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# Comparative phylogeography and connectivity of sibling species of the marine copepod *Clausocalanus* (Calanoida)

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## ABSTRACT

Connectivity of the marine epipelagic environment is subject to presence of subtle barriers that can be difficult to identify and to signals from the geological history of the oceans. This study examines the effects of species' geographical distribution on their population structure as mediated by differential effects of the recent geological history of the oceans. For this purpose, we studied the sequence variation of the mitochondrial cytochrome oxidase *c* subunit I (COI) gene in samples of two sibling species of the calanoid copepod genus *Clausocalanus*. Analyses included molecular population genetic, phylogeographic, and phylogenetic approaches. The cosmopolitan *Clausocalanus arcuicornis* is shown to have a single panmictic population across this species' extensive geographic range, with sufficient gene flow – despite vast distances and geological and oceanographic barriers – to maintain genetic cohesion. In contrast, the biantitropical *Clausocalanus lividus* exhibits clear differentiation between Atlantic and Pacific Ocean populations, suggesting a vicariance process that started after the rise of the Isthmus of Panama.

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## 1. Introduction

Connectivity among the geographic populations of a species is necessary to maintain genetic integrity throughout its distributional range. Barriers to gene flow in the marine pelagic environment are often not clearly identified (Cowen et al., 2007; Goetze, 2005; Knowlton, 2000) and the effect of these barriers will differ depending on the spatial distribution of the species. To examine evidence of barriers to gene flow and cohesion among pelagic populations in different ocean basins, the biogeography of species must be studied in relation to the geological history of the oceans (Bradbury et al., 2008; Hellberg, 2009). Comparative studies of species that overlap in both time and space can provide better understanding of the existence of boundaries and their variable effects (Avise, 2009; Hickerson et al., 2010; McGovern et al., 2010; Peijnenburg et al., 2005; Reece et al., 2010).

Heterogeneous approaches to phylogeographic analysis and dispersal estimates (e.g., tag-and-release) have yielded inconsistent results in the ocean (Cowen and Sponaugle, 2009). In particular, it is uncertain whether previous studies may accurately represent global patterns (Bradbury et al., 2008). The development of molecular markers allowed genetic studies in phylogeography (Avise, 1998, 2009) and yielded improved understanding in the marine environment (Hedgecock et al., 2007; Selkoe et al., 2008). Many studies have used mitochondrial DNA (mtDNA) genes as markers (Avise, 2009; Avise et al., 1987), although multigene analysis including also nuclear loci is a clear and desirable trend in phylogeographic studies (Avise, 2009; Brito and Edwards, 2009). Despite recent doubts about the adequacy of mtDNA for this purpose, these genes have proved to be useful tools to address recent – up to several million years ago – phylogeographic and speciation phenomena (Avise, 2009; Galtier et al., 2009; Knowlton, 2000; Lessios, 2008).

Many studies have focused on species with planktonic larval stages (Bradbury et al., 2008; Weersing and Toonen, 2009), with fewer studies on holoplanktonic taxa (e.g., Caudill and Bucklin, 2004; Eberl et al., 2007; Goetze and Ohman, 2010; Goodall-Copestake et al., 2010; Milligan et al., 2011; Peijnenburg et al., 2006; Unal et al., 2006).

To investigate the presence and effect of barriers to population connectivity and gene flow of marine holoplanktonic species, we chose the calanoid copepod genus *Clausocalanus* (Giesbrecht, 1888). This genus comprises thirteen geographically widespread, epiplanktonic species of small copepods (Frost and Fleminger, 1968) and includes dominant zooplankton taxa from low to high latitudes (Pakhomov and Perissinotto, 1997; Peralba et al., 2010; Peralba and Mazzocchi, 2004; Schnack-Schiel et al., 2010). Despite their overlapping distributions, the species are ecologically, biogeographically, and genetically distinct (Bucklin and Frost, 2009; Cornils et al., 2007; Peralba et al., 2010; Saiz and Calbet, 1999; Schnack-Schiel et al., 2010). This study focuses on two species, *C. lividus* and *C. arcuicornis*. Both species are epipelagic, with distributions in both shelf and open ocean waters (Frost and Fleminger, 1968; Peralba et al., 2010; Peralba and

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Fig. 1. Range of distribution and sample locations for *Clausocalanus lividus* and *Clausocalanus arcuicornis*.

Mazzocchi, 2004; Schnack-Schiel et al., 2010). The species show different geographical ranges (Fig. 1): *C. lividus* has a disjunct antitropical distribution, while *C. arcuicornis* is a cosmopolitan species (Frost and Fleminger, 1968) that is found in all ocean basins between 40° N and 40° S. Although Frost and Fleminger (1968) described the *C. lividus* distributional range as spanning the Pacific and Indian Oceans in the Southern Hemisphere, the species has not to our knowledge subsequently been reported in these regions (M.D. Viñas, INIDEP, Argentina; P. Ayón, IMARPE, Peru; R. Escribano, Universidad de Concepcion, Chile; D. McKinnon, AIMS, and F. Coman, CSIRO, Australia; pers. comm.).

In this work, we examine DNA sequence variation of the mitochondrial cytochrome oxidase c subunit I (COI) gene in samples of two species of copepods collected throughout their distributional ranges. We present here our findings of the comparative effects of barriers to gene flow and recent geological history of the oceans on the phylogeography and connectivity of these epipelagic zooplankton species.

## 2. Methods

#### 2.1. Samples

A total of 87 individuals for *C. lividus* and 96 for *C. arcuicornis* were analyzed, including samples from cruises in the Atlantic, Pacific and Indian Oceans (Fig. 1; Table 1). Samples were preserved in 95% ethanol, which was changed after 24 h. The material analyzed for this study included samples stored in the Census of Marine Zooplankton (CMarZ) archives located at the Department of Marine Sciences, University of Connecticut.

# 2.2. DNA extraction, PCR amplification and sequencing

DNA extractions were carried out using the DNeasy Blood & Tissue Kit (QIAGEN) from whole individuals and with an elution volume of 50 to 300 ul AE buffer. PCR amplifications for a fragment of COI were performed in a total volume of 25 µl, including 5 µl of  $5 \times$  Green GoTaq<sup>®</sup> Flexi Buffer, 2.5 µl of 25 mM MgCl<sub>2</sub>, 1 µl of dNTPs (final concentration 0.2 mM each), 1  $\mu$ l of each primer (10  $\mu$ M), 0.75 units of GoTag<sup>®</sup> Flexi DNA Polymerase (Promega) and 3 µl of DNA sample. Two primer sets were used: the consensus primers LCO1490 and HCO2198 (Folmer et al., 1994) and the specific primers for Clausocalanus spp., COI 5' GAGCCTGGTCAGGAATAATCG 3' (forward) and 5' GGTCTCCTCCTCCAACAT 3' (reverse) (Blanco-Bercial and Álvarez-Margués, 2007). The PCR protocol included an initial denaturation step of 94 °C (4 min), followed by denaturation at 94 °C for 35 s, annealing at 53 °C (Clausocalanus primers) or 45 °C (1490F/2198R) for 45 s, and extension at 69 °C for 45 s for 35 cycles. A final extension phase at 69 °C for 20 min was followed by storage at 4 °C. PCR products were checked by electrophoresis on a 1% agarose/TBE gel; positive results were purified using UltraClean® PCR Clean-Up Kit (Mo Bio). The purified PCR products were sequenced using the same set of primers as in the original amplification and Big Dye Terminator Ver. 3.1 (Applied Biosystems Inc., ABI), and run on an ABI 3130 Genetic Analyzer capillary DNA

#### Table 1

Location, number of individuals (N), collection, date, geographical coordinates, and grouping pattern for the AMOVA pool and for coalescence (Coals., C. lividus) and isolation with migration (lwM, C. arcuicornis) analyses for all samples.

| Clausocalanus lividus   |    |                      |          |             |              |      |          |
|-------------------------|----|----------------------|----------|-------------|--------------|------|----------|
| Location                | Ν  | Cruise               | Date     | Latitude    | Longitude    | Pool | Coals.   |
| Alaska                  | 9  | Seward Line          | Sep 2005 | 58°09.65′ N | 147°47.60′ W | Alk  | Pacific  |
| California Current      | 11 | RR-9610              | Oct 1996 | 32°25.05′ N | 123°08.50′ W | CC1  | Pacific  |
|                         | 23 | RR-9610              | Oct 1996 | 32°20.00′ N | 123°18.70′ W | CC2  | Pacific  |
| Japan                   | 3  | KT 09-4              | Apr 2009 | 35°01.18′ N | 139°22.04′ E | -    | Pacific  |
| Bay of Biscay           | 22 | Radial Cudillero     | Feb 2004 | 43°42.00′ N | 06°09.00' W  | NEA  | Atlantic |
| NW Atlantic             | 6  | RHB-0603             | Apr 2006 | 33°31.47′ N | 69°57.68′ W  | NWA  | Atlantic |
|                         | 4  | DE-0808              | Aug 2008 | 38°16.30′ N | 74°24.40′ W  | NWA  | Atlantic |
|                         | 1  | DE-0711              | Oct 2007 | 38°26.00′ N | 73°46.10′ W  | NWA  | Atlantic |
|                         | 6  | OCE-258              | Apr 1993 | 40°45.80′ N | 62°28.10′ W  | NWA  | Atlantic |
|                         | 2  | OCE-258              | Apr 1993 | 39°46.30′ N | 54°44.70′ W  | NWA  | Atlantic |
| Clausocalanus arcuicorn | is |                      |          |             |              |      |          |
| Location                | Ν  | Cruise               | Date     | Latitude    | Longitude    | Pool | IwM      |
| California Current      | 11 | RR-9610              | Oct 1996 | 32°25.05′ N | 123°08.50′ W | CC   | CC       |
|                         | 11 | RR-9610              | Oct 1996 | 32°20.00′ N | 123°18.70′ W | CC   | CC       |
| Tahiti                  | 21 | S202A                | Jan 2006 | 17°10.60′ S | 150°24.50' W | Tah  | Tah      |
| Central Pacific         | 5  | EUC-FE-2006          | Sep 2006 | 01°20.91′ N | 155°59.71′ E | -    | -        |
| Japan                   | 1  | KT 09-4              | Apr 2009 | 35°01.18′ N | 139°22.04′ E | -    | -        |
| South Africa            | 4  | SARP-OM-EN26/12      | Dec 2005 | 34°13.74′ S | 18°04.46′ E  | SA   | SA       |
|                         | 4  | Pel. Sp. Biomass-225 | Nov 2006 | 33°26.74′ S | 17°48.63′ E  | SA   | SA       |
|                         | 8  | Pel. Sp. Biomass-225 | Nov 2006 | 34°43.68′ S | 24°56.94′ E  | SA   | SA       |
|                         | 6  | Pel. Sp. Biomass-225 | Nov 2006 | 34°25.91′ S | 25°59.01′ E  | SA   | SA       |
| Bay Biscay              | 17 | Radial Cudillero     | Jul 2004 | 43°42.00′ N | 06°09.00' W  | NEA  | NAt      |
| NW Atlantic             | 2  | OCE-258              | Apr 1993 | 40°45.80′ N | 62°28.10′ W  | NWA  | NAt      |
|                         | 6  | RHB-0603             | Apr 2006 | 33°31.47′ N | 69°57.68′ W  | NWA  | NAt      |

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