Color Variation, Cryptic Diversity, and ENSO Driven Range Shifts in the Benthic Marine Invertebrates *Polycera alabe* and *P. atra* in North America

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Introduction and Methods

Opisthobranch sea slugs are soft-bodied marine mollusks. Most species lack an outer shell that is used by other types of mollusks for protection. Therefore, many species of sea slugs have developed chemical defenses to ward off predators. In addition to these chemicals, many species are brightly colored to warn potential predators of their toxicity. As a result, members of the same species are not highly variable in color.

Polycera alabe and *Polyera atra* are sea slugs found in coastal habitats along the eastern Pacific, with *P. atra* described in northernmost regions and *P. alabe* in southernmost regions. Both *P. atra* and *P. alabe* contain populations that are extremely variable in external colorations, along with suggestions of some geographic variation. Anecdotal evidence suggests that El Niño Ocean Oscillation (ENSO) plays significant roles in range expansion and contractions of both species, which otherwise have allopatric ranges.

In order to determine the genetic structure of *P. alabe* and *P. atra* in North America, molecular phylogenies were produced by amplifying both of the following genes using PCR: the nuclear H3 gene and the mitochondrial 16S rRNA gene. The radula of both species were also examined to morphologically support genetic findings. In order to document the effects of past ENSO events in the range of these species, this study also includes museum specimens collected during the 1970's.

Geneious Pro 5.3 was used to build a phylogenetic tree for the genus *Polycera*. The phylogenetic tree includes the species of interest, *P. alabe* and *P. atra*, and outgroups *P. hedgpethi* and *P. cf. capensis*.

Results

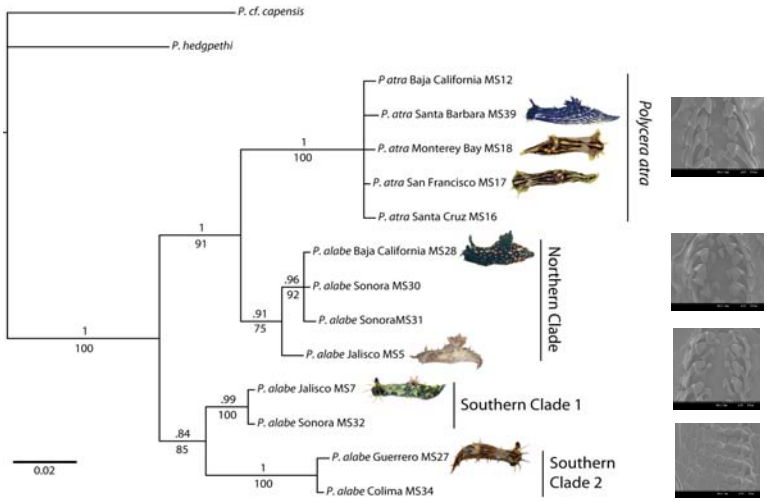

Figure 1. Bayesian tree for the genus *Polycera* using the H3 gene and 16 genes and Radula ESM photographs for each clade of *P. alabe* and *P. atra*.

Discussion

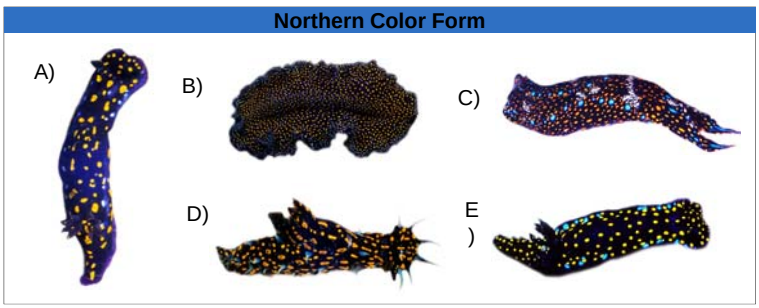

Figure 2. Live photographs of A) *Hypselodoris californiensis*, B) *Pseudoceros bajae*, C) *Navanax aenigmaticus*, D) *Polycera alabe*, and E) *Hypselodoris ghiselini*.

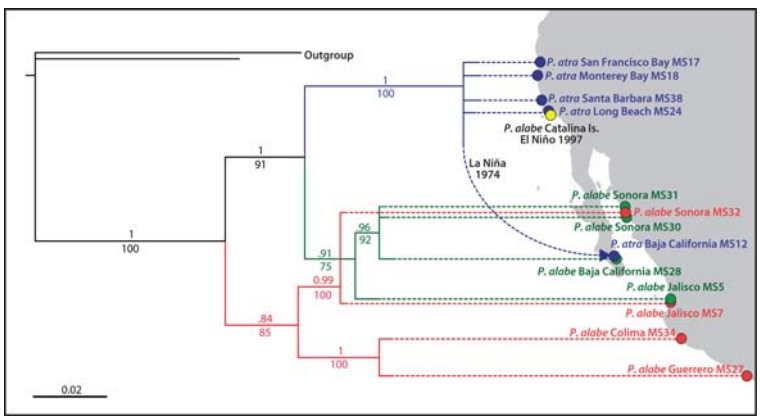

Figure 3. Map of reported sightings of *Polycera atra* (blue), northern *Polycera alabe* (green) , and southern *Polycera alabe* (red). Indicated in yellow is *P. alabe* dispersed during an El Niño event.

Populations of *Polycera atra* are genetically similar and lack geographic structure, suggesting rampant gene flow across the range of the species. *Polycera alabe* forms three distinct clades with geographic structure, divided longitudinally (Figure 1, Figure 3). Southern Clade 2 is further supported by distinct radular morphology, indicating that it is a different species than the two other *P. alabe* clades. The Northern Clade is sister to *P. atra*, thus the current definition of *P. alabe* constitutes a paraphyletic assemblage; an alternative approach would be to transfer the Northern Clade to *P. atra*, leaving Southern Clade 1 and 2 provisionally under *P. alabe*. This indicates that Southern Clade 1 is also a different species since it is genetically different from the Northern Clade, but there are no morphological differences, indicating the need of a larger sample size in study.

A record of *P. atra* from La Paz, Mexico, during La Niña of 1997, and a record of *P. alabe* from Southern California during El Niño of 1997-1998 suggest a broad dispersal of both species possibly limited by water temperature (Figure 3, Figure 4). Overlapping ranges in the Gulf of California of two distinct clades of *P. alabe* may result from water temperature variations. This would make it difficult to conceive of a scenario in which *P. atra* and the three clades assigned to *P. alabe* have diverged allopatrically.

It is possible that mimicry could be one of the driving forces causing divergence within *P. atra* at the southern end of its range. Several species common in the Gulf of California have a similar color pattern and spotted pattern (Figure 2). A large sample size is necessary to determine whether black and spotted *P. alabe* are consistently found in the Gulf of California and caldistically nested in the Northern Clade, which would be a strong indication that mimicry with other benthic invertebrates could have caused parapatric divergence of the Northern Clade.

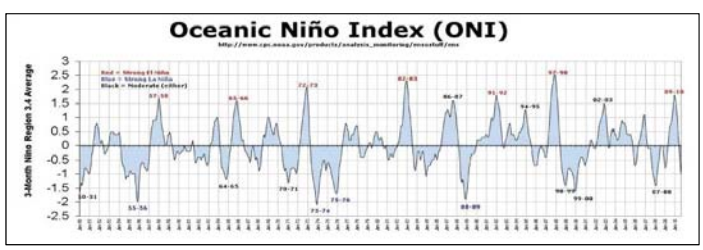

Figure 4. Oceanic Niño Index for the years 1950-2010 during the month of January.

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