

# First record along the Uruguayan coast of the largest sea nettle jellyfish, *Chrysaora plocamia* (Lesson, 1830) (Cnidaria: Scyphozoa)

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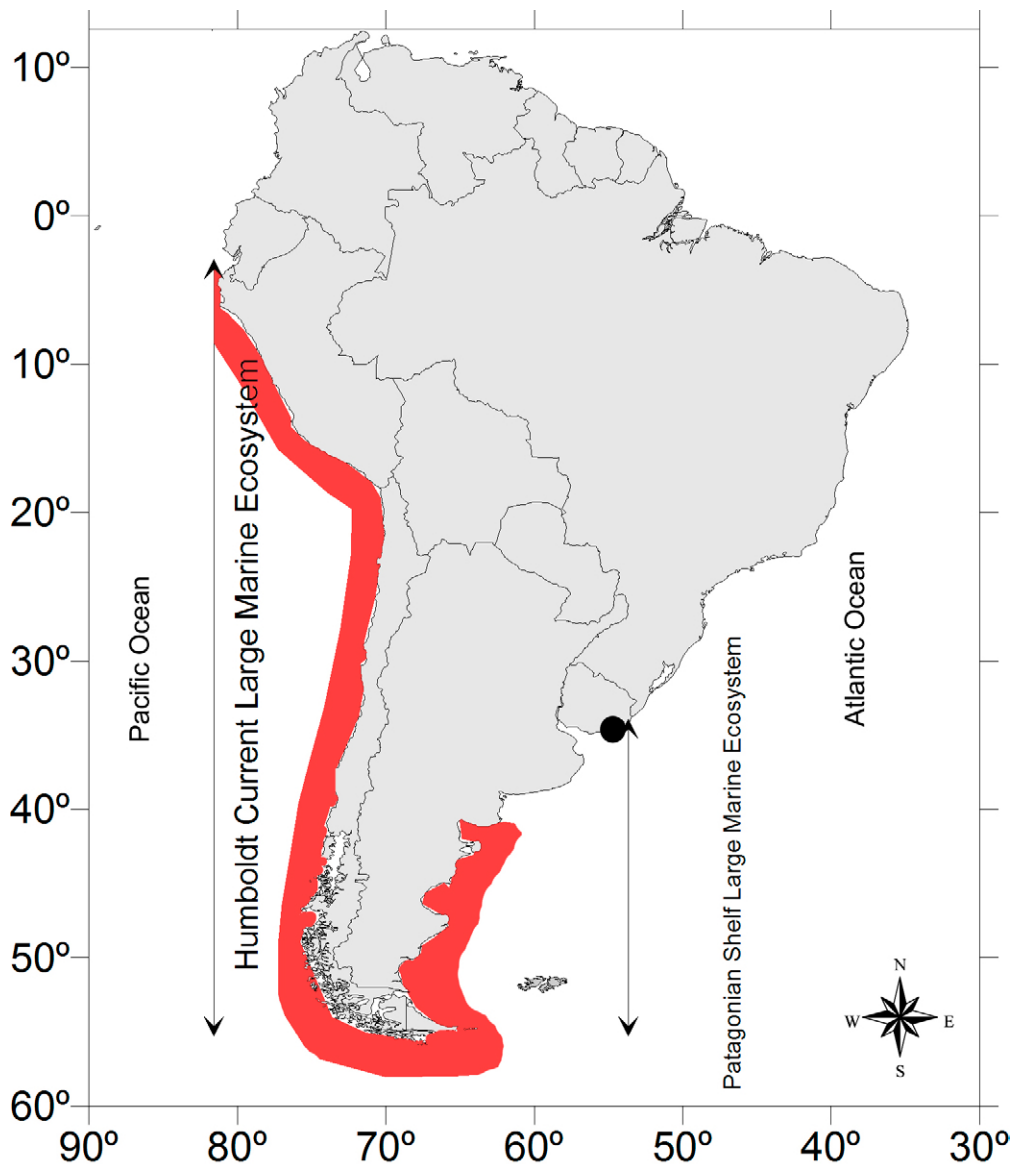
**Abstract:** *Chrysaora plocamia* is one of the 15 species of the jellyfish genus *Chrysaora*. This species has an unusual distribution pattern, occurring on both Atlantic and Pacific coasts of South America. It is distributed along the southeastern Pacific Ocean, encompassing coastal areas of Peru and Chile, and reaching the Patagonian coast of Argentina in the southwestern Atlantic. During two separate events, two large specimens of *Chrysaora* were collected on the east coast of Uruguay at La Paloma. Based on morphology and molecular data, these specimens were identified as *Chrysaora plocamia*. These records are described along with oceanographic features observed at that time. Unusual oceanographic and atmospheric conditions may explain the presence of these specimens 1,100 km north of the current northernmost known distribution.

**Keywords:** taxonomy; oceanography; South Atlantic

There are more than 200 species of scyphozoan jellyfishes in the world (Mianzan and Cornelius 1999). These organisms are well known for their seasonal presence in most oceans. In South America the largest species of scyphozoan jellyfish, *Chrysaora plocamia*, is one of the few that promotes blooms along coasts of the Atlantic and Pacific (see more in Mianzan et al. 2014). First described from Peruvian waters (Lesson 1830) as *Cyanea plocamia*, there is surprisingly little ecological information on this remarkable species (Morandini and Marques 2010). Despite this lack of coverage, *Chrysaora plocamia* has important ecological roles, including their trophic relationship and symbiotic interactions with pelagic fish, sea turtles, association with amphipods, copepods

and anemones. This large jellyfish negatively affects industries in the region when abundant, including fishing, aquaculture, desalination plants and tourism (Mianzan and Cornelius 1999; Mianzan et al. 2005; Mianzan et al. 2014).

Many species of Scyphozoa are distributed in different temperature regimes. Some tropical and subtropical species occur over large areas of the Atlantic, Pacific and Indian oceans; on the other hand, other species may be restricted due to biogeographical barriers (Arai 1997; Morandini et al. 2005). *Chrysaora plocamia* presents an uncommon distribution pattern, occurring on both coasts of southern South America, that is, in the eastern South Pacific (Peru, Chile) (Lesson 1830; Stiasny 1937; Kramp 1952) and western South Atlantic (Argentina) (Mianzan and Cornelius 1999). This pattern of distribution fits with oceanographic data and circulation noted by Acha et al. (2004) and known as the Patagonian cold estuarine zone that connects the Pacific and Atlantic oceans. No morphological difference in *C. plocamia* from these different areas has been noted by previous authors (Stiasny 1937; Morandini and Marques 2010). This species can be found across a range that encompasses two large marine ecosystems (LMEs): the Humboldt Large Marine Ecosystem in the Pacific and the Patagonian Shelf Large Marine Ecosystem in the Atlantic (Heileman 2009; Heileman et al. 2009). These LMEs, with a combined coastline of 13,000 km and surface area of more than 5.5 million km, represent a large fraction of South American coastal waters (Miloslavich et al. 2011). The finding of *C. plocamia* in La Paloma, Uruguay (ca. 34°40'S) is here reported and discussed, including morphological, molecular and oceanographic evidence.



**Figure 1.** Geographic distribution of *Chrysaora plocamia* covering two large marine ecosystems in the Pacific and Atlantic Oceans (red). Circle: location of the stranded specimens reported here, 1,100 km north of the previously known range.

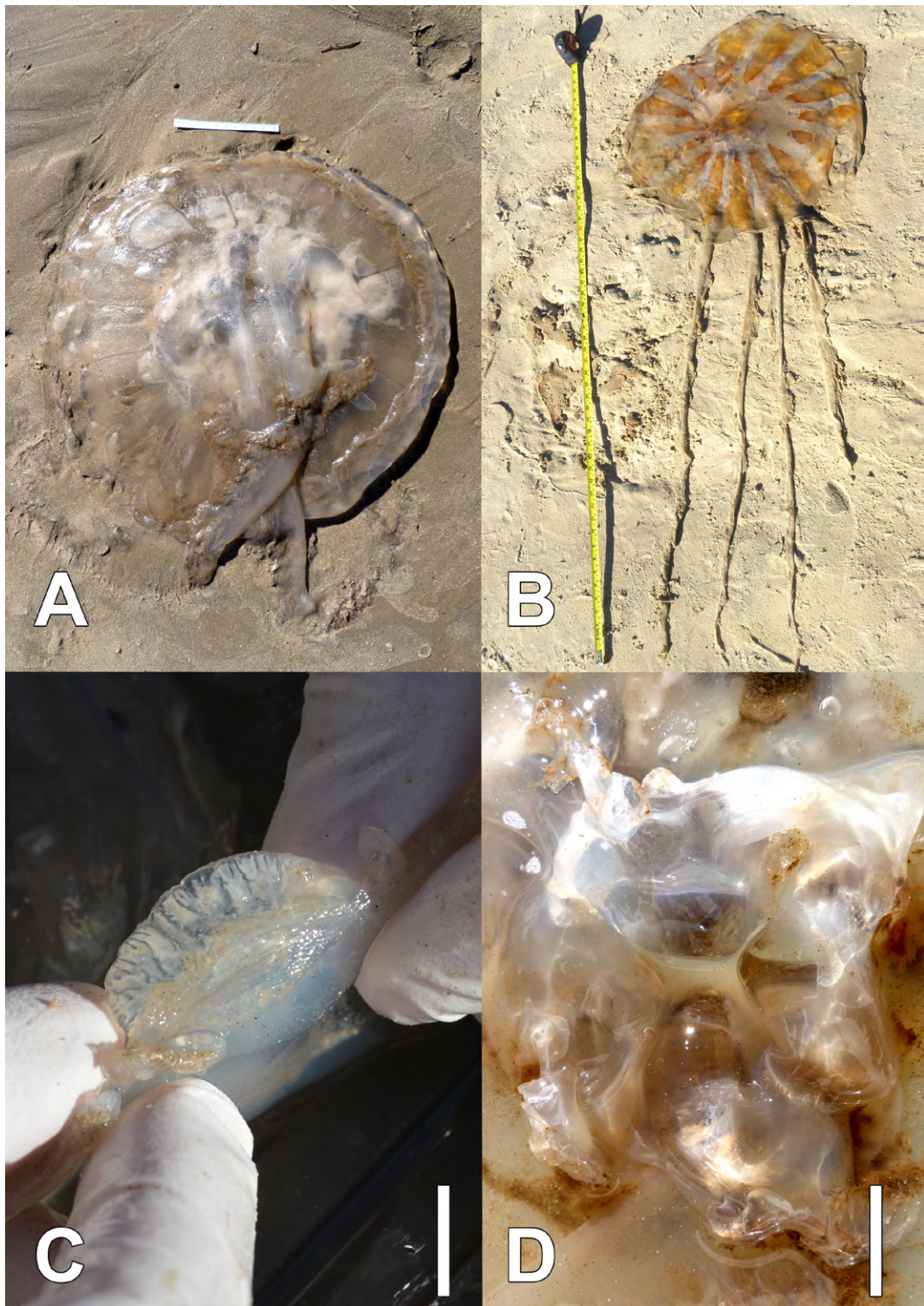
Two large specimens of *Chrysaora plocamia* were collected at La Aguada Beach (34°38'43" S, 054°09'13" W), La Paloma, Uruguay (Figure 1), in two distinct events: 8 December 2012 and 20 July 2014. The two specimens were found stranded on sand at the tide line. The animals were kept in a bucket with seawater for observations and photographing and soon preserved in 4% formaldehyde solution, with the exception of some tentacles that were previously preserved in 95° ethanol. The morphological studies of the preserved specimens were based on Morandini and Marques (2010). Specimens (CHRP001/CHRP002) were deposited in Museo Nacional de Historia Natural (Montevideo, Uruguay).

In addition to the samples collected in Uruguay, two specimens of *Chrysaora plocamia* from Ilo, Peru (17°38'53" S, 071°21'12" W) were utilized in our molecular studies. Specimens of *Chrysaora lactea* collected in La Paloma (December 2012) were also used for genetic comparison.

The molecular study was based on the protocol defined in Stampar et al. (2012). DNA was extracted using InstaGene (Bio-Rad) from single tentacles removed from the specimens. Genes were amplified using the PCR technique, then PCR products purified with AMPure® kit (Agencourt®). The PCR primers CB1 and CB2 (Cunningham and Buss, 1993) were used to amplify part of the 16S gene. Purified PCR products were made ready to sequencing using the BigDye® Terminator v3.1 kit (Applied Biosystems), with the same primers and temperature conditions of the PCR's reactions. The sequencing procedure was carried out on an ABI PRISM®3100 genetic analyzer (Hitachi).

Sequences were assembled and edited (removing ambiguous base calls and primer sequences) using Geneious™ 7 (Drummond et al. 2011). The alignment in every molecular marker were made using MUSCLE (Edgar 2004) in default parameters. Kimura's





**Figure 2.** *Chrysaora plocamia* from Uruguayan coast. **A:** Specimen found in 2012 (Scale bar: 15 cm) (CHRP001). **B:** Specimen found in 2014 (Scale bar: 70 cm) (CHRP002). **C:** Detail of canal system in lappets (Scale bar: 2 cm) (CHRP001). **D:** Quadralinga (Scale bar: 3 cm) (CHRP001).

two-parameter model of base substitution in MEGA6 software (Tamura et al. 2013) and *p-distance* in Geneious 7 was used to calculate genetic distances. The sequences were submitted to GenBank: *Chrysaora plocamia* (Peruvian specimens KT371520/KT371521 and Uruguayan specimen KT371522) and *Chrysaora lactea* (Uruguayan specimen KT371523 - CHRP001).

The Humboldt Current (HCS) LME extends along the west coast of South America from northern Peru to southern Chile and is one of the major upwelling systems of the world. The HCS is characterized by the flow of cold and low salinity waters toward the equator (Heileman 2009; Heileman et al. 2009). Environmental conditions in the HCS are broadly characterized

by nutrient-rich cold waters, showing slight seasonal temperature variability compared to those found in other coastal ecosystems at similar latitudes (Camus 2001; Thiel et al. 2007). The influence of the continuous upwelling of cold subsurface waters, mainly at northern Chile and Peru, and seasonal upwelling in southern to central Chile (Thiel et al. 2007), causes an atypical weak south to north temperature gradient and extends the influence of cold environmental conditions northward (Camus 2001). Therefore, many species in the HCS exhibit broad distributional ranges and are adapted to moderately constant low water temperatures (Riascos et al. 2009).

The Patagonian Large Marine Ecosystem extends from Uruguay to the Strait of Magellan. It is influenced by two major wind-driven currents: the northward flowing Malvinas Current a branch of a Circumpolar Current that flows along the continental shelf of Argentina (Garzoli 1993; Vivier and Provost 1999) and the southward flowing Brazil Current (Stramma et al. 1990). The Brazil and Malvinas currents converge at about 38° S (Saraceno et al. 2004) and generate conspicuous frontal zones and eddies, consequently this area is a region of high energy, primary productivity and spatio-temporal variability, which influences the hydrography of the adjacent continental shelf (Garzoli and Garrafo 1989; Gordon 1989; Goni and Wainer 2001). Additionally, the freshwater discharge from the Río de la Plata, the major freshwater inflow of the area (Guerrero et al. 1997), with seasonal and interannual variations, adds complexity to the system. The Río de la Plata front is characterized by strong vertical stratification, freshwater flows seaward on the surface while denser shelf water intrudes along the bottom, producing a turbidity front (Acha et al. 2004). Over the shelf other thermohaline frontal zones were described by Martínez and Ortega (2007) as well a subsurface front, formed when Subantarctic Shelf Water and Subtropical Shelf Water converge. This generates the Subtropical Shelf Front that can be regarded as an extension of the Malvinas-Brazil Confluence over the shelf (ca. 33° S; Piola et al. 2000). Southward, close to the Argentine continental shelf-break, a permanent thermohaline front separates subantarctic shelf waters from the cooler and more saline waters of the Malvinas current (Acha et al. 2004, 2015 for details).

The Uruguayan continental shelf is characterized by a marked seasonality, with a predominance of cold subantarctic water during austral winter and spring and warm tropical and subtropical waters during austral summer and autumn (Lima et al. 1996; Piola et al. 2000; Ortega and Martínez 2007).

Sea surface temperature anomalies were derived from Reynolds et al. (2002) (<http://iridl.ldeo.columbia.edu>). An 8-day composite of sea surface temperature with a 4 km resolution was obtained from the

Moderate-Resolution Imaging Spectroradiometer (MODIS-Aqua) satellite image and data was extracted using the SeaDAS 7.2 software. Image and contour maps were created using the Kriging method. *In situ* sea temperature data was obtained by means of CTD casts (SBE SECAT19v2) performed during a survey onboard RV “Aldebaran” from DINARA (Uruguay). Only bottom data from two CTD casts close the coast of La Paloma were used as *in situ* temperature register for the zone (27–28 November 2012).

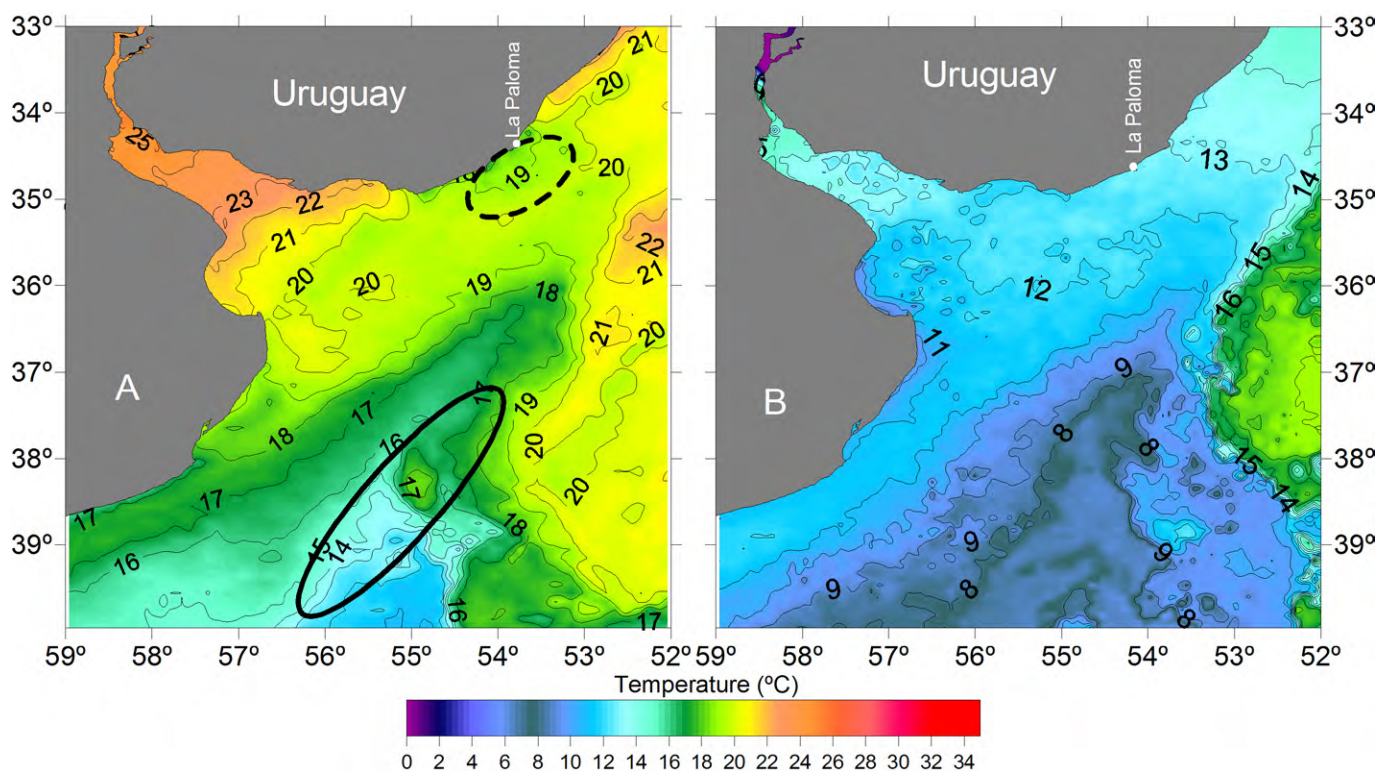
Examined material (Figure 2A–D): MNHNM (code CHRPO01) (~45 cm in diameter, 07.xii.2012, 4% formaldehyde solution, La Paloma, Uruguay); MNHNM (code CHRPO02) (~50 cm in diameter, 20.vii.2014, 4% formaldehyde solution, La Paloma, Uruguay).

Brief description (following Morandini and Marques 2010): Umbrella diameter up to 100 cm (45–50 cm in measured specimens), almost hemispherical. Exumbrellar surface finely granulated; colouration varied, either transparent-whitish with irregular distributed brown-reddish streaks; or completely whitish (Figure 2A–B). Mesoglea flexible, thicker centrally. Marginal lappets wide (Figure 2C), squared, 3 per octant; all lappets of similar size, rhopalar lappets not overlapping (“open rhopalia” condition). Rhopalia 8, without ocelli, in deep clefts; deep exumbrellar sensory pit. Tentacle clefts similar in depth. Tentacles 24 (3 per octant), primary tentacle central. Quadrilinga present (Figure 2D). Subgenital ostia, small, rounded. Oral arms up to 3 times longer than umbrellar diameter, V-shaped, delicate and much convoluted, distal portion slightly spiraled. Central stomach circular, marginal region limited by insertion of radial septa. Stomach pouches 16, width uniform centrally; tentacular pouches enlarged distally. Radial septa thin; rounded at base; straight up to ¼ of margin, then making an “S” (first thinning tentacular pouch, then enlarging it); ending near tentacular base at rhopalar lappet. Gastric filaments present. Gonads outlining gastric filaments, semicircular ring, greatly folded; colour whitish.

The estimated distance between *C. plocamia* specimens from Peru and Uruguay using the mitochondrial marker 16S is 0.003 for K2P and 0.003 for *p-distance*. Actually the difference between obtained sequences is indeed very low (only 3 bp from the 589bp recovered). The genetic distance between the sequences obtained shows that there is some correlation (exchange) between populations. The estimated distance between *C. plocamia* (Uruguay) and *C. lactea* (Uruguay) is 0.082 for K2P and 0.077 for *p-distance*.

Close to the date of the record in 2012 the presence of cold bottom water (15.6–13.7°C) was observed in front of La Paloma (data collected by RV Aldebaran 27–28 November 2012). Coastal upwelling was also recorded (surface temperature <18°C); during that





**Figure 3.** Sea surface temperature (SST) distribution during late spring, 2–9 December 2012 (A) highlighting the cold front offshore (full ellipse) and the coastal upwelling (dashed ellipse) and location of the stranded specimens (La Paloma), (B) SST distribution during winter (20–27 July 2012).

period (Figure 3A). In addition, a dominance of negative sea surface temperature anomalies over large parts of the Argentine and Uruguayan continental margin were observed (<http://iridl.ldeo.columbia.edu>), reinforcing the presence of a cold water core offshore (Figure 3A). During 2014, winter temperatures  $< 13^{\circ}\text{C}$ , indicative of the influence of cold Subantarctic Shelf Waters, were recorded throughout the Uruguayan and Argentine shelf (Figure 3B).

The distribution of large jellyfish is mainly related to physical factors. These factors include: currents, swirls, upwelling, and presence of islands, tides and ocean fronts (Haury et al. 1978). *Chrysaora plocamia* can be found across a range that encompasses two LMEs, Humboldt Current Large Marine Ecosystem in the Pacific Ocean and the Patagonian Large Marine Ecosystem in the Atlantic Ocean. The records of *C. plocamia* in Uruguay are especially relevant because the closest confirmed, published record is from Golfo de San Matías, (Patagonia, Argentina; ca.  $42^{\circ}\text{S}$ ), ca. 1,100 km south) (Mianzan and Cornelius 1999; Morandini and Marques 2010; Mianzan et al. 2014). The Uruguay records were collected in late spring 2012 and winter 2014, close to when, in 2012, the presence of cold bottom water ( $15.6\text{--}13.7^{\circ}\text{C}$ ) was observed off La Paloma (data collected by RV Aldebaran 27–28 November 2012).

The presence of this large, easy-to-detect species, on the Uruguayan coast is exceptional, and there are no records from La Paloma during at least the last 25 years (M. Abreu, pers. obs; G. Fabiano, pers. com.). Although

some exceptional and unverified historical records off the coast of Uruguay and Buenos Aires province, Argentina, (ca.  $34\text{--}38^{\circ}\text{S}$ ;  $50\text{--}300\text{ m}$  depth) may belong to this species, extensive trawling for fisheries assessments since 2005 failed to detect any large jellyfish (L. Ortega and F. Scarabino obs. pers.). Thus, these occasional records must be related with singular climatic and/or oceanographic events. Ocean temperatures have warmed in most regions over the last century. Consistent with the view that marine species are thermally constrained, there is growing evidence that many marine species have already undergone poleward range shifts in line with warming trends (Cheung et al. 2013; Sen Gupta 2014). In fact, the increasing frequency of records of species with tropical affinities in the Southwestern Atlantic (Segura et al. 2009; Martínez et al. 2009) agrees with the climate change scenario. In that sense, the geographical distribution of species is delimited by range edges by climate changes and the species has been shown to respond to such modifications. Range edges that advance into previously unoccupied habitat (e.g., under global warming, habitat previously too cool to accommodate a given species) are known as leading range edges, whereas those that contract into habitat currently occupied (under global warming, occupied habitat that has come to exceed upper thermal limits of the species in question) are known as trailing range edges (Schoeman et al. 2014). So it is important to stress that *C. plocamia* is associated with cold neritic waters and its northern distribution limit is probably being

constrained by ocean temperature and global warming. This is particularly evident in the Atlantic where there is a steep latitudinal thermal gradient in comparison with the Humboldt system as well as a pronounced warming trend in the coastal system (Zavialov et al. 1999; Ortega et al. 2013). Thus, these occasional records could be seen as the product of natural variability in the coastal circulation or rare incidents.

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## LITERATURE CITED

- Acha, E.M., H.W. Mianzan, R.A. Guerrero, M. Favero and J. Bava. 2004. Marine fronts at the continental shelves of austral South America: Physical and ecological processes. *Journal of Marine Systems* 44(1–2): 83–105. doi: [10.1016/j.jmarsys.2003.09.005](https://doi.org/10.1016/j.jmarsys.2003.09.005)
- Acha, E.M., A. Piola, O. Iribarne and H. Mianzan 2015. *Ecological Processes at Marine Fronts*. Cham: Springer International Publishing. 68 pp.
- Arai, N.A. 1997. *A functional biology of Scyphozoa*. New York: Chapman & Hall. 316 pp.
- Camus, P.A. 2001. Biogeografía marina de Chile continental. *Revista Chilena de Historia Natural* 74(3): 587–617. doi: [10.4067/S0716-078X2001000300008](https://doi.org/10.4067/S0716-078X2001000300008)
- Cheung, W.W.L., R. Watson and D. Pauly. 2013. Signature of Ocean Warming in Global Fisheries Catch. *Nature* 497: 365–368. doi: [10.1038/nature12156](https://doi.org/10.1038/nature12156)
- Cunningham, C.W. and L.W. Buss 1993. Molecular evidence for multiple episodes of pedomorphosis in the Family Hydractiniidae. *Biochemical Systematics and Ecology* 21(1): 57–69. <http://sites.biology.duke.edu/cunningham/pdfs/CunninghamBuss1993.pdf>
- Drummond, A.J., B. Ashton, S. Buxton, M. Cheung and A. Cooper. 2011. Geneious v5.4. Accessed at <http://www.geneious.com/>, 20 August 2015.
- Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792–1797. doi: [10.1093/nar/gkh340](https://doi.org/10.1093/nar/gkh340)
- Garzoli, S.L. and Z. Garraffo 1989. Transports, frontal motions and eddies at the Brazil-Malvinas Currents confluence. *Deep Sea Research Part A* 36(5): 681–703. [ftp://ftp.io.usp.br/lado/papers/garzoli\\_garraffo\\_1989.pdf](ftp://ftp.io.usp.br/lado/papers/garzoli_garraffo_1989.pdf)
- Garzoli, S.L. 1993. Geostrophic velocity and transport variability in the Brazil–Malvinas confluence. *Deep Sea Research Part A* 40(7): 1379–1403. [ftp://ftp.io.usp.br/lado/papers/garzoli\\_1993.pdf](ftp://ftp.io.usp.br/lado/papers/garzoli_1993.pdf)
- Gordon, A.L. and C.L. Greengrove. 1986. Geostrophic circulation of the Brazil–Falkland Confluence. *Deep Sea Research Part A* 33(5): 573–585. [http://www.ldeo.columbia.edu/~agordon/publications/Gordon\\_Greengrove\\_BZ-Falk\\_conflu\\_DSR86.pdf](http://www.ldeo.columbia.edu/~agordon/publications/Gordon_Greengrove_BZ-Falk_conflu_DSR86.pdf)
- Guerrero, R.A. and A.R. Piola 1997. Masas de agua en la Plataforma Continental; pp. 107–118, in: E.E. Boschi (ed.). *El Mar Argentino y sus Recursos Pesqueros*, Volume 1. Mar del Plata: Instituto Nacional de Investigación y Desarrollo Pesquero.
- Haurv, L.R., J.A. McGowan and P.H. Wiebe 1978. Patterns and processes in the time-space scales of plankton distributions; pp. 277–327, in: J. Steele (ed.). *Spatial Patterns in Planktonic Communities*. New York: Plenum Press.
- Heileman, S. 2009. Patagonian Shelf LME; pp. 735–746, in: K. Sherman and G. Hempel (eds.). *The UNEP Large marine ecosystem report: a perspective on changing conditions in LMEs of the world's regional seas*. UNEP Regional Seas Report and Studies N° 182, Nairobi, United Nations Environment Programme.
- Heileman, S., R. Guevara, F. Chávez, A. Bertrand and H. Soldi. 2009. XVII-56 Humboldt Current LME; pp. 1–14, in: K. Sherman and G. Hempel (eds.). *The UNEP large marine ecosystems report: a perspective on changing conditions in LMEs of the world's regional seas*. UNEP Regional Seas Report and Studies N° 182, Nairobi: United Nations Environment Programme.
- Kramp, P.L. 1952. Reports from the Lund University Chile expedition 1948–1949. 2. Medusae collected by the Lund University Chile Expedition 1948–1949. *Lunds Universitets Årsskrift N.F. Avd2*. 47(7): 3–19.
- Larkin, N.K. and D.E. Harrison. 2001. Tropical Pacific ENSO cold events, 1946–1995: SST, SLP, and surface wind composite anomalies. *Journal of Climate* 14: 3904–3931.
- Lesson, R.P. 1830. Voyage autour du monde, exécuté par ordre du roi sur la corvette La Coquille, pendant les années 1822, 1823, 1824, et 1825. *Zoologie* 2(2): 1–360. doi: [10.5962/bhl.title.57936](https://doi.org/10.5962/bhl.title.57936)
- Lima, I.D., C.A.E. Garcia and O.O. Möller. 1996. Ocean surface processes on the southern Brazilian shelf: characterization and seasonal variability. *Continental Shelf Research* 16(10): 1307–1317.
- Mianzan, H.W. and P.F.S. Cornelius 1999. Cubomedusae and Scyphomedusae; pp. 513–559, in: D. Boltovskoy (ed.) *South Atlantic Zooplankton*, vol. I. Leiden: Backhuys.
- Mianzan, H.W., F. Ramirez, J. Costello and L. Chiaverano. 2005. Un Mar de gelatina? *Ciencia Hoy* 15(86): 48–55. [http://aquaticcommons.org/16706/2/CienciaHoy2005\\_15\\_86\\_48.pdf](http://aquaticcommons.org/16706/2/CienciaHoy2005_15_86_48.pdf)
- Mianzan, H.W., J. Quiñones, S. Palma, A. Schiariti, M. Acha, K. Robinson and W.M. Graham. 2014. *Chrysaora plocamia*: A Poorly Understood Jellyfish from South American Waters; pp. 219–236, in: K.A. Pitt and C.H. Lucas (eds.) *Jellyfish Blooms*. Leiden: Springer.
- Miloslavich, P., E. Klein, J.M. Díaz, C.E. Hernández, G. Bigatti, L. Campos, F. Artigas, J. Castillo, P.E. Penchaszadeh, P.E. Neill, A. Carranza, M. V. Retana, J. M. Díaz de Astarloa, M. Lewis, P. Yorio, M.L. Piriz, D. Rodríguez, Y. Yoneshigue-Valentin, L. Gamboa and A. Martín. 2011. Marine Biodiversity in the Atlantic and Pacific Coasts of South America: Knowledge and Gaps. *PLoS ONE* 6(1): e14631. [10.1371/journal.pone.0014631](https://doi.org/10.1371/journal.pone.0014631)
- Morandini, A.C., D. Ascher, S.N. Stampar and J.F.V. Ferreira. 2005. Cubozoa e Scyphozoa (Cnidaria: Medusozoa) de águas costeiras do Brasil. *Iheringia, Série Zoologia* 95(3): 281–294. doi: [10.1590/S0073-47212005000300008](https://doi.org/10.1590/S0073-47212005000300008)
- Morandini, A.C. and A.C. Marques. 2010. Revision of the genus *Chrysaora* Péron & Lesueur, 1810 (Cnidaria: Scyphozoa). *Zootaxa* 2464: 1–97. <http://www.mapress.com/zootaxa/list/2010/2464.html>
- Ortega, L. and A. Martínez 2007. Multiannual and seasonal variability of water masses and fronts over the Uruguayan shelf. *Journal of Coastal Research* 23(3): 618–629. doi: [10.2112/04-0221.1](https://doi.org/10.2112/04-0221.1)
- Piola, A.R., E.J.D. Campos, O.O. Möller Jr., M. Charo and C. Martinez 2000. Subtropical shelf front off eastern South America. *Journal of Geophysical Research* 105(3): 6565–6578. [ftp://io.usp.br/lado/papers/piola\\_et\\_al\\_2000.pdf](ftp://io.usp.br/lado/papers/piola_et_al_2000.pdf)

- UNEP. 2006. Permanent Commission for the South Pacific (CPPS). Humboldt Current, GIWA Regional assessment 64. University of Kalmar, Kalmar, Sweden.
- Reynolds, R.W., Rayner N.A., Smith T.M., Stokes D.C. and Wang W. 2002. An improved in situ and satellite SST analysis for climate. *Journal of Climate* 15: 1609–1625. doi: [10.1175/1520-0442\(2002\)015<1609:AIISAS>2.0.CO;2](https://doi.org/10.1175/1520-0442(2002)015<1609:AIISAS>2.0.CO;2)
- Riascos, J.M., D. Carstensen, J. Laudien, W.E. Arntz, M.E. Oliva, A. Güntner and O. Heilmayer 2009. Thriving and declining: climate variability shaping life-history and population persistence of *Mesodesma donacium* in the Humboldt Upwelling System. *Marine Ecology Progress Series* 385: 151–163. doi: [10.3354/meps08042](https://doi.org/10.3354/meps08042)
- Riascos, J.M., L. Paredes, K. González, I. Cáceres and A.S. Pacheco. 2013. The larval and benthic stages of the scyphozoan medusa *Chrysaora plocamia* under El Niño–La Niña thermal regimes. *Journal of Experimental Marine Biology and Ecology* 446: 95–101. doi: [10.1016/j.jembe.2013.05.006](https://doi.org/10.1016/j.jembe.2013.05.006)
- Saraceno, M., C. Provost, A.R. Piola, J. Bava and A. Gagliardini. 2004. Brazil Malvinas Frontal System as seen from 9 years of advanced very high resolution radiometer data. *Journal of Geophysical Research* 109: C05027. doi: [10.1029/2003JC002127](https://doi.org/10.1029/2003JC002127)
- Schoeman, D.S., T.A. Schlacher and O. Defeo. 2014. Climate-change impacts on sandy-beach biota: crossing a line in the sand. *Global Change Biology* 20: 2383–2392. doi: [10.1111/gcb.12505](https://doi.org/10.1111/gcb.12505)
- Sen Gupta, A., J.N. Brown, N.C. Jourdain, E. van Sebille, A. Ganachaud and A. Vergés. 2014. Episodic and non-uniform shifts of thermal habitats in a warming ocean. *Deep Sea Research Part II: Topical Studies in Oceanography* 113: 59–72. doi: [10.1016/j.dsr2.2013.12.002](https://doi.org/10.1016/j.dsr2.2013.12.002)
- Stampar, S.N., M.M. Maronna, M.J.A. Vermeij, F.L.d. Silveira and A.C. Morandini. 2012. Evolutionary Diversification of Banded Tube-Dwelling Anemones (Cnidaria; Ceriantharia; *Isarachnanthus*) in the Atlantic Ocean. *PLoS ONE* 7(7): e41091. [10.1371/journal.pone.0041091](https://doi.org/10.1371/journal.pone.0041091)
- Stramma, L., Y. Ikeda and R.G. Peterson. 1990. Geostrophic transport in the Brazil Current region north of 20°S. *Deep Sea Research Part A. Oceanographic Research Papers* 37(12): 1875–1886. doi: [10.1016/0198-0149\(90\)90083-8](https://doi.org/10.1016/0198-0149(90)90083-8)
- Stiasny, G. 1937. Über *Chrysaora plocamia* (Lesson) Haeckel von Toxopila (Nord-Chile). *Zoologischer Anzeiger* 119 (11/12): 273–284.
- Tamura, K., G. Stecher, D. Peterson, A. Filipiński and S. Kumar. 2013. MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* 30(12): 2725–2729. [10.1093/molbev/mst197](https://doi.org/10.1093/molbev/mst197)
- Thiel, M., E.C. Macaya, E. Acuña, W.E. Arntz, H. Bastidas, K. Brokordt, P.A. Camus, J.C. Castilla, L.R. Castro, M. Cortés, C.P. Dumont, R. Escibano, M. Fernandez, J.A. Gajardo, C.F. Gaymer, I. Gomez, A.E. Gonzales, H.E. Gonzalez, P.A. Haye, J.E. Illanes, J.L. Iriarte, D.A. Lancellotti, G. Luna-Jorquera, C. Luzoro, P.H. Manriquez, V. Marín, P. Muñoz, S.A. Navarrete, E. Perez, E. Poulin, J. Sellanes, H. Sepúlveda, W. Stotz, F. Tala, A. Thomas, C.A. Vargas, J.A. Vasquez and J.M.A. Vega. 2007. The Humboldt Current System of Northern and Central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. *Oceanography and Marine Biology: An Annual Review* 45: 195–344. [http://www.ieb-chile.cl/uploads/publicaciones/-1\\_Thiel\\_et\\_al\\_2007\\_Ocean\\_Marin\\_Biol\\_AnuarRew.pdf](http://www.ieb-chile.cl/uploads/publicaciones/-1_Thiel_et_al_2007_Ocean_Marin_Biol_AnuarRew.pdf)
- Vivier, F. and C. Provost. 1999. Direct velocity measurements in the Malvinas Current. *Journal of Geophysical Research* 104: 21083–21103. doi: [10.1029/1999JC900163](https://doi.org/10.1029/1999JC900163)

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