



Southern Right Whales

Population histories of right whales (Cetacea; Balaenidae; *Eubalaena spp.*) inferred from population structures of their whale lice (Amphipoda; Cyamidae; *Cyamus spp.*)

Historia populacji wielorybów biskajskich (Cetacea; Balaenidae; *Eubalaena spp.*) określona na podstawie struktury populacji ich wszy wielorybich (Amphipoda; Cyamidae; *Cyamus spp.*)

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Cyamus ovalis and *Cyamus gracilis*

Abstract

Right whales occur in all of the world's major oceans. Whether they comprise one, two, or three species has been controversial. Right whales carry large populations of three species of permanent, obligate crustacean ectoparasites called whale lice. We studied patterns of mt sequence variation in all three species from right whales in the North Pacific, North Atlantic, and three locations in the Southern Hemisphere. North Atlantic and Southern Ocean populations of whale lice are reciprocally monophyletic, and their levels of sequence divergence imply separation around 6 MYA, consistent with estimates of divergences of right whales. There is little genetic differentiation of cyamid populations on individual whales, and no differentiation between the Southern Ocean breeding aggregations off South America, southern Africa, and Australia, indicating large effective population sizes and high rates of transfer between whales and geographic subpopulations. Preliminary data for nuclear genes suggest that right-whale cyamid populations have been consistently large since the late Miocene, and thus that right whales did not experience severe or prolonged bottlenecks for millions of years, prior to human exploitation.

Abstrakt

Wieloryby biskajskie żyją w oceanach świata pomiędzy 40 i 60 stopniami szerokości. To, czy są jednym, dwoma czy trzema gatunkami było do tej pory kontrowersyjne. Na wielorybach biskajskich żyją duże populacje trzech stałych gatunków skorupiaków, zwane wszami wielorybimi, i które żyją tylko i wyłącznie na wielorybach. Zespół nasz badał wzory z wariacji w genach mitochondriów we wszystkich trzech gatunkach wszy wielorybich z wielorybów biskajskich z północnego Pacyfiku, północnego Atlantyku i z trzech okolic południowej półkuli. Populacje z północnego Atlantyku i południowej półkuli są wzajemnie monofiletyczne i poziomy rozbieżności w ich mitochondriach sugerują rozdzielenie się gatunków 6 milionów lat temu, co zgadza się z rozdzieleniem się wielorybów biskajskich. Nie ma dużej rozbieżności genetycznej populacji wszy wielorybich na pojedynczych wielorybach i nie ma różnicy pomiędzy południowo oceanicznymi terenami legowymi niedaleko Południowej Ameryki, południowej Afryki i Australii, co wskazuje na duży rozmiar populacji i wysokie tempo przeniesienia pomiędzy wielorybami i pomiędzy geograficznymi pod-populacjami. Wstępne dane z jądrowych genów sugerują, że populacje wszy wielorybów biskajskich były stale duże od okresu późno miocenu jak również, że wieloryby biskajskie nie doświadczyły przedłużających się niesprzyjających warunków od milionów lat, nim ludzie zaczęli je eksploatować.



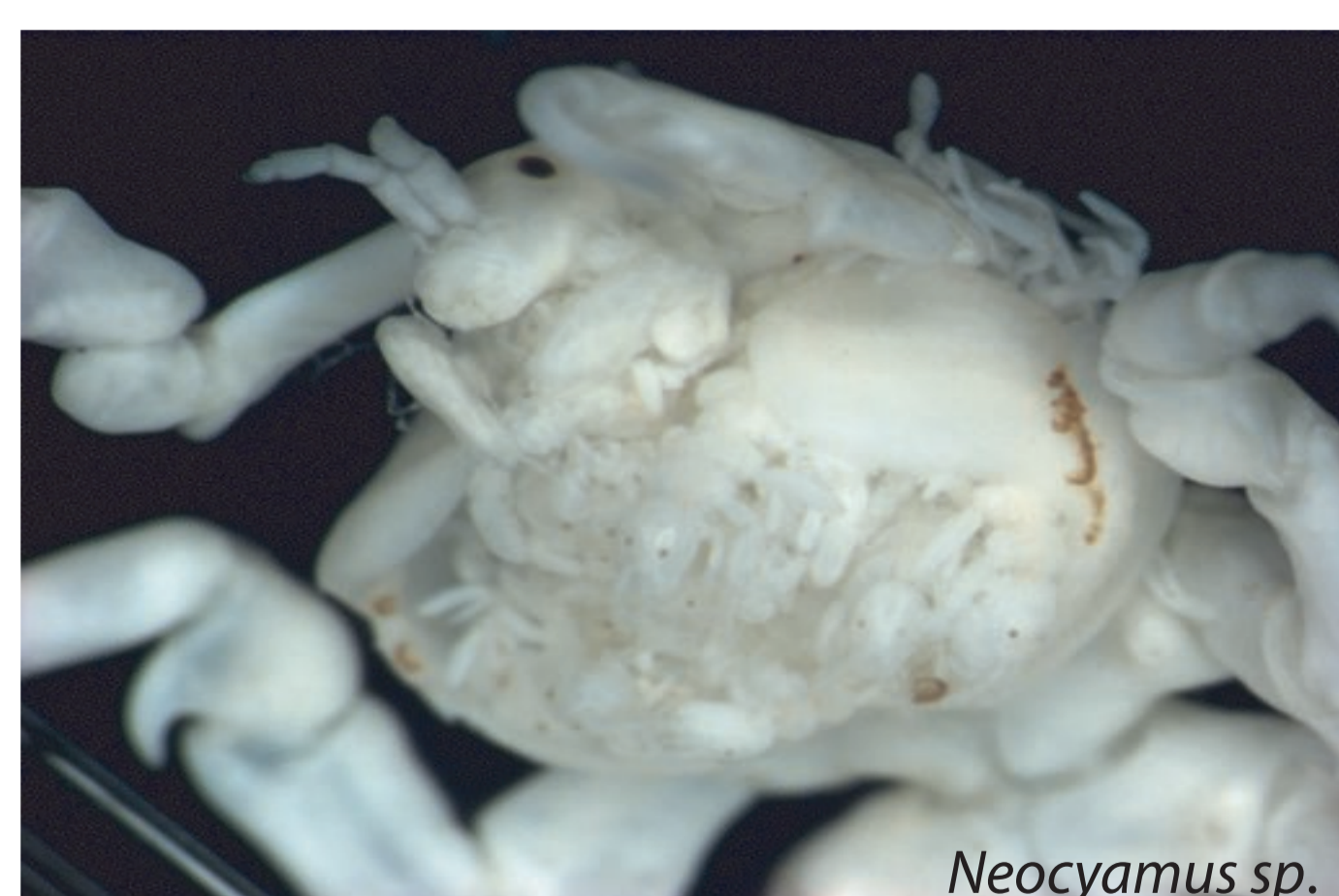
Right Whale Nursery Grounds

Background

Whale lice are Amphipod crustaceans in the family Cyamidae. All of their life stages are spent clinging to whales. They cannot swim and cannot survive if they become dislodged from their host. Thus they spend their entire lives on a single host species, and often on a single host individual. Right whales carry large populations of three recognized species of cyamids: *Cyamus ovalis*, *C. gracilis* and *C. erraticus*.

Right whales occur in all the major oceans of the world between 40 and 60 degrees latitude. They have been hunted nearly to extinction over the last 1000 years. There are three species of right whales: the North Atlantic right whale (*Eubalaena glacialis*) – 300 individuals remaining – the southern right whale (*E. australis*) – 7500 individuals – and the poorly studied North Pacific right whale (*E. japonica*) – probably 100-200 individuals remaining. Right whales do not cross the equator, and the three species appear to have been separated for at least a few million years. Southern right whales gather in coastal aggregations to calve and nurse their young during the austral winter. The three largest populations of southern right whales calve off the coasts of South America, South Africa and Australia. The wintering aggregations are subpopulations among which relatively little migration occurs.

Because cyamids have no free-swimming stage, they can transfer only between whales that rub against each other. The genetic structure of cyamid populations might thus provide clues about social interactions, migratory patterns and population history of their hosts.



Neocyamus sp.

Methods

We sequenced 819 bp of COI for 250 cyamids, from 16 whales. We also sequenced the full-length COI, 5kb spanning 6 mitochondrial gene regions and 1.4kb of an EF-1 α paralog for selected subsets of cyamids. Then we estimated maximum likelihood gene trees using PAUP, PHYLIP and PHYML, and estimated polymorphism, molecular clock and population-structure parameters using DnaSP, codeml, and Arlequin.

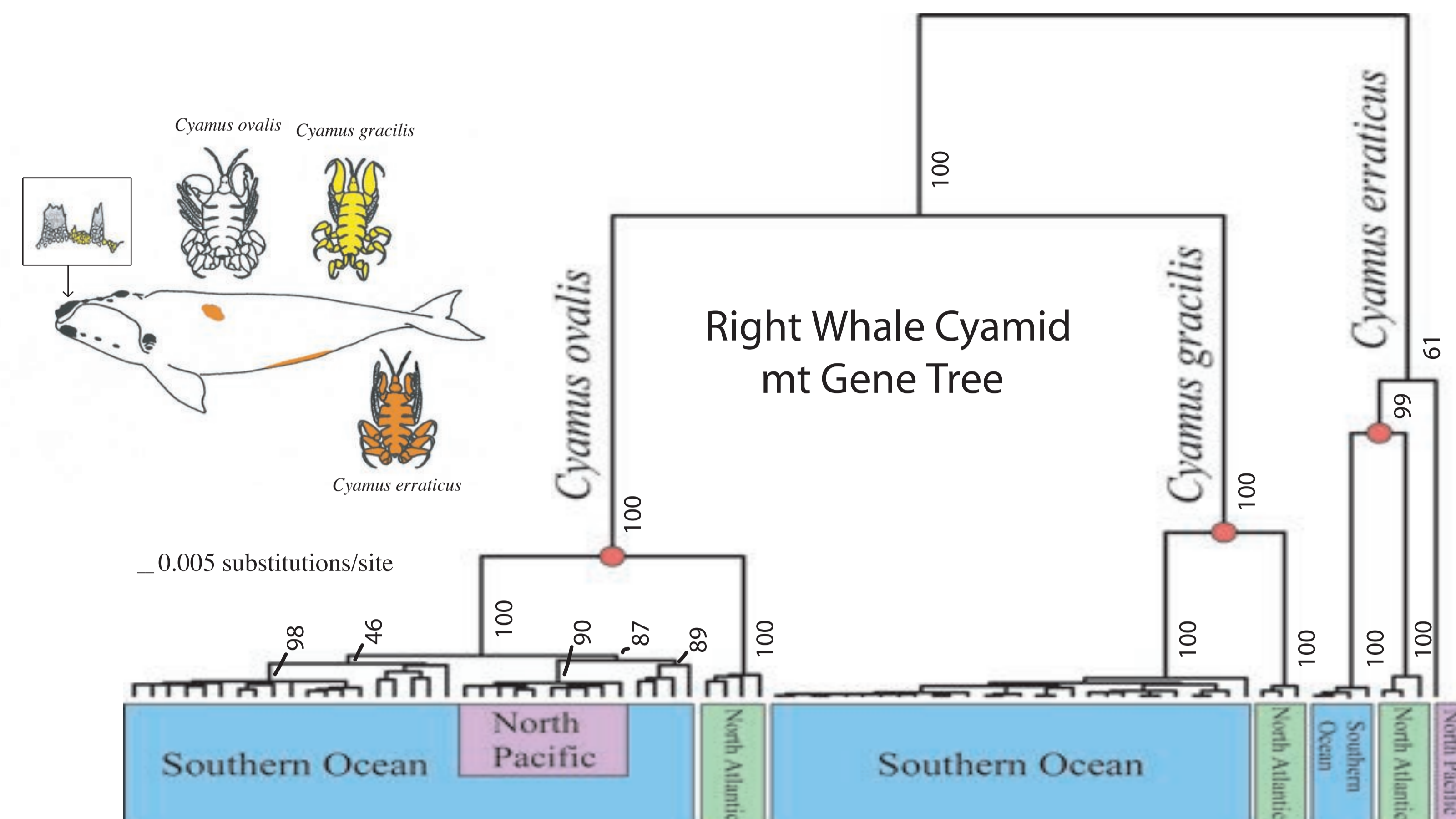
Results

1. The mitochondrial genetic variation of northern and southern hemisphere cyamids shows that they (and their right whale hosts) are genetically distinct and that they have been separated for about 6 million years.

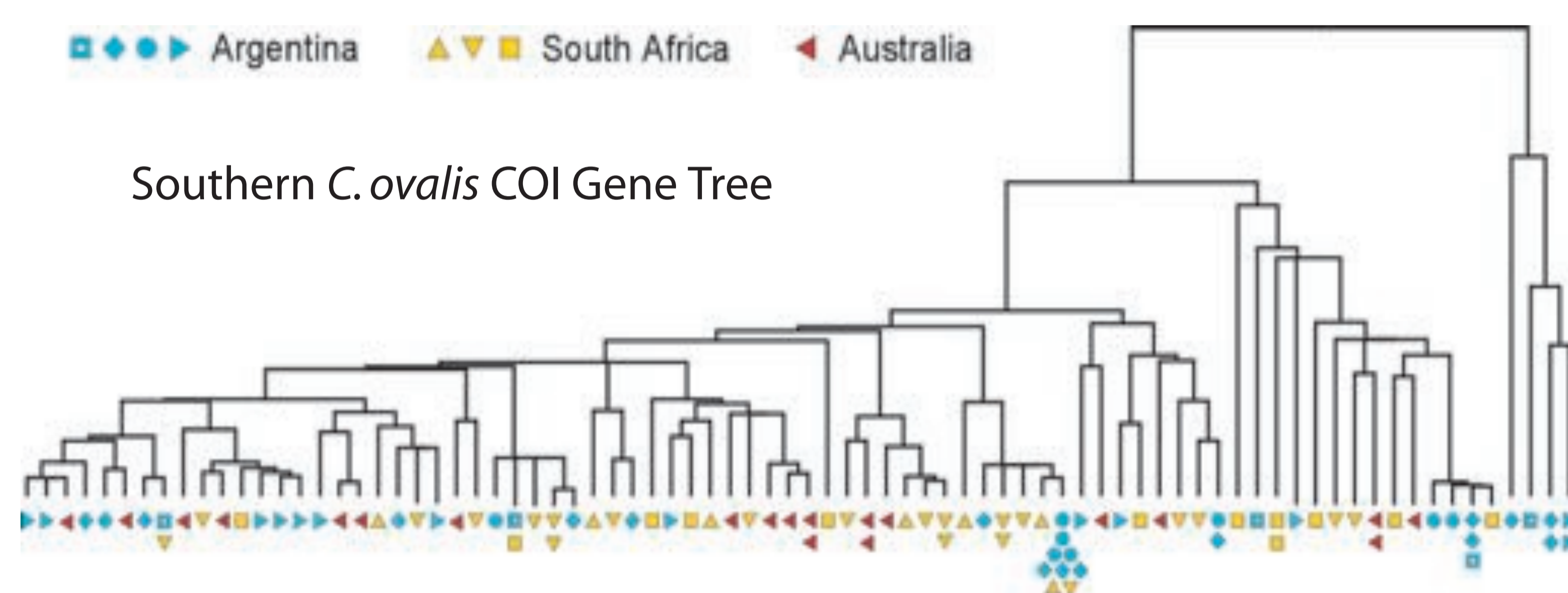
2. Right whale cyamids show no detectable differentiation among whales within nursery areas or between nursery areas within the southern ocean.

3. Right whale cyamid populations have been consistently large since the late Miocene, and thus right whales have not experienced severe or prolonged bottlenecks for millions of years, prior to human exploitation.

For more about this study, for citations of relevant literature, and for many heartfelt acknowledgments, please see: Kaliszewska ZA, Seger J, Rowntree VJ, Barco SG, Benegas R, Best PB, Brown MW, Brownell Jr. RL, Carribero A, Harcourt R, Knowlton AR, Marshall-Tilias K, Patenaude NJ, Rivarola M, Schaeff CM, Sironi M, Smith WA, Yamada TK (2005) Population histories of right whales (Cetacea: *Eubalaena*) inferred from mitochondrial sequence diversities and divergences of their whale lice (Amphipoda: *Cyamus*) *Molecular Ecology* 14(10), (published electronically August 10, 2005, <http://www.blackwell-synergy.com/loi/mec>).



All three North Atlantic and southern clades are reciprocally monophyletic. The North Pacific *C. erraticus* is at least as distant from North Atlantic and southern ocean *C. erraticus* as they are from each other. The North Pacific *C. ovalis*, however, form a clade nested within the southern *C. ovalis* gene tree. Divergence times indicate that the northern and southern right whales are two distinct species. Data presented here suggest that the northern and southern hemisphere sister pairs of cyamids separated 6 million years ago and thus should also be considered distinct species.



There is very little genetic differentiation in cyamids among whales within nursery areas (shapes), $F_{ST} \sim 0$ and no detectable genetic differentiation in cyamids among nursery areas within the southern ocean (colors), $F_{ST} = 0$. This well-mixed population structure, with many diverse mitochondrial lineages on each whale, indicates that cyamids often move between whales during social interactions, and that whales from different nursery grounds sometimes interact.

Levels of mitochondrial polymorphisms are high. Assuming two generations per year and typical arthropod mitochondrial mutation rates, these diversities imply effective population sizes in the millions.

Species	N	Distinct Haplotypes	Segregating Sites (θ_s)	Mean Heterozygosities per site (π)
North Atlantic <i>C. ovalis</i>	33	30	0.021	0.012
Southern Ocean <i>C. ovalis</i>	104	81	0.030	0.015
North Pacific <i>C. ovalis</i>	12	10	0.013	0.009
North Atlantic <i>C. gracilis</i>	30	8	0.007	0.007
Southern Ocean <i>C. gracilis</i>	28	19	0.010	0.008
North Atlantic <i>C. erraticus</i>	22	15	0.013	0.013
Southern Ocean <i>C. erraticus</i>	21	16	0.013	0.009

Polymorphism at the nuclear EF-1 α locus is nearly half as large as at the mitochondrial COI locus, even though the nuclear mutation rate appears to be about 40 times lower. Northern and Southern Hemisphere sibling species still share many polymorphisms and show modest F_{ST} values, indicating very low rates of drift (hence very large effective population sizes) at this nuclear locus.

Species	N	Segregating Sites (θ_s)	Mean Heterozygosities per site (π)	$F_{ST}(NA/SO)$
North Atlantic <i>C. ovalis</i>	20	0.005	0.003	0.48
Southern Ocean <i>C. ovalis</i>	24	0.003	0.002	
North Pacific <i>C. ovalis</i>	8	0.003	0.004	
North Atlantic <i>C. gracilis</i>	18	0.006	0.006	0.48
Southern Ocean <i>C. gracilis</i>	12	0.006	0.005	
North Atlantic <i>C. erraticus</i>	12	0.005	0.005	0.17
Southern Ocean <i>C. erraticus</i>	18	0.007	0.005	



Southern Right Whale