 3730 48-well capillary DNA analyser (Applied Biosystems Inc.) using LIZ GS500 size standard (Applied Biosystems Inc.). Allele sizes were assigned using the GENEMAPPER v3.7 software (Applied Biosystems Inc.).

Relatedness between individuals was estimated with SPAGEDI (Hardy & Vekemans 2002) using Queller and Goodnight's (1989) measure of relatedness. Relatives were removed and departure from Hardy–Weinberg equilibrium (HWE; $P < 0.05$) and linkage disequilibrium (LD) were calculated using GENEPOP (Raymond & Rousset 1995; Rousset 2008). LD was assessed using 1000 iterations per population and *P*-values corrected using the False Discovery Rate adjustment (FDR; Verhoeven *et al.* 2005). Corrections were made on a population-by-population basis to avoid overinflating the number of tests in which the correction was required. Each microsatellite locus was assessed to estimate the frequency of null alleles and identify scoring errors due to stutter using MICRO-CHECKER (Van Oosterhout *et al.* 2004). Null allele frequency per locus was estimated using CERVUS v3.0 (Kalinowski 2005). To assess genotyping error rate, 60% of samples were re-extracted and re-genotyped across all loci. Error rates per reaction were calculated according to Hoffman & Amos (2005).

Population Structure

Three Bayesian clustering methods were used to determine the most likely number of genetic clusters within the data set: STRUCTURE (Pritchard *et al.* 2000), TESS (Durand *et al.* 2009) and GENELAND (Guillot *et al.* 2005). The software STRUCTURE was run with an admixture model and no prior information on the sampling locations (Supplementary Material Table 1). To avoid the influence of kinship on inferred structure, all individuals within a population with a relatedness of 0.5 were removed from the dataset before analysis (Queller & Goodnight 1989). Plotting the natural logarithm of the posterior probability (P_P) of K given the data over multiple runs determined the predicted number of clusters (Supplementary Material Fig. 2), and this was compared with ΔK (Evanno *et al.* 2005) as determined in STRUCTURE HARVESTER v.0.6.93 (Earl & VonHoldt 2011). Independent runs for all datasets were averaged in CLUMPP v.1.1.2 (Jakobsson & Rosenberg 2007) using the *Greedy* algorithm with 10,000 repeats to develop a consensus value for K. Graphical representation was produced in DISTRUCT v.1.1 (Rosenberg 2003). Bayesian clustering of TESS was run without admixture and K was inferred from the modal value of the replicate with the highest likelihood. A correlated allele frequency model was used in GENELAND and the burn-in length was based on the appearance of the posterior density log, as suggested by the software manual. The number of proposed clusters was selected from the highest mean log P_P (Guillot *et al.* 2009).

MICROSATELLITE ANALYSER (Dieringer & Schlötterer 2003) was used to calculate pairwise F_{ST} values (Weir & Cockerham 1984) between sampling locations, with Bonferroni corrections applied. To test for an association between F_{ST} and geographical distance, Mantel's test for isolation by distance (IBD) was performed in SPAGEDI with 10,000 randomisations. A regression of the spatial distance against $F_{ST}/(1-F_{ST})$ was performed (Rousset 1997). Jost's differentiation index (D_{est}) values (Jost 2008) across loci were calculated using DEMETICS (Gerlach *et al.* 2010).

Approximate Bayesian Computation Methods

To test alternative hypotheses that could explain the genetic similarity between PH and WA samples (see Results), we conducted an ABC analysis (Beaumont *et al.* 2002). ABC aims to obtain the joint posterior distribution of complex models for which the likelihood function can be difficult or impossible to solve analytically, allowing a great flexibility in the scenarios being investigated (Marjoram & Tavaré 2006). Its rationale is to bypass the need of an exact likelihood function by comparing summary statistics from observed data to the summary statistics obtained by simulating the models of interest (Beaumont 2010; Csilléry *et al.* 2010).

We compared three evolutionary scenarios (Fig. 3). Model IWOM assumes that an ancestral population of size N_A split t generations ago into two daughter populations, PH and WA, of effective sizes N_1 and N_2, respectively (Fig. 3b). Model IM (Nielsen & Wakeley 2001) is equivalent to Model IWOM with the adjustment that populations PH and WA have constantly exchanged migrants since their split at rates m_{12} and m_{21}, respectively (Fig. 3c). A null model was also tested as Model PAN; this assumes that PH and WA are part of the same panmictic population of effective size N_P (Fig. 3a). Note that to compute summary statistics comparable to the observed data (i.e. from two different populations), we set $\text{Model}_{\text{PAN}}$ using $\text{Model}_{\text{IWOM}}$ parameters but fixed the divergence time to 1 generation – effectively modelling the samples as a panmictic population throughout their whole history.

The prior distributions were uniform for all demographic parameters and the same range was used for common parameters between models (Table 2). For all demographic models, we assumed that microsatellites evolved under a stepwise-mutation model. Mean mutation rates across loci were extracted from a normal prior distribution, and single-locus mutation rates were drawn from a Gamma distribution as parameterized in ABC TOOLBOX (Wegmann *et al.* 2010), using uniform priors for the two parameters of the distribution. To avoid effects of substructure within the WA clade, and due to similar sample size, Ashmore Reef was chosen to represent the WA clade.

Summary statistics and simulations

ABC analyses were conducted using the package ABC TOOLBOX (Wegmann *et al.* 2010). One limitation of ABC is that models can appear more or less likely dependent on the range of the parameter values and the weight assigned to them by the priors (Sousa *et al.* 2012). Exploratory simulations were therefore performed with varied sets of priors to allow an assessment of their effect on the posterior distribution and ensure that the whole posterior was contained within the final prior range.

We used FASTSIMCOAL (Excoffier & Foll 2011; Excoffier *et al.* 2013) to run one million coalescent simulations of our dataset of 14 microsatellites under each model. ARLSUMSTAT (Excoffier & Lischer 2010) was used to calculate a set of 30 summary statistics (within and between populations; Supplementary Material Table 2), chosen based on those shown to be informative in previous studies (Palero *et al.* 2009; Sousa *et al.* 2012; Butlin *et al.* 2013). To reduce the high dimensionality of the summary statistics, we used a partial least-squares (PLS) transformation (Wegmann *et al.* 2009) to extract their orthogonal components. PLS identifies components to explain variability of response variables (model parameters) by maximising the covariance matrix of predictor (raw summary statistics) and response variables (Wegmann *et al.* 2009).

Model choice and parameter estimation

For model comparison, marginal densities comparable between models were produced using the PLS-transformed summary statistics for the rejection step, while all raw summary statistics were used to perform the post-sampling adjustment step using the ABC-GLM (General Linear Model) in ABC TOOLBOX (Wegmann *et al.* 2009). We retained the 5% of simulations closest to the observed data. We checked that our observed summary statistics (for both PLS components and raw summary statistics) fell within the distribution of summary statistics from the simulations retained. Bayes Factors and P_P were derived from the model choice procedure (Supplementary Material Table 3). *P*-values were taken as an indication of each model's ability to explain the data.

To validate our model choice procedure, we simulated 1000 pseudo-observed data sets for each model using the original priors. The original results files (of one million simulated data sets for each model) were used to perform our model choice procedure using each of the 1000 pseudo-observed data sets in turn. To test the robustness of discrimination between models using our model choice procedure, each pairwise comparison of simulated and observed data for the two models was performed. A model's original data were compared with the pseudo-data of the same model and those of the model being compared. Posterior probabilities were compared with a logistic regression. Confidence in model choice was calculated by estimating the FDR (Verhoeven *et al.* 2005): the frequency of the P_P being equal to or larger than the real P_P of the best model.

For parameter estimation, the distance step and post-sampling adjustment were both carried out using PLS components. This was performed independently for each model because different PLS components are extracted for each model. The GLM method implemented in ABC TOOLBOX (Leuenberger & Wegmann 2010) was used for post-sampling adjustment. Parameter estimation was verified by ensuring *P*-values were reasonably large (>0.05 as suggested in the ABC TOOLBOX manual) and checking that posterior distributions were within the prior ranges (Supplementary Material Fig. 3). The pseudo-observed data were also used to check for uniformity of the posterior quantiles; a departure from uniformity suggests a parameter is over- or underestimated.

Results

Genotyping Validation

A genotyping error rate of zero was determined between replicates. No evidence was found for frequent allelic drop-out across any loci in any sampling locations. A shortage of heterozygous genotypes was found for locus *Npom08* in the Osprey Reef and Scott Reef populations, possibly resulting from scoring errors due to stutter. This locus was retained in analyses due to its quality in other reef populations. The estimated frequency of null alleles was low for all loci (≤ 0.05). Departure

from HWE was not detected consistently across all sampling locations at any loci. No pairs of loci consistently showed LD in all populations, suggesting that no loci were physically linked. F_{ST} values ranged from -0.04 to 0.35, D_{est} ranged from -0.04 to 0.75 (Table 1). IBD analysis revealed no overall association between F_{ST} and geographical distance and was not significant ($r^2 = 0.139$; $P = 0.095$).

Population Structure

Shark Reef was grouped with Osprey Reef for analyses based on their close geographical location and high degree of relatedness (Table 1); they will hereafter be referred to as Osprey Reef. Results incorporating spatial data in TESS (Fig. 2a) and GENELAND (Supplementary Material Fig. 1) returned three and five genetic clusters, respectively. TESS returned the first cluster, including PH and all WA reefs, the second cluster of the Great Barrier Reef, and third cluster of Osprey Reef. GENELAND divided samples into five genetic clusters of: (i) PH, (ii) Ashmore, Imperieuse and Clerke Reefs, (iii) Scott Reef, (iv) Great Barrier Reef and (v) Osprey Reef.

Plots of ΔK and LnP(K) generated from STRUCTURE results indicated four as the most likely number of genetic clusters present in the full dataset (Fig. 2). The first two genetic clusters consisted of populations PH and WA, the third cluster consisted of EA Great Barrier Reef, and cluster four consisted of Coral Sea's Osprey Reef (Fig. 2b). Sub-setting the data to look for further division within clusters returned validating results (Fig. 2c and 2d).

Approximate Bayesian computation analysis

The model comparison gave strong support to $model_{IWOM}$ ($P_P = 1.0$, Supplementary Material Table 3) and the FDR was low (0.2%), indicating with high confidence that the data were not the result of sustained migration between the Philippines and WA (see also Supplementary Material Fig. 4). Moreover, this model fitted the data well (the observed summary statistics lay within the range of both the untransformed and PLS-transformed post-rejection simulated summary statistics), indicating that its best score was not a result of a bad fit by all models to the data. Parameter estimation under

model$_{IWOM}$ enabled estimation of the ancestral effective population size (median: 2,035,120; highest posterior density (HPD95 low, high): 62,816.9, 4,508,320), which was smaller than the estimated current population sizes of PH (median: 3,080,000) and WA (median: 2,610,000). The distribution of posterior quantiles did not show strong departures from uniformity, which is indicative of a lack of bias in parameter estimation (Wegmann *et al.* 2009).

Discussion

We detected population structure among east Australian sampling sites, indicating genetic isolation of Osprey Reef and Shark Reef from the Great Barrier Reef. West Australian samples revealed limited population structure but with significant pairwise F_{ST} and D_{est} between Scott Reef and the other west Australian reefs. The genetic similarity found between the Philippines and west Australia was unexpected. Further investigation modelling different demographic scenarios revealed that this similarity was not the result of migration, but may be attributable to ancestral population sizes that were until recently large (population declines have been shown in areas under fishing pressure; Barord et al. 2014), and consequently exhibiting limited genetic drift.

Mechanisms for population structure

Results from software STRUCTURE, TESS and GENELAND showed Osprey Reef and Shark Reef populations in the Coral Sea to be genetically distinct from the Great Barrier Reef, west Australia, and Philippine populations. Ocean physiography (the physical geography of the ocean floor) appears to have been influential in this differentiation. Ocean depths in the Coral Sea between Osprey Reef and the Great Barrier Reef exceed 1700 m (Dunstan *et al.* 2011), and while movement through open water is feasible, it leaves individuals vulnerable to predation (Yomogida & Wani 2013). The response of *N. pompilius* individuals to attacks by teleosts showed that that they retreated into their shells and demonstrated no defence or escape response (Saunders & Landman 2010). The Great Barrier Reef was shown to be distinct, not only from Osprey Reef but also from the western populations, which supports

the conclusions of previous evolutionary studies using partial *COI* sequences (Sinclair *et al.* 2007, 2011; Bonacum *et al.* 2011; Williams *et al.* 2012).

West Australian results were not consistent across software; STRUCTURE and TESS assigns the Philippines and west Australia to the same genetic population, whereas GENELAND designates the Philippines and Scott Reef as separate genetic clusters. Geographically, Scott Reef is located between Ashmore and Clerke Reef, and the differentiation is seen between Scott Reef and surrounding west Australian reefs, despite shallower surrounding sea depths. F_{ST} measures deviation from panmixia, D_{est} measures deviations from total differentiation (Whitlock 2011); both F_{ST} and D_{est} values distinguish Scott Reef as a separate genetic cluster.

Due to their residing depth, data on currents at the surface cannot explain *N. pompilius* dispersal patterns (Biuw *et al.* 2007). Currents have been shown to impact individual positions on a reef (O'Dor *et al.* 1993), with recorded movements of up to 6 km that may have been facilitated by currents (Dunstan *et al.* 2011). However, *N. pompilius* has also demonstrated strong resistance to currents and an ability to utilise them to obtain food (O'Dor *et al.* 1990). The overall impact of currents on the species' population distribution is poorly documented.

No significant correlation was found between F_{ST} and linear geographic distance (Rousset 1997). IBD has been shown in other cephalopods (Pérez-Losada *et al.* 2002; Kassahn *et al.* 2003; Cabranes *et al.* 2008) but, like *Nautilus,* the octopus *Octopus vulgaris* (Moreira *et al.* 2011), the cuttlefish *Sepia esculenta* (Zheng *et al.* 2009) and the squid *Loligo pealeii* (Buresch *et al.* 2006) have all demonstrated genetic distances disproportionate to geographical distances. It has been hypothesised that this was in each case due to natal philopatry (Kassahn *et al.* 2003; Buresch *et al.* 2006). It has been speculated that this behaviour does not occur in nautiloids (Crook & Basil 2013), but gaps remain in our knowledge of *N. pompilius* ecology. Despite lacking the lensed eye and vertebrate-like brain of other cephalopods (including dedicated lobes for learning and memory), *N. pompilius* has been shown to be

capable of both spatial learning and navigational strategy (Crook *et al.* 2009; Crook & Basil 2013). Migration on a small scale is not completely unfeasible, but seems unlikely at the scale investigated in our study.

Divergence without migration

Our ABC model does not support the possibility of sustained migration between the Philippines and west Australia as an explanation for the genetic admixture shown in the structural analyses. Movement of individuals between the two sites was unknown, but depth limitations of *N. pompilius* are indicative of isolation over such a geographical distance; it is possible that the genetic similarity observed has resulted from incomplete lineage sorting. Marker data can be misleading about relationships among populations due to the retention and stochastic sorting of ancestral polymorphisms. This is especially likely if the effective population size is large relative to lineage length (the time since the populations split; Maddison & Knowles 2006). Alleles can then persist in both populations due to limited genetic drift. $Model_{IWOM}$ indicated extremely large ancestral and current effective population sizes, resulting in a lower probability of alleles becoming fixed before divergence (Pamilo & Nei 1988). Current population size estimates for the Philippines (median = 3,190,920) and Ashmore Reef (median = 2,562,800) suggest that genetic drift has yet to have a significant impact. Such large current population estimates are potentially due, in part, to substructure within the sampled areas. Sampling from the Philippines was conducted in several locations, the connectivity between which was assumed but not confirmed. West Australian samples were from the most northern of these reefs, Ashmore Reef; gene flow was previously established between the sampled west Australian reefs (Williams *et al.* 2012). This local gene flow may have inflated the population estimate for Ashmore Reef, reflecting the population size of the NW shelf populations.

Population density estimates made using baited remote underwater video systems were calculated as 13.6 and 0.03 individuals per km^2 for Osprey Reef and Bohol Sea (Philippines), respectively (Barord *et al.* 2014). Using different methods to generate these results produced predictably dissimilar

abundance data. Additionally, Barord *et al.* (2014) documents evidence of a sudden population size reduction, but our data showed that allelic richness in the Philippines was no lower than at other locations sampled (Fig. 4). It is possible that the genetic consequences of population reduction have yet to take effect; low fecundity and long developmental time (Carlson *et al.* 1984; Landman *et al.* 2010) of nautiloids results in a long generation time compared to other cephalopods. Fishing for shells is relatively new, with no cultural or historical significance in studied areas such as Palawan (Dunstan *et al.* 2010), and so it is possible that we will see a genetic response to exploitation that is not yet detectable with our current set of markers.

The allelic richness in Philippine samples also supports the proposed direction of colonisation from the progenitor population located in the Philippines (Wray *et al.* 1995). There is lower allelic richness in the Great Barrier Reef, with a further decline in the more genetically distinct Osprey and Shark Reefs of the Coral Sea (Fig. 4). The time split estimation (median = 296,495 generations/1,660,366 years based on a generation time of 5.6 years (Saunders & Landman 2010)) by $model_{IWOM}$ indicates that current populations have been evolving independently for a similar time as the accepted species of modern *N. pompilius* (Kröger *et al.* 2011).

Management implications

The absence of migration between the Philippines and west Australia highlights the need for mechanisms to protect these populations as discrete conservation units (Moritz 1994). Environmental differences between sites have not been measured and so it is unknown if resulting divergent selection has occurred, but as a unique population with the possibility of local adaptation, adequate protection for the Philippines is imperative to the long-term survival of this genetic cluster. The absence of contemporary migration indicates that it is unlikely that the Philippines would be repopulated, should fishing in this area continue to extinction. Informative results must now reach policy makers to enable legislative protection.

The variation seen in IBD within cephalopods demonstrates the need for species-specific range studies, especially when results are extrapolated for fisheries management. As fin fish stocks decline and the fishing industry targets novel resources, it is likely that cephalopod stocks will experience increased fishing pressure (Dillane *et al.* 2005). The data supporting the need for *Nautilus* and *Allonautilus* protection is ever increasing (Dunstan *et al.* 2010; Bonacum *et al.* 2011; Williams *et al.* 2012; De Angelis 2012; Barord *et al.* 2014). Overexploitation is threatening marine species world-wide (Hutchings 2000; Worm *et al.* 2006; Doukakis *et al.* 2009; Neubauer *et al.* 2013; Watson *et al.* 2013) and our study highlights the need for multiple or finer-scale markers to determine connectivity patterns and establish adequate protection. For example, mitochondrial DNA data on the west Australian reefs (Williams *et al.* 2012) suggested that the population was panmictic, but the higher-resolution data presented here reveals substructure. Our results show how management plans should incorporate discrete management units and should account for more than separation by geographic distance.

Conclusions

A range of molecular studies has been conducted on coleoids (Allcock *et al.* 2015), including population structure analysis using minisatellites, microsatellites and mitochondrial DNA (Dillane *et al.* 2005; Zheng *et al.* 2009; Moreira *et al.* 2011), but this is the first study to use microsatellite markers in a nautiloid. We had hypothesised genetic division between east and west Australia based on previous evolutionary studies on these populations (Sinclair *et al.* 2007, 2011; Bonacum *et al.* 2011; Williams *et al.* 2012), but we found a greater degree of genetic similarity between samples from the Philippines and west Australia than had been previously considered. Our conclusion that this similarity was not the result of migration emphasises the need to reduce over-exploitation and prevent the local extinction of *N. pompilius* in the Philippines. Protection for *Nautilus* and *Allonautilus* under CITES would decrease the incentive for continued exploitation. In relatively inaccessible species, genetic data can provide an insight into migration and population dynamics. Such genetic studies should be utilised to develop efficient species-specific management plans for declining populations.

Enforcing these, in collaboration with legislative protection, is imperative for the conservation of marine populations (Neubauer *et al.* 2013).

Acknowledgements

We thank Rikki Gumbs and Aaron Comeault for comments on the manuscript, and Martin Hinsch for support with analyses. We thank Steeves Buckland, Rachel Tucker and Kim Mortega for advice throughout the project. We are grateful to members of the Sheffield Molecular Ecology Laboratory for helpful discussion. The laboratory work and data analyses were supported by the UK Natural Environment Research Council (NERC) at the NERC Biomolecular Analysis Facility. LD was supported by the Leverhulme trust (grant number RPG-2013-198).

Author Contributions

RCW and WS obtained samples. RCW performed the genotyping. RCW and DAD assessed the marker quality. RCW, BCJ and LD analysed and interpreted the data. WS, DAD, TB oversaw the project. RCW drafted the manuscript and all authors contributed edits and comments.

Data accessibility

Microsatellite primer sequences for *N. pompilius* are available through NCBI: accession numbers HG918068-HG918111. Microsatellite genotyping data and the geographic information for the Mantel's test are available in Dryad, doi:10.5061/dryad.j251f.

References

Allcock A, Lindgren A, Strugnell J (2015) The contribution of molecular data to our understanding of cephalopod evolution and systematics: a review. *Journal of Natural History*, **49**, 1373–1421.

De Angelis P (2012) Assessing the impact of international trade on chambered Nautilus. *Geobios*, **45**, 5–11.

Barord GJ, Dooley F, Dunstan A *et al.* (2014) Comparative population assessments of Nautilus sp. in the Philippines, Australia, Fiji, and American Samoa using baited remote underwater video systems. *PLoS One*, **9**, e100799.

Baums IB, Boulay JN, Polato NR, Hellberg ME (2012) No gene flow across the Eastern Pacific Barrier in the reef-building coral Porites lobata. *Molecular Ecology*, **21**, 5418–33.

Beaumont MA (2010) Approximate Bayesian Computation in evolution and ecology. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 379–406.

Beaumont MA, Zhang W, Balding DJ (2002) Approximate Bayesian computation in population genetics. *Genetics*, **162**, 2025–2035.

Biuw M, Boehme L, Guinet C *et al.* (2007) Variations in behavior and condition of a Southern Ocean top predator in relation to *in situ* oceanographic conditions. *Proceedings of the National Academy of Sciences of the USA*, **104**, 13705–13710.

Bonacum J, Landman NH, Mapes RH *et al.* (2011) Evolutionary radiation of present-day *Nautilus* and *Allonautilus*. *American Malacological Bulletin*, **29**, 77–93.

Buresch KC, Gerlach G, Hanlon RT (2006) Multiple genetic stocks of longfin squid *Loligo pealeii* in the NW Atlantic: stocks segregate inshore in summer, but aggregate offshore in winter. *Marine Ecology Progress Series*, **310**, 263–270.

Butlin RK, Saura M, Charrier G *et al.* (2013) Parallel evolution of local adaptation and reproductive isolation in the face of gene flow. *Evolution*, **68**, 935–949.

Cabranes C, Ernandez-Rueda P, Martínez J (2008) Genetic structure of *Octopus vulgaris* around the Iberian Peninsula and Canary Islands as indicated by microsatellite DNA variation. *ICES Journal of Marine Science*, **65**, 12–16.

Carlson BA, McKibben J, DeGruy M (1984) Telemetric investigation of vertical migration of *Nautilus belauensis* in Palau. *Pacific Science*, **38**, 183–188.

Carvalho GR, Hauser L (1994) Molecular genetics and the stock concept in fisheries. *Reviews in Fish Biology and Fisheries*, **4**, 326–350.

CITES (2015) Convention on International Trade in Endangered Species of Wild Fauna and Flora. *http://www.cites.org/eng*.

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, **1**, 443–466.

Crick RR (1993) Biogeography of Early and Middle Paleozoic nautiloid Cephalopods: evidence for barriers to dispersal and evolution. *Geobios*, **15**, 91–105.

Crook RJ, Basil JA (2013) Flexible spatial orientation and navigational strategies in chambered *Nautilus*. *Ethology*, **119**, 77–85.

Crook RJ, Hanlon RT, Basil JA (2009) Memory of visual and topographical features suggests spatial learning in nautilus (*Nautilus pompilius* L.). *Journal of Comparative Psychology*, **123**, 264–274.

Csilléry K, Blum MGB, Gaggiotti OE, François O (2010) Approximate Bayesian Computation (ABC) in practice. *Trends in Ecology & Evolution*, **25**, 410–418.

Davidson AD, Boyer AG, Kim H *et al.* (2012) Drivers and hotspots of extinction risk in marine mammals. *Proceedings of the National Academy of Sciences of the USA*, **109**, 3395–3400.

Dieringer D, Schlötterer C (2003) Microsatellite analyser (MSA): a platform independent analysis tool for large microsatellite data sets. *Molecular Ecology Notes*, **3**, 167–169.

Dillane E, Galvin P, Coughlan J, Lipinski M, Cross TF (2005) Genetic variation in the lesser flying squid *Todaropsis eblanae* (Cephalopoda, Ommastrephidae) in east Atlantic and Mediterranean waters. *Marine Ecology Progress Series*, **292**, 225–232.

Doukakis P, Parsons ECM, Burns WCG *et al.* (2009) Gaining traction: retreading the wheels of marine conservation. *Conservation Biology*, **23**, 841–846.

Dunstan A, Alanis O, Marshall J (2010) *Nautilus pompilius* fishing and population decline in the Philippines: a comparison with an unexploited Australian Nautilus population. *Fisheries Research*, **106**, 239–247.

Dunstan AJ, Ward PD, Marshall NJ (2011) Vertical distribution and migration patterns of *Nautilus pompilius*. *PLoS One*, **6**, e16311.

Durand E, Jay F, Gaggiotti OE, François O (2009) Spatial inference of admixture proportions and secondary contact zones. *Molecular Biology and Evolution*, **26**, 1963–1973.

Earl DA, VonHoldt BM (2011) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, **4**, 359–361.

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology*, **14**, 2611–2620.

Excoffier L, Dupanloup I, Huerta-Sánchez E, Sousa VC, Foll M (2013) Robust demographic inference from genomic and SNP data. *PLoS Genetics*, **9**, e1003905.

Excoffier L, Foll M (2011) Fastsimcoal: a continuous-time coalescent simulator of genomic diversity under arbitrarily complex evolutionary scenarios. *Bioinformatics*, **27**, 1332–1334.

Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, **10**, 564–567.

Galarza JA, Carreras-Carbonell J, Macpherson E *et al.* (2009) The influence of oceanographic fronts and early-life-history traits on connectivity among littoral fish species. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 1473–1478.

Gerlach G, Jueterbrock A, Kraemer P, Deppermann J, Harmand P (2010) Calculations of population differentiation based on GST and D: forget GST but not all of statistics ! *Molecular Ecology*, **19**, 3845–3852.

Griffiths AM, Miller DD, Egan A *et al.* (2013) DNA barcoding unveils skate (Chondrichthyes: Rajidae) species diversity in "ray" products sold across Ireland and the UK. *PeerJ*, **1**, e129.

Grüss A, Kaplan DM, Guénette S, Roberts CM, Botsford LW (2011) Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation*, **144**, 692–702.

Guillot G, Leblois R, Coulon A, Frantz AC (2009) Statistical methods in spatial genetics. *Molecular Ecology*, **18**, 4734–4756.

Guillot G, Mortier F, Estoup A (2005) Geneland: a computer package for landscape genetics. *Molecular Ecology Notes*, **5**, 712–715.

Hardy JO, Vekemans X (2002) SPAGeDi : a versatile computer program to analyse spatial. *Molecular Ecology Notes*, **2**, 618–620.

Hobson K a. (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*, **120**, 314–326.

Hoffman JI, Amos W (2005) Microsatellite genotyping errors: detection approaches, common sources and consequences for paternal exclusion. *Molecular Ecology*, **14**, 599–612.

Hutchings JA (2000) Collapse and recovery of marine fishes. *Nature*, **406**, 882–885.

Jakobsson M, Rosenberg N (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, **23**, 1801–1806.

Jost L (2008) GST and its relatives do not measure differentiation. *Molecular Ecology*, **17**, 4015–4026.

Kalinowski ST (2005) Hp-Rare 1.0: a computer program for performing rarefaction on measures of allelic richness. *Molecular Ecology Notes*, **5**, 187–189.

Kanie Y, Fukuda Y, Nakayama H, Seki K, Hattori M (1980) Implosion of living *Nautilus* under increased pressure. *Paleobiology*, **6**, 44–47.

Kassahn KS, Donnellan SC, Fowler AJ *et al.* (2003) Molecular and morphological analyses of the cuttlefish *Sepia apama* indicate a complex population structure. *Marine Biology*, **143**, 947–962.

Koch PL, Barnosky AD (2006) Late Quaternary Extinctions: State of the Debate. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 215–250.

Kröger B, Vinther J, Fuchs D (2011) Cephalopod origin and evolution: A congruent picture emerging from fossils, development and molecules: Extant cephalopods are younger than previously realised and were under major selection to become agile, shell-less predators. *BioEssays : news and reviews in molecular, cellular and developmental biology*, **33**, 602–613.

Landman NH, Cochran JK, Saunders WB (2010) Growth and longevity of *Nautilus*. In: *Nautilus: Biology and Paleobiology of a Living Fossil* , pp. 401–420. Plenum Press, New York.

Lessios HA, Kane J, Robertson DR (2003) Phylogeography of the pantropical sea urchin Tripneustes: contrasting patterns of population structure between oceans. *Evolution*, **57**, 2026–2036.

Leuenberger C, Wegmann D (2010) Bayesian computation and model selection without likelihoods. *Genetics*, **184**, 243–252.

Levin L (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integrative and Comparative Biology*, **46**, 282–297.

Maddison WP, Knowles LL (2006) Inferring phylogeny despite incomplete lineage sorting. *Systematic Biology*, **55**, 21–30.

Marjoram P, Tavaré S (2006) Modern computational approaches for analysing molecular genetic variation data. *Nature Reviews. Genetics*, **7**, 759–770.

McCauley DJ, Pinsky ML, Palumbi SR *et al.* (2015) Marine defaunation: Animal loss in the global ocean. *Science*, **347**, 1255641.

Mirams AGK, Treml EA, Shields JL, Liggins L, Riginos C (2011) Vicariance and dispersal across an intermittent barrier: population genetic structure of marine animals across the Torres Strait land bridge. *Coral Reefs*, **30**, 937–949.

Moreira AA, Tomás ARG, Hilsdorf AWS (2011) Evidence for genetic differentiation of *Octopus vulgaris* (Mollusca, Cephalopoda) fishery populations from the southern coast of Brazil as revealed by microsatellites. *Journal of Experimental Marine Biology and Ecology*, **407**, 34–40.

Moritz C (1994) Defining "Evolutionarily Significant Units" for conservation. *Trends in ecology & evolution*, **9**, 373–375.

Neubauer P, Jensen OP, Hutchings JA, Baum JK (2013) Resilience and recovery of overexploited marine populations. *Science*, **340**, 347–349.

Nielsen R, Wakeley J (2001) Distinguishing migration from isolation: a Markov chain Monte Carlo approach. *Genetics*, **158**, 885–896.

O'Connor S, Ono R, Clarkson C (2011) Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. *Science*, **334**, 1117–1121.

O'Dor RK, Forsythe J, Webber DM, Wells J, Wells MJ (1993) Activity levels of *Nautilus* in the wild. *Nature*, **362**, 626–628.

O'Dor RK, Wells J, Wells MJ (1990) Speed, jet pressure and oxygen consumption relationships in free-swimming *Nautilus*. *Journal of Experimental Biology*, **154**, 383–396.

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) Micro-Checker: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, **4**, 535–538.

Palero F, Lopes J, Abelló P *et al.* (2009) Rapid radiation in spiny lobsters (Palinurus spp) as revealed by classic and ABC methods using mtDNA and microsatellite data. *BMC Evolutionary Biology*, **9**, 263.

Palumbi SR (1994) Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics*, **25**, 547–572.

Pamilo P, Nei M (1988) Relationships between gene trees and species trees. *Molecular Biology and Evolution*, **5**, 568–583.

Pearse DE, Crandall KA (2004) Beyond FST : Analysis of population genetic data for conservation. *Conservation Genetics*, **5**, 585–602.

Pérez-Losada M, Guerra A, Carvalho GR, Sanjuan A, Shaw PW (2002) Extensive population subdivision of the cuttlefish *Sepia officinalis* (Mollusca: Cephalopoda) around the Iberian Peninsula indicated by microsatellite DNA variation. *Heredity*, **89**, 417–424.

Pimm SL, Jenkins CN, Abell R *et al.* (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**, 1246752.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.

Raymond M, Rousset F (1995) GENEPOP (Version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.

Rocha LA (2003) Patterns of distribution and processes of speciation in Brazilian reef fishes. *Journal of Biogeography*, **30**, 1161–1171.

Rosenberg N (2003) Distruct: a Program for the Graphical Display of Population Structure. *Molecular Ecology Notes*, **4**, 137–138.

Rousset F (1997) Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics*, **145**, 1219–1228.

Rousset F (2008) GENEPOP'007: a complete re-implementation of the genepop software for Windows and Linux. *Molecular Ecology Resources*, **8**, 103–106.

Sale PF, Cowen RK, Danilowicz BS *et al.* (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution*, **20**, 74–80.

Sambrook J, Fritsch E, Maniatis T (1989) *Molecular cloning. A laboratory manual*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.

Sauer W, Lipinski M, Augustyn C. (2000) Tag recapture studies of the chokka squid Loligo vulgaris reynaudii d′Orbigny, 1845 on inshore spawning grounds on the south-east coast of South Africa. *Fisheries Research*, **45**, 283–289.

Saunders WB, Landman NH (2010) *Nautilus: The Biology and Paleobiology of a Living Fossil*. Springer, London.

Saunders WB, Wehman DA (1977) Shell strength of Nautilus as a depth limiting factor. *Paleontological Society*, **3**, 83–89.

Semmens JM, Pecl GT, Gillanders BM *et al.* (2007) Approaches to resolving cephalopod movement and migration patterns. *Reviews in Fish Biology and Fisheries*, **17**, 401–423.

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. *Reviews in Fish Biology and Fisheries*, **17**, 223–235.

Sinclair W, Newman SJ, Vianna GMS, Williams S, Aspden WJ (2011) Spatial subdivision and genetic diversity in populations on the east and west coasts of Australia: The multi-faceted case of *Nautilus pompilius* (Mollusca, Cephalopoda). *Reviews in Fisheries Science*, **19**, 52–61.

Sousa VC, Beaumont MA, Fernandes P, Coelho MM, Chikhi L (2012) Population divergence with or without admixture: selecting models using an ABC approach. *Heredity*, **108**, 521–530.

Stark K, Jackson G, Lyle J (2005) Tracking arrow squid movements with an automated acoustic telemetry system. *Marine Ecology Progress Series*, **299**, 167–177.

Verhoeven KJF, Simonsen KL, Mcintyre LM (2005) Implementing false discovery rate control: increasing your power. *Oikos*, **108**, 643–647.

Watson R a, Cheung WWL, Anticamara J a *et al.* (2013) Global marine yield halved as fishing intensity redoubles. *Fish and Fisheries*, **14**, 493–503.

Wegmann D, Leuenberger C, Excoffier L (2009) Efficient approximate Bayesian computation coupled with Markov chain Monte Carlo without likelihood. *Genetics*, **182**, 1207–1218.

Wegmann D, Leuenberger C, Neuenschwander S, Excoffier L (2010) ABCtoolbox: a versatile toolkit for approximate Bayesian computations. *BMC Bioinformatics*, **11**, 116.

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.

White C, Selkoe KA, Watson J *et al.* (2010) Ocean currents help explain population genetic structure. *Proceedings of the Royal Society B*, **277**, 1685–1694.

Whitlock MC (2011) *G'*ST and *D* do not replace *F*ST. *Molecular Ecology*, **20**, 1083–1091.

Williams RC, Dawson DA, Horsburgh GJ, Sinclair W (2015) Isolation and characterisation of microsatellite loci for the ancient cephalopod, Nautilus pompilius. *Conservation Genetics Resources*, **7**, 107–111.

Williams RC, Newman SJ, Sinclair W (2012) DNA barcoding in *Nautilus pompilius* (Mollusca : Cephalopoda): evolutionary divergence of an ancient species in modern times. *Invertebrate Systematics*, **26**, 548–560.

Worm B, Barbier EB, Beaumont N *et al.* (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**, 787–790.

Wray C, Landman N, Saunders W, Bonacum J (1995) Genetic divergence and geographic diversification in Nautilus. *Paleobiology*, **21**, 220–228.

Yomogida S, Wani R (2013) Higher risk of fatality by predatory attacks in earlier ontogenetic stages of modern *Nautilus pompilius* in the Philippines: evidence from the ontogenetic analyses of shell repairs. *Lethaia*, **46**, 317–330.

Zardi G, McQuaid C, Teske P, Barker N (2007) Unexpected genetic structure of mussel populations in South Africa: indigenous *Perna perna* and invasive *Mytilus galloprovincialis*. *Marine Ecology Progress Series*, **337**, 135–144.

Zheng X, Ikeda M, Kong L *et al.* (2009) Genetic diversity and population structure of the golden cuttlefish, *Sepia esculenta* (Cephalopoda: Sepiidae) indicated by microsatellite DNA variations. *Marine Ecology*, **30**, 448–454.

Population	Philippines	Ashmore Reef	Scott Reef	Clerke Reef	Imperieuse Reef	Great Barrier Reef	Osprey Reef	Shark Reef
Philippines (N = 27)	-	0.015*	0.044*	0.014*	0.024*	0.130*	0.330*	0.237*
Ashmore Reef (N = 29)	0.136*	-	0.018*	-0.004	0.006	0.121*	0.319*	0.228*
Scott Reef (N = 30)	0.263*	0.097*	-	0.015*	0.015*	0.173*	0.354*	0.268*
Clerke Reef (N = 32)	0.114*	-0.028	0.084*	-	0.004	0.124*	0.322*	0.234*
Imperieuse Reef (N = 31)	0.158*	0.044	0.111*	-0.042	-	0.144*	0.343*	0.255*
Great Barrier Reef (N = 13)	0.527*	0.485*	0.586*	0.494*	0.528*	-	0.312*	0.229*
Osprey Reef (N = 45)	0.693*	0.696*	0.740*	0.703*	0.745*	0.5*	-	0.012
Shark Reef (N = 8)	0.651*	0.612*	0.736*	0.678*	0.731*	0.483*	-0.014	-

Parameters	Prior range	Mean	Median	Mode	HPD95 low	HPD95 high
ARG_K	Uniform [0 - 6]	1.78785	1.62815	1.35678	0.105534	3.72541
MUT_U	Uniform [10^{-6} - 5×10^{-4}]	5.00E-05	4.11E-05	2.61E-05	-2.53E-07	0.000122236
N_A	Uniform [0 - 5×10^{6}]	2.17E+06	2.04E+06	1.31E+06	62816.9	4.51E+06
N_1	Uniform [0 - 5×10^{6}]	3.08E+06	3.19E+06	3.79E+06	1.05E+06	4.99E+06
N_2	Uniform [0 - 5×10^{6}]	2.61E+06	2.56E+06	2.09E+06	665830	4.77E+06
t	Uniform [0 - 10^{6}]	353845	296495	105529	-2511.56	839452