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Research Article

Austinotheres angelicus (Lockington, 1877): the correct name for the symbiotic crab *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001) (Crustacea, Brachyura, Pinnotheridae)

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ABSTRACT. The taxonomic identity of the symbiotic crabs *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001) was revised. The morphology of these specimens, collected in the estuary of Punta Morales, Pacific coast of Costa Rica, in the oyster *Saccostrea palmula* did not agree with *J. muliniarum* but concurs well with topotypes and voucher material of *Austinotheres angelicus* from the Gulf of California, Mexico. *Austinotheres angelicus* belongs to the subfamily Pinnotherinae *sensu* Campos, 2009, and the morphology of *A. angelicus* supports its close relationship with *Bonita mexicana* and *Enigmatheres canfieldi*. The presence of a soft and thin carapace colored with deep chocolate brown with dark purple tones, a conspicuous protuberance in the basal antennal article, a third maxilliped with an ischio-merus fused with its inner margin angled, a carpus larger than the propodus, and a digitiform and small dactylus subdistally inserting on the ventral margin of the propodus are diagnostic features for *A. angelicus*. These characteristics separate this species from other pinnotherid crabs from the entire Pacific Ocean.

Keywords: *Juxtafabia muliniarum*, taxonomy, Pinnotheridae, Brachyura, Crustacea.

Austinotheres angelicus (Lockington, 1877): nombre correcto para el cangrejo simbiótico *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001) (Crustacea, Brachyura, Pinnotheridae)

RESUMEN. Se revisó la identidad taxonómica del cangrejo simbionte *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001). La morfología de los especímenes recolectados en el estuario de Punta Morales, costa Pacífica de Costa Rica, en el ostión *Saccostrea palmula* no concordaron con *J. muliniarum* pero concurren bien con topotipos y material verificado de *Austinotheres angelicus* del Golfo de California, México. *Austinotheres angelicus* pertenece a la subfamilia Pinnotherinae *sensu* Campos, 2009 y su morfología apoya su cercana relación con *Bonita mexicana* y *Enigmatheres canfieldi*. La presencia de un caparazón blando y delgado, de color chocolate intenso con tonos purpura oscuros, una conspicua protuberancia en el artejo basal de la antena, un tercer maxilipedio con el isquio-merus fusionado con su margen interno angulado, un carpus más grande que el propodus y el pequeño dáctilo digitiforme que se inserta sobre el margen ventral del propodus son características diagnosticas para *A. angelicus*. Estas características separan a esta especie de otros pinotéridos del océano Pacífico.

Palabras clave: *Juxtafabia muliniarum*, taxonomía, Pinnotheridae, Brachyura, Crustacea.

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INTRODUCTION

Ongoing studies on the pinnotherid crabs of Costa Rica continue to yield new information on the species recorded for this country. The present study deals with *Juxtafabia muliniarum sensu* Cabrera-Peña *et al.* (2001), a symbiont of the oyster *Saccostrea palmula* Carpenter, 1857. *Juxtafabia* Campos, 1993 is a monotypic genus, closely related to *Fabia* Dana, 1851 (Campos, 1993, 1996). Females of both genera share an asymmetrical pair of pereopods 3 (walking legs 2), longer than the others, and males possess two or more abdominal somites fused (Campos, 1993, 1996). In addition, both males and females in both genera lack a tubercle on the basal article of the antennae (Campos, 2009). Recently, Dr. Maurizio Protti-Quesada (Escuela de Ciencias Biológicas, Universidad Nacional, Heredia, Costa Rica) allowed us to examine some of the specimens formerly studied by Cabrera-Peña *et al.* (2001) in order to revise their taxonomic identification. Specimens studied by these authors were compared with all the known genera and species of the American Pinnotheridae, including the type species of the genus *Juxtafabia* (Campos, 1993), *J. muliniarum* (Rathbun, 1918). The morphology of males and females of the symbiotic crab of the oyster *S. palmula* did not match with that of *Juxtafabia*. In the present study, the taxonomic identity of *J. muliniarum sensu* Cabrera-Peña *et al.* (2001) is emended, providing a diagnostic description for this species and a morphological comparison with all pinnotherid crabs of America.

MATERIALS AND METHODS

Both, specimens studied by Cabrera-Peña *et al.* (2001) and new material collected in the intertidal zone of the estuary of Punta Morales, Puntarenas, Pacific coast of Costa Rica, in the oyster *Sacosstrea palmula* (see details in the next section) were analyzed. In addition, 26 species of different pinnotherid genera were studied for a comparative purpose. Material obtained from the following institutions were analyzed: Laboratorio de Sistemática de Invertebrados, Universidad Autónoma de Baja California, México (UABC); Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México, Distrito Federal, Mexico (CNCR); Colección Nacional de Equinodermos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Distrito Federal, Mexico (CNE); Colección de Macroinvertebrados, Instituto de Ciencias del Mar y Limnología (Estación Mazatlán), Universidad Nacional Autónoma de México, Sinaloa, Mexico (EMU); Crustacean Collection, Department of Biology, University of Louisiana, Lafayette, USA (ULLZ); Muséum national d'Histoire naturelle, Paris, France (MNHN); National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM); Natural History Museum of Los Angeles County, California, USA (formerly at the Allan Hancock Foundation) (AHF), and Naturalis, Nationaal Naturhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH). The species studied include: *Austinotheres angelicus* (Lockington, 1877), USNM 71334, 67723, UABC, EMU; *Austinotheres* sp., ULLZ 5547; *Calyptraeotheres granti* (Glassell, 1933), UABC, CNCR 1425; *Epulotheres* sp., UABC; *Fabia subquadrata* Dana, 1851, UABC, USNM, AHF 1467-42; *Fabia* sp., ULLZ 8563, 8564, 8565; *Gemmotheres chamae* (Roberts, 1975), USNM 139098; *Glassella costaricana* (Wicksten, 1982), UABC; *Holothuriophilus pacificus* (Poeppig, 1836), ULLZ 5569; *Holothuriophilus trapeziformis* Nauck, 1880, UABC; *Juxtafabia muliniarum* (Rathbun, 1918), UABC, USNM 23443, 18217, 229724; *Limotheres nasutus* Holthuis, 1975, USNM 151039; *Opisthopus transversus* Rathbun, 1893, USNM 50997, UABC; *Orthotheres ungifalcula* Glassell, 1936, USNM; *Ostracotheres tridacnae* (Ruppell, 1830) MNHN B.10578, RMNH-D 1542; *Parapinnixa nitida* (Lockington, 1877), EMU 3753; *Pinnaxodes floridensis* H.W. Wells & Wells, 1961, ULLZ, USNM 186366; *P. chilensis* (Milne-Edwards, 1837), USNM 22112, 49238; *P. gigas* Green, 1992, UABC; *Pinnixa* spp, UABC; *Pinnotheres pisum* (Linnaeus, 1758), UABC; *Pinnotherelia laevigata* H. Milne Edwards & Lucas, 1843, UABC, USNM 125585; *Raytheres clavapedatus* Glassell, 1935, UABC; *Scleroplax granulata* Rathbun, 1893, UABC, ULLZ, USNM 17497; *Tetrias scabripes* Rathbun, 1898, EMU 3744, 4026; *Tumidotheres margarita* (Smith, 1969), UABC, USNM 229723, EMU; *Tunicotheres moseri* (Rathbun, 1918), USNM 74954; *Zaops geddesi* (Miers, 1880), USNM 23767, 51000; *Z. ostreum* Rathbun, 1900, UABC, USNM, CNCR 2252, 2571.

Other abbreviations used include: MZUCR: Museo de Zoología, Universidad de Costa Rica; SDNH: San Diego Natural History, California, USA; CL: carapace length; CW: carapace wide; MXP3: third maxilliped; P1: pereopod 1 (cheliped), P2-P5: pereopods 2-5 (walking legs 1-4).

Systematics

Order Decapoda Latreille (1802)
Suborder Pleocyemata Burkenroad (1963)
Infraorder Brachyura Linnaeus (1758)
Section Eubrachyura de Saint Laurent (1980)
Family Pinnotheridae de Haan (1833)
Genus *Austinotheres* Campos (2002)
Austinotheres angelicus (Lockington, (1877)
(Figs. 1a-1f, 2a)

Synonymy: For previous synonymy, see Schmitt *et al.* (1973): 10, 38.

Pinnotheres angelicus: Lemaitre & Alvarez-Leon (1992): 36-76; Hendrickx (1995): 142.

Austinotheres angelicus: Campos (2002): 328-335; 2009: 30, 40; Ng *et al.* (2008): 248; Palacios-Theil *et al.* (2009): 459, 464, 466; Campos & Hernández-Ávila (2010): 42. *Juxtafabia muliniarum* [not *J. muliniarum* (Rathbun, 1918)]: Cabrera-Peña *et al.* (2001): 889-894.

Type species

Pinnotheres angelicus Lockington 1877, by the original designation and monotypy.

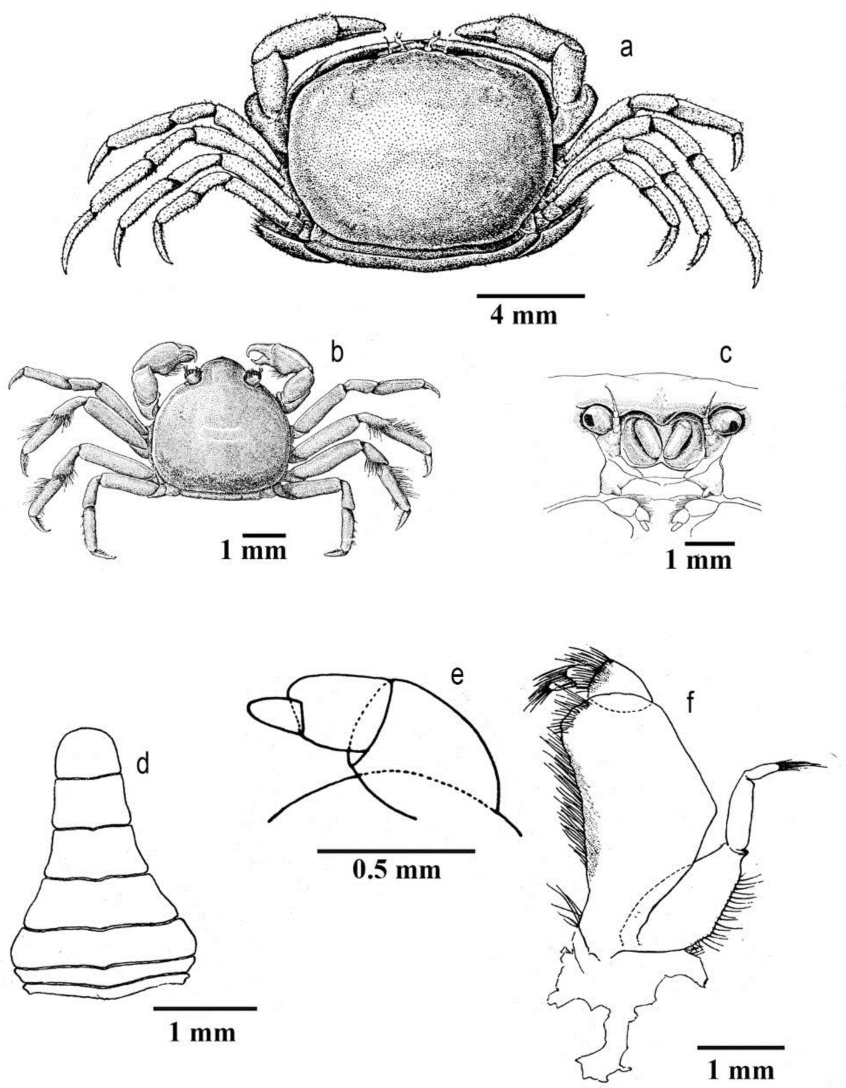

Figure 1. *Austinotheres angelicus*. a,c,e,f) adult female, b, d) adult male, from Bahia de los Angeles, Baja California, Mexico, SDNH 759: a) dorsal view, b) dorsal view, c) frontal region of carapace, d) abdomen, e) palp of MXP3, f) MXP3, (a-f, from Glassell, 1935).

Geographic distribution and host

San Felipe, Baja California, upper Gulf of California, Mexico to Colombia (Lemaitre & Alvarez-León, 1992; Campos, 2002). In *Myrakeena angelica* (Rochebrune, 1895) and Saccostrea palmula Carpenter, 1857.

Material examined

1 ♂, 4 ♀, San Felipe, Baja California, Mexico, USNM 71334, 67723; 30 ♀, 30 ♂, Campo E1 Pescador, 4 km north of San Felipe, Baja California, Mexico, 18 September 1986, in the oyster *Mayrakeena angelica* (Rochebrune, 1895), UABC, USNM 205688; 5 ♀, San José Island, Baja California Sur, Mexico, Albatross, 16 May 1889, USNM 17467; 3 ♀, Bahía de los Ángeles, BC, Mexico, May 1982, in *Mayrakeena angelica*, USNM210921; 2 ♀, Punta Morales Beach, Puntarenas, Costa Rica, 7 June 1992, USNM 256984; 2 ♂, 8♀ (4 ovigerous) Punta Morales, Playa Blanca (Golfo de Nicoya) in *Saccostrea palmula*, M. Protti & A. Baeza, coll, MZUCR 2617-01; 34 ♂, 107 ♀, 15 juveniles, same locality, habitat and host, 18-19 April 2009, MZUCR-2782-01; same locality, habitat and host, 7 November 2009, MZUCR 2782-01; 4 ♂, 12 ♀ (1 juvenile), same locality, habitat and host, 30 October 2010, MZUCR 2832-01; 4 ♂, 9 ♀ (2 ovigerous), same locality, habitat and host, 30 October 2010, MZUCR-2831-01; 11 ♂, 61 ♀ (6 juveniles, 28 ovigerous), same locality, habitat and host, 30 October 2010, MZUCR-2833-01, Rita Vargas coll.

Description

Female (after Campos, 2002). Carapace suborbicular, regions ill-defined, smooth, shiny, thin, easily wrinkled; anterior margin strongly arcuate and not protruding anteriorly; posterior margin wide, slightly sinuous, sides rounded. Front advanced, laterally rounded. Orbits and eyes oval, hidden from dorsal view. Antenna with a prominent tubercle at posterior end of basal joint of antenna. MXP3 obliquely placed on buccal cavity, ischium and merus indistinguishably fused, palp of three articles, joined end to end; carpus larger than propodus and dactylus combined, propodus extending distally, small dactylus distally inserted on ventral margin of propodus. Exopod of MXP3 with a 2-segmented flagellum. Pereopod 1 (chelipeds) elongate, manus slightly compressed and increasing in width distally; pollex slightly deflexed, swollen in basal half, with small teeth on cutting edge; dactylus slightly curved, with small proximal tooth on cutting edge; curved tips cross each other and leave a small gape when fingers are closed. P2-P5 slender, relative length P3 > P4 > P2 > P5; P3 asymmetrical, right from 1.10 to 1.22 longer than left. Dactyli of P2-P5 slightly curved at tip, relative length 3 > 4 > 2 > 5, those of P3 subequal to or longer than respective propodi. Abdomen extremely large, with six somites, and telson free articulated; margin with tomentum, laterally covering ischia and distally buccal cavity and eyes.

Male

(After Campos, 2002). Much smaller than female. Carapace flat, suborbicular; front projecting, triangular, tip bent ventrally to a blunt point, not visible in dorsal view; surface hard, lightly pubescent, punctuate; cardiac region faintly defined. Eyestalk large and stout, diminishing from base to tip; pubescent on upper frontal surface; cornea large. A small tubercle at posterior end of basal joint of antenna. MXP3 similar to that of female. Pereopod 1 (chelipeds) stout, similar, slightly pubescent, palm smooth, swollen on basal half, tapering distally; exterior of manus crossed longitudinally by granulated ridge. Pollex short, stout, hooked at tip; a large ridge-like tooth occupying entire central portion; a deep notch at gape. Dactyli long and curved at tip; armed with two well-developed teeth at proximal end, the distal one the larger; fingers fitting together when closed, curved tips crossing each other; a row of setae on ventral margin of hand. P2-P5 slender, relative length P3 = P4 > P2 > P5. Dactyli long and straight, with tips hooked, acuminate. Propodus of P3-P5 crested with setae. Lower distal edges of carpus of P3-P4 with setae. Abdomen of six somites, and telson free articulated, widest at third segment, which represents almost ¾ of entire length; gradually narrowing from third somite to telson, which is obtusely rounded. Abdomen and sternum pubescent.

Color in life

Carapace and chelipeds of male a deep chocolate brown; finger of chelipeds and ambulatory legs much lighter. Carapace and chelipeds of female a deep chocolate brown; ambulatory legs from light cream color to white (modified from Glassell, 1935).

Hosts

Austinotheres angelicus is a holosymbiont of oysters (Ostreidae) including *Myrakeena angelica* (Rochebrune, 1895) and *Saccostrea palmula* (Carpenter, 1857). The only other two American pinnotherid crabs, which are symbionts of oysters of the genus *Crassostrea* in the Atlantic Ocean include *Zoaps ostreum* and *Z. geddesi* (see Rathbun, 1918; Schmitt *et al.*, 1973; Campos & Manning, 2000). In addition, several hundreds of *Modiolus capax* (Conrad, 1837) from the Gulf of California were collected in the intertidal zone of San Felipe, and Los Angeles Bay, Baja California, and La Paz Bay, Baja California Sur, Mexico. Like Glassell (1935) we were unable to verify Rathbun´s (1918) record of *A. angelicus* in *M. capax*. Only *Fabia concharum* (Rathbun, 1893) and *Opisthopus transversus* Rathbun, 1893 have been confirmed as symbionts of *M. capax* but from the west coast of Baja California Sur, Mexico (Campos *et al.*, 1992; Campos, 1996).

DISCUSSION

The morphological analyses of the specimens collected in Punta Morales, Pacific coast of Costa Rica, in *Saccostrea palmula* and their comparison with topotypes of *Austinotheres angelicus* collected in Los Angeles Bay and another in San Felipe, Baja California, in *Mayrakeena angelica*, has led to the conclusion that the Costa Rican specimens belong to *A. angelicus* (Fig. 1). The genus *Austinotheres* Campos, 2002 along with other 17 genera worldwide has been included in the subfamily Pinnotherinae *sensu stricto* by Campos (2009). The consistent and distinct characters of this group include a soft and thin carapace, and a conspicuous protuberance at the basal antennal article, which is conspicuous in *A. angelicus* (Fig. 2a). Although *Juxtafabia muliniarum* has a carapace soft and thin, it is lacking such a protuberance at the basal antennal article (Fig. 2b). In addition, adult females of *J. muliniarum* have the dactyl of P5 longer than the other pereopods (Fig. 3a); males of this genus, and those of *Fabia* share long swimming setae on external face of carpus and propodus of P3 and P4, and two or more abdominal somites fused (Figs. 3b, 3d; Campos, 1993, 1996; Campos & Manning, 1998). Females of *A. angelicus* have the dactylus of P3 longer than the others pereopods, and males have all abdominal somites and

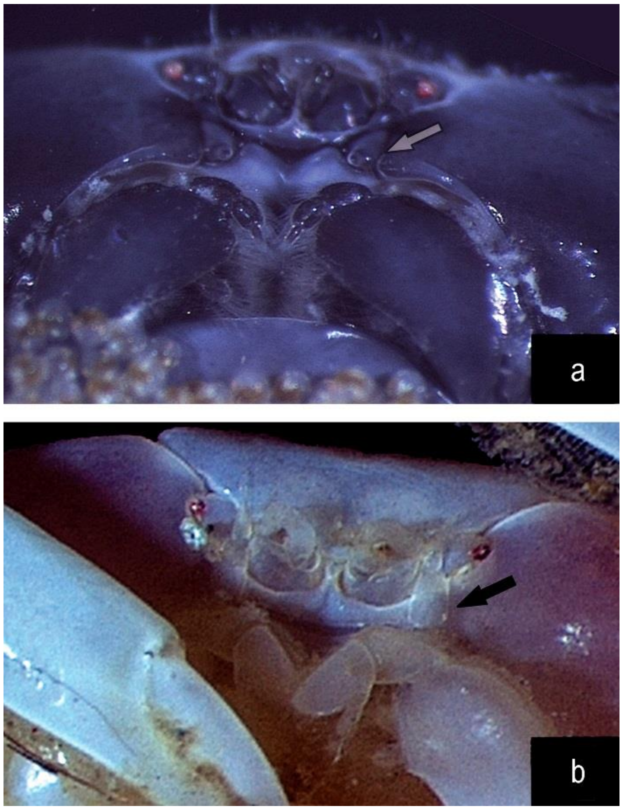

Figure 2. Frontal view. a) *Austinotheres angelicus* from San Felipe, Baja California, Mexico, UABC uncatalogued, arrow indicates the conical tubercle of basal antennal segment; b) *Fabia subquadrata*, Todos Santos Bay, Ensenada, Baja California, Mexico, UABC uncatalogued, arrow indicate the basal antennal segment without a conical tubercle. a) CL = 9.9 mm, b) CL = 13.4 mm.

telson well separated (Fig. 1d). The oyster crab, *A. angelicus,* as well as *Enigmatheres canfieldi* (Rathbun, 1918) (type species of *Enigmatheres* Campos, 2009) and *Bonita mexicana* Campos, 2009 (type species of *Bonita* Campos, 2009) comprise a subgroup within the Pinnotherinae *sensu* Campos (2009) that share a third maxilliped with a palp of three segments, being the carpus longer than the propodus (Figs. 1e, 1f). These shared and exclusive features of these species allow their taxonomic separation from other members of this subfamily. The presence of an even and smooth carapace, and the P3 longer than the others (Fig. 1a) permit to separate *A. angelicus* from *B. mexicana*, which has the carapace tumid with two longitudinal sulci arising from the orbits and extending to the middle the of carapace, and the P4 longer than the others. On the other hand, *E. canfieldi* and *A. angelicus* can be distinguished from other pinnotherines by the asymmetrical P3 and because the propodus of the third maxilliped is shorter than the carpus (Figs. 1e, 1f).

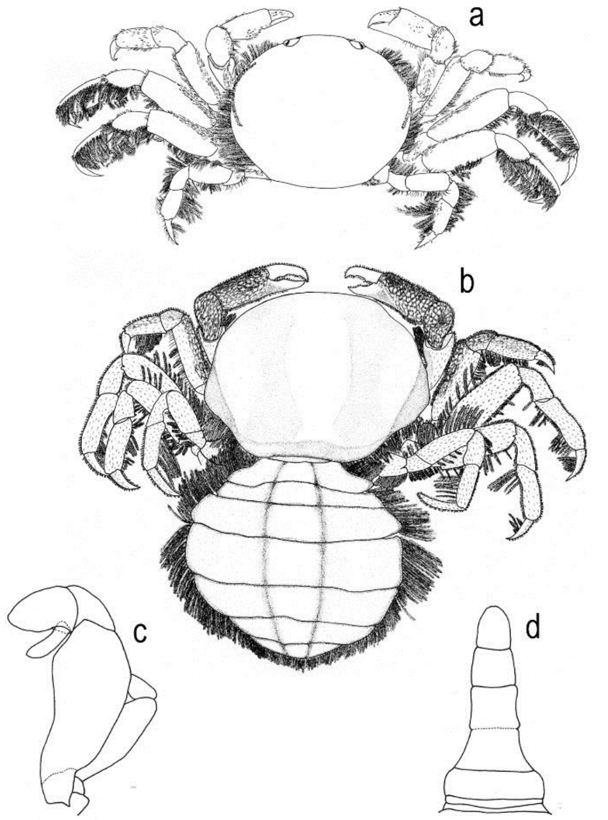

Figure 3. *Juxtafabia mulimiarum*: a,c) adult male, b,d) adult female, from Laguna Percebú, San Felipe, Baja California, México, UABC uncatalogued: a) dorsal view; b) dorsal view; c) third maxilliped; d) abdomen. a) CL = 7 mm, b) CL = 3.14 mm.

Others species in the Pinnotherinae *sensu* Campos, 2009, except *B. mexicana,* have symmetrical walking legs, and the propodus of the third maxilliped is always larger than the carpus (Figs. 2b, 3c). *A. angelicus* differs from *E. canfieldi* in the obtuse angle of the outer margin of the ischium-merus of the third maxilliped (Fig. 1f) and by the insertion of the dactylus of this appendage on the distal third of the ventral margin of the propodus (Figs. 1e, 1f). *E. canfieldi* has a gently curved outer margin of the MXP3, and the insertion of the dactylus is on the middle third of the ventral margin of the propodus. The oyster crab, *A. angelicus,* can be also distinguished from *E. canfieldi* by its slender and long walking legs with long, blade-shaped and slightly curved dactyli. The walking legs of *E. canfieldi* are relatively stouter, and the dactyli are shorter, conical and slightly curved up to hooked and hard tip.

In summary, the following diagnostic characteristics as well as its symbiotic relationship with oysters (Ostreidae) permit to distinguish *A. angelicus* from other pinnotherid crabs from the entire Pacific Ocean: 1) the presence of a soft and thin carapace colored deep chocolate brown with dark purple tones, 2) a conspicuous protuberance in the basal antennal article (Fig. 2a), 3) a third maxilliped with a ischium-merus fused with its inner margin angled, 4) a carpus longer than the propodus, and 5) a digitiform dactylus insert subdistally (Figs. 1e, 1f).

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Research Article

Massive salp outbreaks in the inner sea of Chiloé Island (Southern Chile): possible causes and ecological consequences

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ABSTRACT. During 2010 several massive salp outbreaks of the Subantarctic species *Ihlea magalhanica* were recorded in the inner sea of Chiloé Island (ISCh, Southern Chile), affecting both phytoplankton abundance and salmon farmers by causing high fish mortality. First outbreaks were recorded during February 2010 when *Ihlea magalhanica* reached up to 654,000 ind m^{-3} close to the net pens in Maillen Island and consecutive outbreaks could be followed during March and from October to November 2010. One month prior to the first recorded salp outbreak, the adjacent oceanic region and ISCh showed a sharp decline of *ca.* 1.0ºC in sea surface temperature and an atypical pattern of oceanic sea surface currents, changing from a predominantly meridional (northward) to a zonal (eastward) direction, probably causing a massive Subantarctic Water parcel to enter the ISCh. During the outbreaks, surface chlorophyll concentration decreased from an historical mean of 13.8 to less than 4 mg Chl-*a* m^{-3}, and did not return to normal conditions throughout the entire year, and similar results were also observed in phytoplankton abundance. The abundance of salp aggregations were highest close to the salmon net pens, which acted as physical barriers, and may have favored the successful reproduction and persistence of the outbreaks during 2010. The possible impact of these outbreaks on phytoplankton quality and quantity, as well as potential scenarios for the development of further outbreaks is discussed.

Keywords: *Ihlea magalhanica*, outbreak, salmon mortality, Chiloé Island, southern Chile.

Proliferaciones masivas de salpas en el mar interior de la isla de Chiloé (sur de Chile): posibles causas y consecuencias ecológicas

RESUMEN. Durante 2010 varias proliferaciones masivas de salpa subantártica, *Ihlea magalhanica*, fueron registrados en el mar interior de Chiloé (MICh, sur de Chile), que afectó la abundancia de fitoplancton y a los productores de salmón al causar altas mortalidades de peces. Las primeras proliferaciones se registraron en febrero de 2010, cuando la abundancia de *I. magalhanica* alcanzó 654.000 ind m^{-3} cerca de las balsas jaulas en isla Maillen. Proliferaciones consecutivas fueron posteriormente registradas durante marzo y de octubre a noviembre de 2010. Un mes antes de los registros de las primeras proliferaciones, la región oceánica adyacente y el MICh evidenciaron un fuerte descenso en la temperatura superficial del mar de *ca.* 1ºC y un patrón atípico de las corrientes oceánicas superficiales, cambiando desde una circulación predominantemente meridional (norte) a zonal (hacia el este), probablemente causando el ingreso de una parcela de agua subantártica al mar interior de Chiloé. Durante las proliferaciones, la concentración de clorofila (Clor-*a*) superficial disminuyó de una media histórica de 13,8 a menos de 4 mg Clor-*a* m^{-3}, manteniéndose bajo los promedios históricos durante todo año 2010. Resultados similares se observaron también en la abundancia de fitoplancton. La abundancia de las concentraciones de salpas fueron mayores cerca de las balsas jaulas de salmón, que actúan como barreras físicas, concentrando los organismos y posiblemente favoreciendo el éxito reproductivo y la persistencia de estas proliferaciones durante el 2010. Se discute el posible impacto de estas proliferaciones en la calidad y cantidad de fitoplancton, así como los posibles escenarios para el desarrollo de nuevos eventos.

Palabras clave: *Ihlea magalhanica*, proliferaciones, mortalidad de salmones, isla de Chiloé, sur de Chile.

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INTRODUCTION

The sudden increase of massive gelatinous zooplankton outbreaks in several coastal areas around the world has become more frequent, especially during the last few decades. The most documented case is the intrusion of the non-indigenous ctenophore species *Mnemiopsis leidyi* in the Black Sea during the 80's, which latter spread into the Caspian, Baltic, and North Seas (Shiganova *et al.*, 2001; Faasse & Bayha, 2006; Javidpour *et al.*, 2006), considerably affecting the food web structure and possibly helping to promote the collapse of fisheries in the Black Sea (Kideys, 1994, 2002). Major gelatinous outbreaks were also reported in 2011 and serious problems in nuclear plants in Israel, Japan and USA were reported where the seawater cooling systems became clogged with jellyfish (Purcell, 2012). In addition, the bursting of fishing nets caused by the giant *Nemopilema nomurai* in the coasts of Japan have forced fishermen to adapt fishing equipment in order to keep out jelly swarms (Uye, 2008).

The impacts of these gelatinous zooplankton outbreaks on tourism have also increased considerably and include the temporary closing of beaches, as well as cases of bathers being injured and even killed. It seems that human alterations to major ecosystems, which in turn have caused jelly outbreaks, are behind planktonic ecosystem shifts, and some anticipate that this will worsen in the future (Richardson *et al.*, 2009). Meanwhile, a recent review (Condon *et al.*, 2012) brings some caution to these findings based on the little knowledge of the historical ecosystem baseline for almost all jelly plankton species. The lack of historical background, the inaccuracy of the plankton nets used and sporadic sampling efforts is the main drawback to solve the paradigm of the abundance of these groups.

In most cases, harmful gelatinous outbreaks are referred to as carnivorous zooplankton, mainly cnidarians and occasionally ctenophores. Records of filter feeding zooplankton (salps, doliolids and pyrosomes) are less frequent and in most cases not even properly recorded. The latter group of zooplankton, due to its nature, is harmless to humans and therefore not of general concern. Salps have the ability to increase in number in short periods of time by the use of a complex life cycle with an obligatory alternation of sexual and asexual generations, allowing them to make rapid use of resources when environmental conditions are favorable (Goy *et al.*, 1989; CIESM, 2001; Molinero *et al.*, 2005). Salps are capable of filtering particles even in the 0.1 to 1 µm range, making them able to feed upon small bacteria, *Prochlorococcus* and colloids (Sutherland *et al.*, 2010), thereafter inducing an exceptional food web shortcut between small particles and higher trophic levels, bypassing the microbial loop. The wide size range of potential food sources, high clearance rates (250-801 mL mg^{-1} h^{-1}) (Deibel, 1982a; Mullin, 1983), and reproductive cycle strategy allows them to achieve exceptional growth rates, ranging between 0.3% and 28% body length per hour (Deibel, 1982b; Le Borgne & Moll, 1986). Each solitary individual (oozooid) produces, by budding, a stolon which strobilates into chains, between 25 and 75 aggregated individuals (blastozooids), depending on the oozooid size (Heron & Benham, 1985), for *Thalia democratica*. These chains are fertilized shortly after they detach from the stolon to form a free living, pseudo-colonial group. The latter process allows salps to achieve high densities in short periods of time, while mortality is likely minimal as a result of viviparity (Heron, 1972), and causes the overgrazing of food resources during these short burst increases. This can come from rapid reproduction and growth during highly favorable environmental conditions where asexual propagation exceeds physical dilution.

In situ evidence and anecdotic information on the salp outbreak formation

During the 2010 austral summer, several warnings of salp outbreaks of the species *Ihlea magalhanica* were recorded, mainly by salmon farmers, in the ISCh, southern Chile. The first report occurred on 25 February, and lasted until 3 March 2010, when a massive outbreak was recorded close to Quemchi (Fig. 1a).This bloom was the onset of the first alert which was followed by several observations in diverse areas of the ISCh. During this outbreak, pictures were taken by local salmon farmers and dissections of dead salmon were performed in order to determine causes of *ca.* 25,000 salmon mortalities (Fig. 2a). Local salp abundances were not recorded, however farmer´s estimate, indicate abundances of a couple of thousand per cubic meter. Massive concentrations clogged fish gills, probably the primary cause of fish deaths. Dissections of fish revealed the magnitude of this outbreak as depicted by gut content analyses that sho-

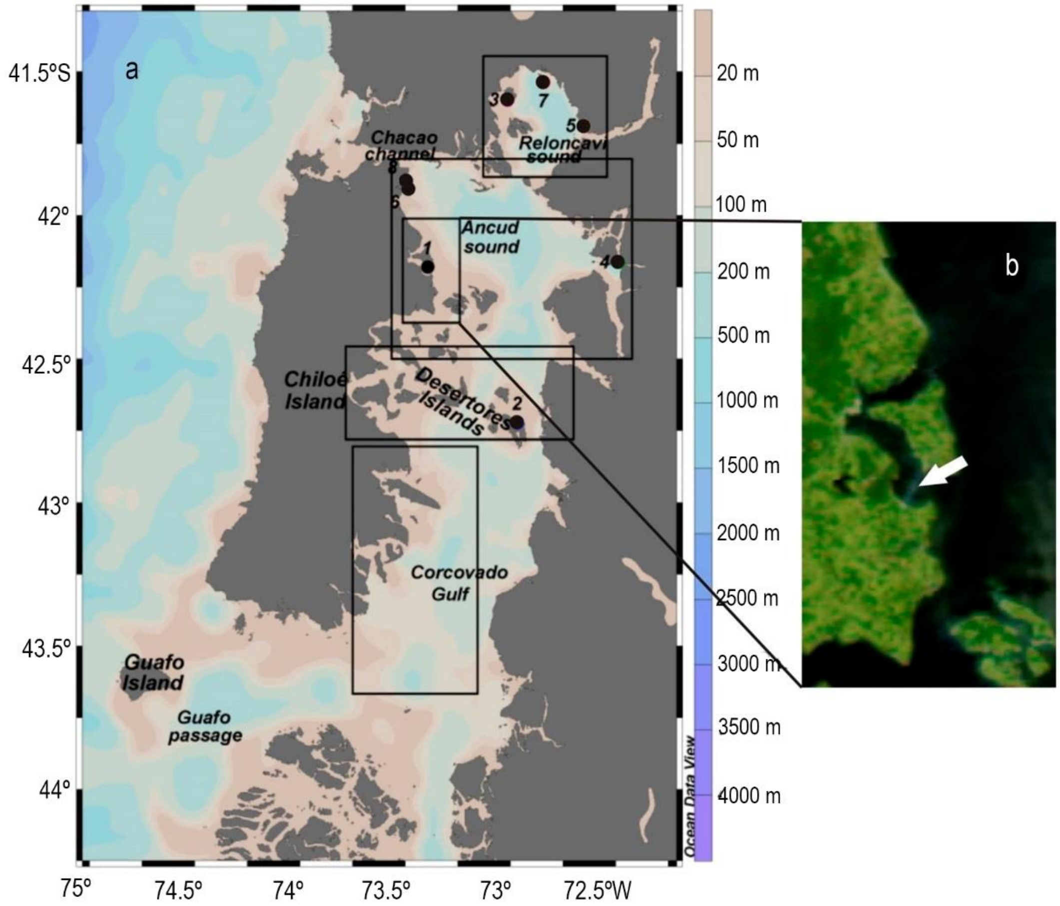

Figure 1. a) Locations and dates where *Ihlea maghalanica* outbreaks were recorded along the coasts of the ISCh during 2010, 1) Quemchi (25 February-3 March), 2) Chaiten (10 March), 3) Maillen Island (20 March), 4) Cholgo Channel (24 March), 5) Caleta Arena (29 March), 6) Hueihue Bay (5 September), 7) Reloncaví (14 September -27 October), 8) Huelden (5 and 25-28 September). The color bar on the right hand side of (a) shows bathymetry (m), b) SeaWiFS true color image of whitish structure of 5 km in length by *ca.*1 km in width crossing the Cacahue Channel where an *I. magalhanica* outbreak was recorded during February 2010.

wed guts almost entirely filled with salps (Fig. 2b), which ultimately could cause fish starvation due to the low energy content of salps compared to food pellets. SeaWiFS true color images taken on 26 February unveiled a whitish structure, 5 km in length by *ca.*1 km in width, crossing the Cacahue Channel, which was most likely a result of this unusual outbreak (Fig. 1b). One week later, a second event was registered on March 10, close to Chaiten, 90 km away from the first report (Fig. 1a). After this, several warnings were received during March across the ISCh: March 20 at Maillen Island (600 thousand oozooids and 54 thousand blastozooids per m^{-3}), March 24 at Cholgo Channel and March 29 at Caleta Arena (Fig. 2c). No more warnings of salp outbreaks were recorded until September in the north of Chiloé Island (Huelden Bay) and Ancud Sound (September to October 2010).

Ihlea magalhanica is a subantarctic species with an oceanic distribution centered between the subtropical convergence and the Antarctic convergence (Esnal & Daponte, 1999). It is usually described as a steno-thermal cold water species (Ihle, 1958; Foxton, 1971), adapted to a temperature range between 4-16.8ºC (Foxton, 1971; Daponte *et al.*, 1993) while highest abundances are usually recoded in association to cold water masses (5-7ºC, Daponte *et al.*, 1993). Few organisms were collected at the Magellan region (Michaelsen, 1907), south of 43.5ºS (F. Cabello, *pers. comm.*) and off Valparaiso (Chile) (~33ºS, Fagetti, 1959), the later being the most northerly location ever recorded.

Ihlea magalhanica, as most salp species, is usually found in large numbers in open ocean waters and exceptionally in neritic regions. Thus, the presence of

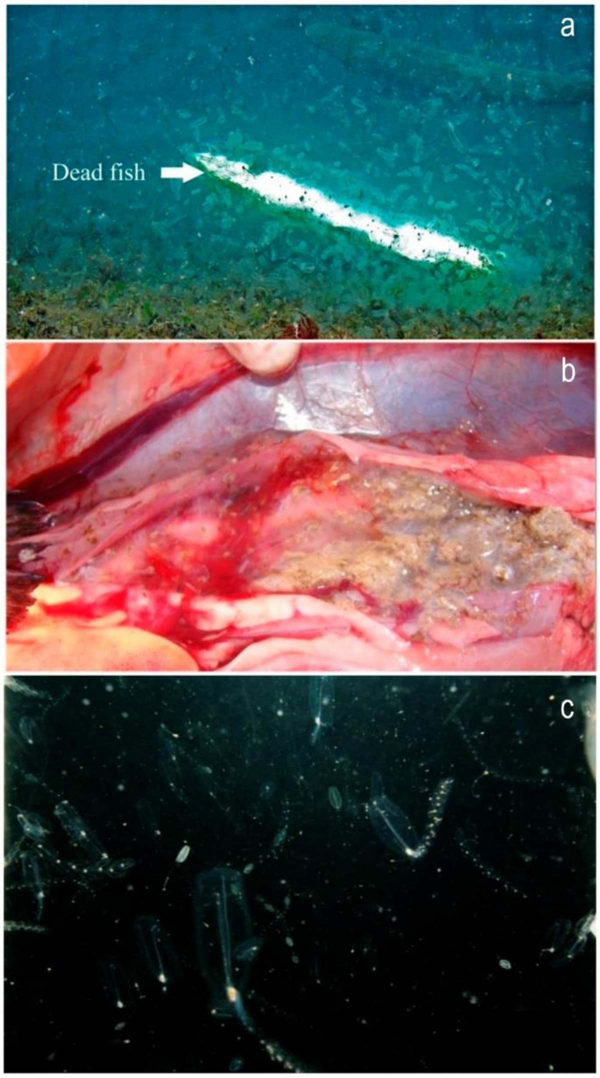

Figure 2. a) Salp abundance in a fish cage showing dead salmons in the Maillen Island, b) gut content of dead salmon, c) salp abundance taken by scuba divers at Caleta Arena.

this species in coastal waters is usually linked to the horizontal advection of oceanic water masses into coastal areas. The area of the east Pacific where salp outbreaks were observed during 2010 coincides with the region in which the South Pacific Current (SPC) reaches the eastern margin of the Pacific Ocean. Here, the SPC splits into two branches; to the north, the Humboldt Current or Chile-Peru Current and to the south the Cape Horn Current. Forced by the SPC, Subantarctic Water (SAAW) mass penetrates the inlets of the ISCh through the Guafo Passage, where it mixes with the Estuarine Water (EW), forming the Subantarctic modal water (Silva *et al.*, 1998; Sievers & Silva, 2006). We hypothesize that temporal anomalies in the currents (*i.e.*, displacement of the SPC, intrusion of anomalous cold water masses into the ISCh), may favor the entrance and establishment of salp populations, while local food availability conditions could have allowed the massive increase in population abundance which were observed during 2010.

The aim of this study was to explore the scenarios which have lead to the intrusion of *I. magalhanica* into the ISCh, as well as the environmental conditions which allowed the persistency and development of a several massive outbreaks in this region during 2010.

MATERIALS AND METHODS

Sea surface temperature and surface current along the outer coast off Chiloé Island and the Patagonian fjord region

Field data with a spatial resolution of 1/12º x 1/12º were obtained from the model outputs of Hybrid coordinate Ocean Model [HYCOM; Chassignet *et al.* (2009)] with a Navy Coupled Ocean Data Assimilation (NCODA) System (Cummings, 2005) for data assimilation. The hybrid coordinate in HYCOM is isopycnal in the open, stratified ocean, but smoothly reverts to a terrain-following coordinate in shallow coastal regions, NCODA uses the model forecast as a first guess in a multivariate Optimal Interpolation scheme and assimilates available satellite altimeter observations satellite and *in situ* SST as well as available *in situ* vertical temperature and salinity profiles from XBTs, ARGO floats and moored buoys. Monthly means and their anomalies from January to March were calculated from daily sea surface temperature and the ocean surface velocity field (42º-46ºS, 74º-76ºW) from 2004 to 2011.

Chlorophyll-*a* and sea surface temperature in the ISCh

In order to explore the general scenario in which *I. magalhanica* outbreaks were established and developed, we analyzed monthly means of historical satellite-derived chlorophyll-*a* (Chl-*a*) and sea surface temperatures (4×4 km pixels, 11 µm night product) and compared them with the monthly mean values for the year 2010. SST and Chl-*a* values were estimated from the Moderate Resolution Imaging Spectro-radiometer Aqua sensor (MODIS Aqua) from July 2002 to July 2010. Data were averaged over an area which included all the locations where salps were seen (*ca.* 4000 km^2) (Fig. 1a). Analysis used in this study was produced with the Giovanni online data system, developed and maintained by the NASA GES DISC (Acker & Leptoukh, 2007).

Sampling and analysis

On 5 September, during the first outbreak recorded in Huelden Bay (northern Chiloé Island), vertical zooplankton samples (20-0 m) were collected on the third (and last) day of the outbreak with a WP-2 net (200 µm mesh size) equipped with a calibrated flowmeter. Zooplankton samples were collected along a transect consisting of five stations, 500 m apart, starting from close to the coast (*ca.* 100 m) into the ISCh. After collection, the samples were fixed in 5% buffered formaldehyde in sea water and stored for further analysis. Abundance and identification of salp species and life history phases were determined under a stereo microscope at 20x, by observing the entire sample. Salps were identified using the taxonomic literature (Fagetti, 1959; Foxton, 1971; Esnal & Daponte, 1999).

In order to explore the *in situ* potential effect of salps on the autotrophic community, water samples for determining phytoplankton and chlorophyll-*a* were collected using 5-L PVC Go-Flo bottles at three depths (0, 5 and 10 m). Subsamples (300 mL) were filtered through 0.7 µm GFF filters, immediately frozen (-20^{o}C) for later pigment extraction and fluorometric analysis (Turner Design TD-700), according to Parsons *et al.* (1984). To quantify phytoplankton abundance, 250 mL subsamples were fixed in acid Lugol's solution (1% final concentration) for phytoplankton cell counts. A 50 mL aliquot was taken from each subsample and placed in a settling chamber for 30 h prior to analysis under an inverted microscope (Zeiss Axiovert 200, 400x magnification) and counted using standard counting methods (Utermöhl, 1958).

During the second salp outbreak at Huelden Bay which occurred between 25 and 28 September, salmon farm workers collected water samples using a 15 L bucket at irregular intervals (0.5 to 10.5 h) at a fixed point within a salmon cage. The sampling point was located on the edge of the salmon cage facing the inner sea. Salps were sieved and directly counted (no distinction between oozooids and blastozooids were made). Salp samples were fixed and sent to the laboratory for later taxonomic identification.

Time series of salp abundance at the Reloncaví Sound

Zooplankton samples were collected monthly by oblique tows using a Tucker trawl net (0.5 m^{-2} mouth area, 300 µm mesh size) equipped with a digital flowmeter for water volume quantification, during daytime from July to November 2010 at a fixed station (41º32.6'S, 72º52'W). Samples were collected at 9 depth intervals, from 5 to 100 m (0-5-10, 10-15, 15-20, 20-30, 30-40, 40-50, 50-75 and 75-100 m) and preserved in borax buffered formalin (10%) for later analysis. Salps were identified up to species level and measured from the oral to the cloacal opening (excluding posterior projections). Along with the zooplankton samples, vertical CTD casts (Seabird 19 plus) were obtained during each sampling date from the surface down to 91 m.

Time series of phytoplankton functional group abundances prior to and after salp outbreaks

Phytoplankton abundance from January 2009 to December 2011 was obtained for the three major basins along the ISCh: Reloncaví Sound, Ancud Sound, and Corcovado Gulf, and the region of the Desertores Islands. The amount of stations per basin varied from between 2 (Reloncaví Sound) up to 52 (Desertores Islands), while each basin was sampled between 1 and 24 times per month. Integrated samples (0-20 m) were collected using a 2.5 cm diameter hose raised vertically and preserved in an acid Lugol's solution. From these samples, a 12 mL subsample was analyzed for diatom and flagellate counting using standard methods (Utermöhl, 1958).

RESULTS

Large scale offshore temperature and sea surface current climatology during austral summer

HYCOM model output derived SST climatology revealed the presence of cold SAAW water surrounding the outer coast from southern Chile during January (Fig. 3a), this cold water approached the coast from the south-west around 45º30'S (Fig. 3d). Close to the coast, the northward current deflected into two branches south of the Guafo Island (~44ºS), one continued equatorward around Guafo Island, while the second entered the ISCh through the Guafo Passage at a speed of 0.06 m s^{-1} (Fig. 3d). Equatorward currents flowed relatively slow close to the coast (0.05 m s^{-1}) and tended to increase along a narrow band between 75º20'-75º40'W which expanded north of the Guafo Island where it reached the coast of Chiloé Island up to 75º4'W.

During February, the currents ran in a predominately meridional direction to the north with an increase in velocity over a wider zonal range, while eastward currents along the western margin were less intense and only apparent south of 45ºS (Fig. 3e). There was also an increase in SST of *ca.* 1ºC associated with modifications in meridional currents over the entire study area (Fig. 3b). The northern warm core tended to show a displacement to the south-east and low SST was only seen in a restricted area close to the outer coast of the Patagonian fjord region and the Guafo Passage.

During March, SST conditions were more similar to those in January (Figs. 3a, 3c), with a cold SST in the outer fjord region, coupled with a change in the meridional currents to a more oblique zonal current plane (eastward) during March (Fig. 3f). The oceanic

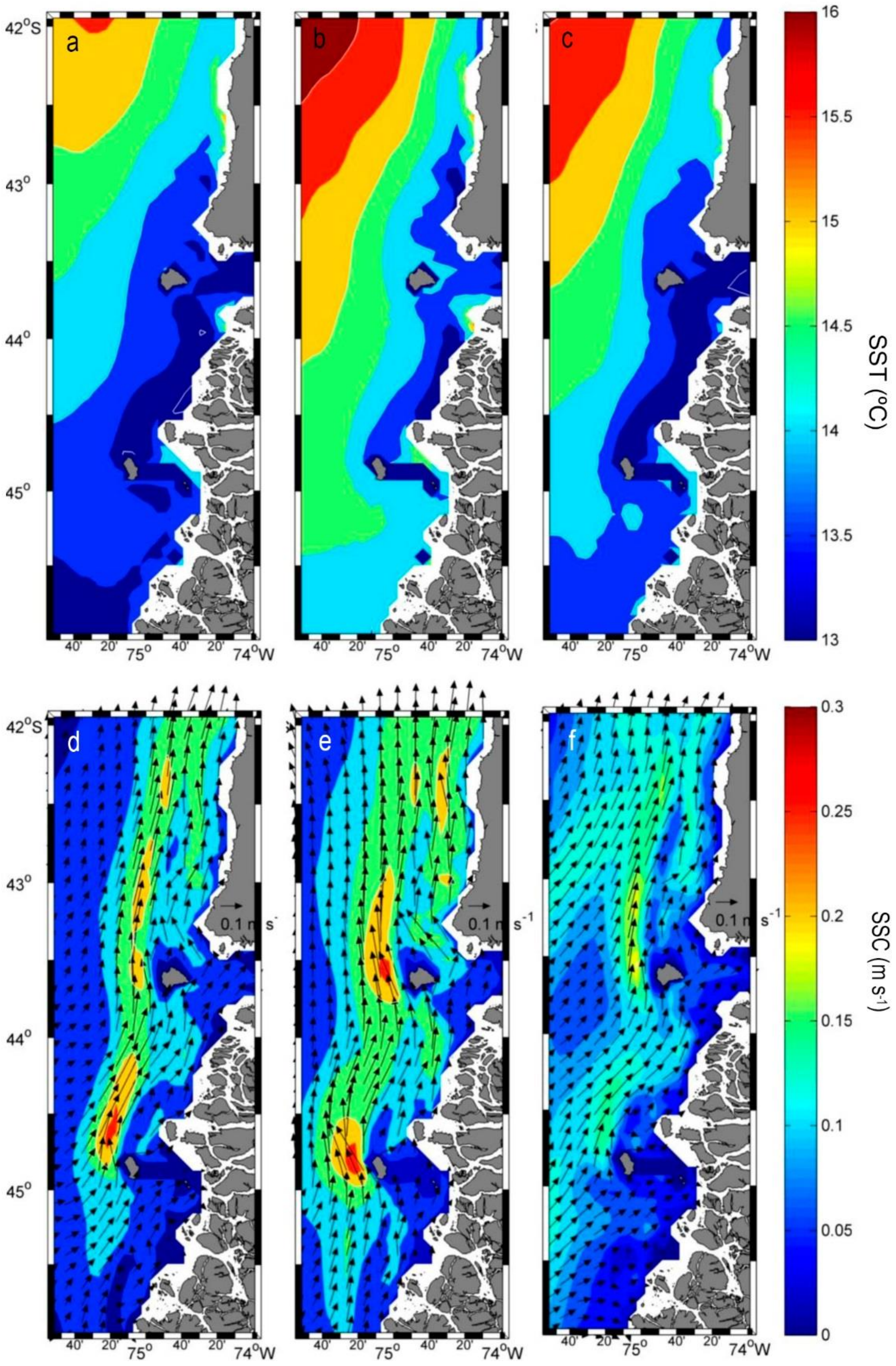

Figure 3. Climatology of sea surface temperature (SST) for a) January, b) February, and c) March and climatology of sea surface currents (SSC) for d) January, e) February, f) March, along the outer coast off Chiloé Island.

meridional currents were weaker and more homogeneous (0.05-0.15 m s^{-1}) with a slight increase in speed close to the continent (Fig. 3f). As in January, a branch of cold water was projected to the ISCh, through the Guafo Passage.

Large scale offshore SST anomalies and currents prior to and during outbreaks in austral summer 2010

During January 2010 the oceanic region off Chiloé Island and the fjord region experienced a cooling in relation to its climatology (Figs. 4a, 5a). South of the Guafo Passage a decrease of *ca.* 0.5ºC was observed, while positive anomalies were mainly located in the northern region close to the coastal environment. Sea surface currents during this month displayed a wider predominance of shoreward zonal currents (Fig. 4d), which deflected to the north as they approached the continent. Meridional currents along outer Patagonia displayed a similar spatial trend, while slowing down in relation to its climatology. During February, the entire area exhibited a decrease in SST (Fig. 4b) and sea surface currents (Fig. 4e). Offshore negative SST anomalies reached as low as -1.5ºC, covering almost the entire south western area. The rest of the area experienced an SST drop of 0.5 and 1ºC. Concomitant to the decrease in SST a significant decrease in offshore current was observed. Meridional surface currents decreased to less than 0.05 m s^{-1} in the oceanic region, while currents close to the coast and interior of the Guafo Passage did not change significantly with respect to the climatology (Figs. 4b, 4e). Zonal currents were weak, always heading north, similar to climatologically conditions. During March, conditions tended to stabilize; SST showed a slight decrease of 0.5ºC over the entire area, while currents remained close to that which can be expected for this month (Figs. 4c, 4f).

General scenario in the ISCh (Ancud Sound) prior to and during salp outbreaks in summer 2010

On an annual time scale, temperatures displayed a typical seasonality with maximum values during austral summer (14-13ºC, January to March) and a continuous decline from autumn to winter, with minimum SST during July and August (9.8ºC) (Fig. 5a). Subsequently, temperatures started to rise during spring through to summer. Surface Chl-*a* however presented a more variable cycle during the year and is partially decoupled with temperature (Fig. 5b). High concentrations of Chl-*a* were typically observed in austral autumn rather than in summer. During January and February (austral summer), Chl-*a* concentrations fluctuated around 10 mg Chl-*a* m^{-3}, March and April being the months with the highest satellite Chl-*a* concentrations (~13.5 mg Chl-*a* m^{-3}). Usually after May there is a substantial drop of one order in magnitude in Chl-*a* (10.5 to 0.9 mg Chl-*a* m^{-3}) when it reaches its lowest value along the annual cycle (Fig. 5b).

During 2010, SST in the Ancud Sound experienced the similar annual drop as that seen offshore, although in a more restricted range. During January, SST and satellite derived Chl-*a* were close to their historical mean (14.1ºC and 10 mg m^{-3}, respectively). However, during February the basin experienced a significant cooling of 1ºC in relation to its historical mean and 0.7ºC below standard error (Fig. 5a). This drop was not followed by any significant change in Chl-*a* concentration, which increased slightly during this month. After this event, temperatures rose again to "normal" conditions while chlorophyll experienced a substantial drop from normal values of 13.5 to 4 mg Chl-*a* m^{-3} (Fig. 5b). After this drop, Chl-*a* did not recover and remained low throughout the entire year. Unfortunately during June, satellite images could not be obtained due to cloud cover (Fig. 5b).

Time series of phytoplankton functional groups in the four major regions in the ISCh

Throughout the annual cycle, the three basins and Desertores Islands were dominated by chain forming diatoms such as *Chaetoceros* spp., *Skeletonema* spp. and *Thalassiosira* spp. In the austral spring and summer (September to May), these species tend to form blooms, especially in the three largest regions (Ancud Sound, Desertores Islands and Corcovado Gulf) while the Reloncaví Sound has a less marked seasonality with sporadic autumn and winter blooms (Fig. 6). Phytoplankton cell concentrations show a north to south gradient with higher concentrations in the Reloncaví and Ancud sounds, declining in the Desertores Islands. This region functions as a barrier between the highly productive northern Ancud Sound and the southern Corcovado Gulf, where the lowest phytoplankton abundances were measured.

A marked reduction in phytoplankton spring bloom in 2010 was evident in the Ancud Sound, Desertores Islands and Corcovado Gulf, in which phytoplankton abundance decreased down to half of what was later recorded in 2011, with no evident change in species composition between years. From May through September 2010, there was a marked reduction in abundance of large phytoplankton cells at Reloncaví Sound, during which small cell numbers of the genus *Chaetoceros* and other less representative algae's dominated. During 2009 the Ancud Sound experienced an unusual extension for *ca.* two months of this less productive phase due to the early decline of the summer bloom and coincided with a drop in cell abundance which lasted until the end of 2010. The Ancud Sound experienced a massive bloom of small flagellates *Tetraselmis* spp., during the end of spring 2009 and beginning of summer 2010, just after the last recorded outbreak of *I. magalhanica* in 2010.

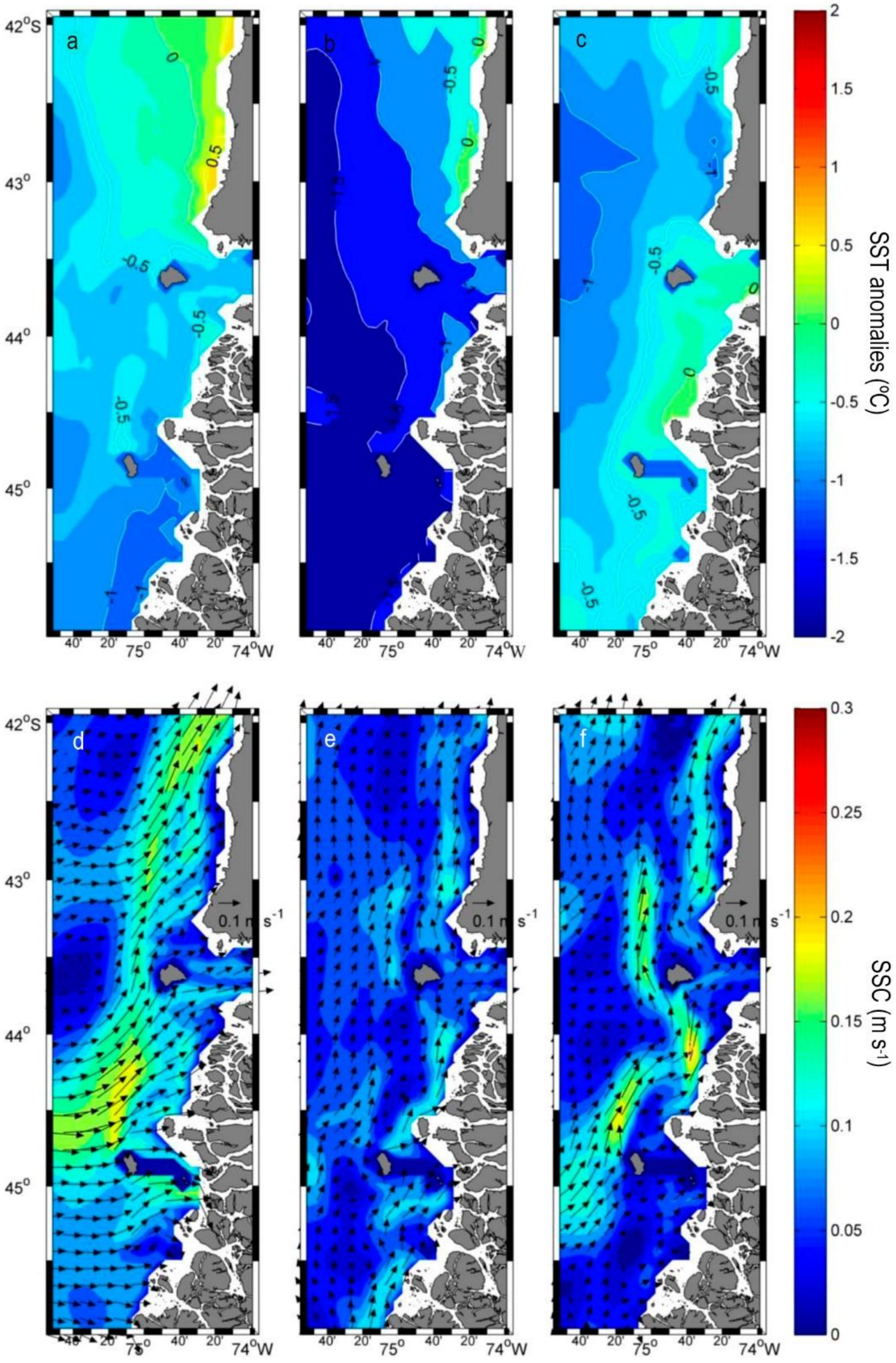

Figure 4. Mean monthly sea surface temperature anomalies (SST) during a) January, b) February and c) March 2010, and sea surface currents (SSC) recorded during d) January, e) February and f) March 2010 along the outer coast off Chiloé Island.

Ihlea magalhanica sampling and analysis

Huelden (Ancud Sound)

Zooplankton samples taken during the first outbreaks in Huelden (5 September 2010), were low in salp abundance compared to the outbreaks reported during the austral summer by local salmon farmers at the same location almost three weeks later. The total abundance of aggregate and solitary forms reached up to 1.13 ind m^{-3} (Fig. 7a) and were dominated by aggregate individuals (93% of the total population) as expected.

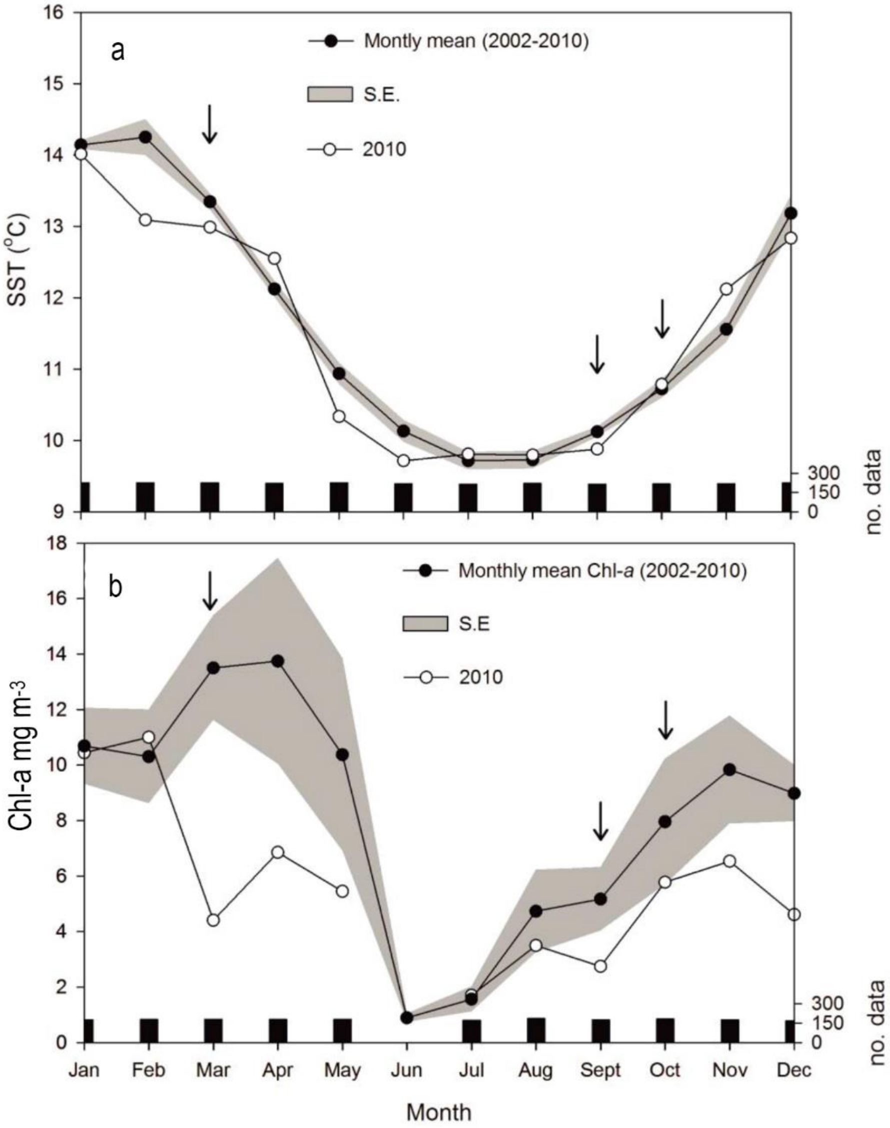

Figure 5. a) Monthly mean climatology (black dots) and standard error (grey area) of SST, compared with monthly mean SST (white dots) recorded during 2010 in Ancud Sound, b) monthly mean climatology (black dots) and standard error (grey area) of satellite Chl-*a*, compared with monthly mean satellite Chl-*a* (white dots) recorded during 2010 in Ancud Sound. Black arrows indicate months in which *Ihlea magalhanica* outbreaks were recorded. Vertical bars denote number of pixel counts used to compute mean values of SST and Chl-*a* in monthly averages during 2010.

The size of the aggregate phase was of 7.7 ± 5.3 mm in length (mean ±; n = 79) while small buds (~1 mm length) which were not considered for the abundance counts, represented 31% of total measured individuals. Solitary forms were only collected at stations 1 and 2, with a mean size of 22 ± 4 mm (mean ± SD; n = 6). The total abundance was higher at the two stations located close to the coast with 0.9-1.13 ind m^{-3}. These stations experienced a sharp decline of Chl-*a* (Fig. 7a) associated with the decline of flagellates, which were the dominant microplankton group in all stations with over 58% of the total abundance (mean 64%) (Fig. 7b).The main contributors (over 98.7%) to flagellate abundance were small sized (<20 µm) loricated flagellates, followed by small (<20 µm) naked dinoflagellates (0.5%), *Gonyaulax* spp. (0.4%), *Diplopsalis* spp. (0.3%) and others (0.1%). Diatoms, coccolitophores and ciliates did not show any apparent change in their relative abundances that could be associated with changes in salp abundance (Fig. 7b).

Twenty days after this event and in this same location, a massive outbreak of *I. magalhanica* took place (Fig. 7b). Abundance on this occasion was around 10,000 ind m^{-3} in the first 3 h after the first measure-

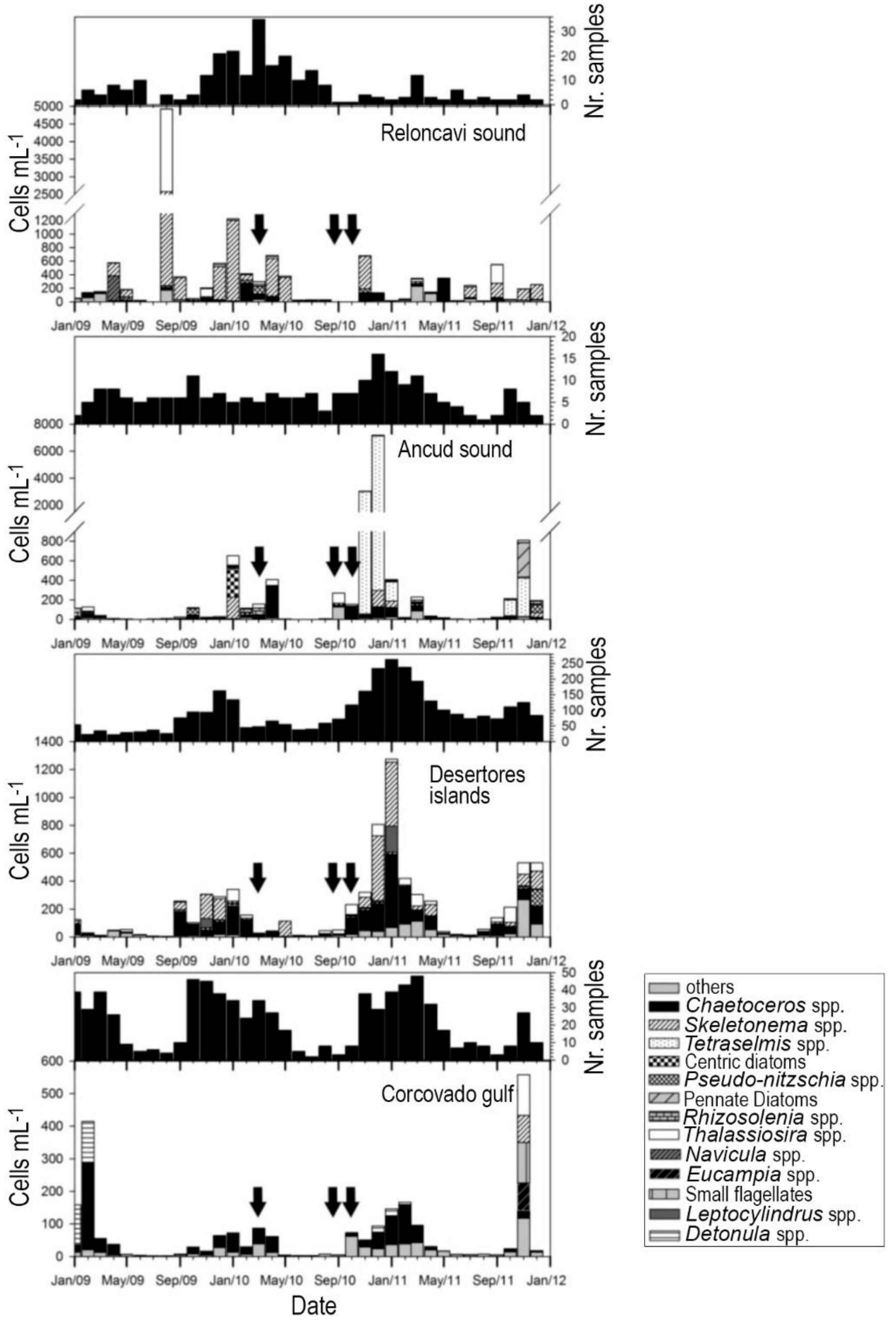

Figure 6. Average (2009-2011) of monthly time series of abundance of the dominant phytoplankton (cells mL^{-1}) of the upper 20 m water column along the four major basins in the ISCh. Black bars above each graph indicate the number of samples collected per month in each basin, used to calculate the monthly mean values while arrows show months in which *Ihlea magalhanica* outbreaks were recorded.

ments were taken. Afterwards, their abundance increased steadily over the next 21 h, reaching a maximum of 33,330 and 32,000 ind m^{-3} at 21:30 and 24:00 on 25 September 2010, respectively. This drastic increase is most likely a result of aggregation rather than reproduction taking into account the rapid increase in just a couple of hours. Consecutive changes in abundance were of great magnitude, increasing/decreasing approximately 4-fold in a range of just 3 h. These temporal oscillations in abundance were coupled with the tidal phase. The highest abundances usually recorded in periods of tidal rise, while decreases were observed during the ebbing tide (Fig. 7c). The zooplankton samples were taken from a salmon cage facing towards the inner sea, and therefore, observed increases are mainly a result of the aggregation and clo-

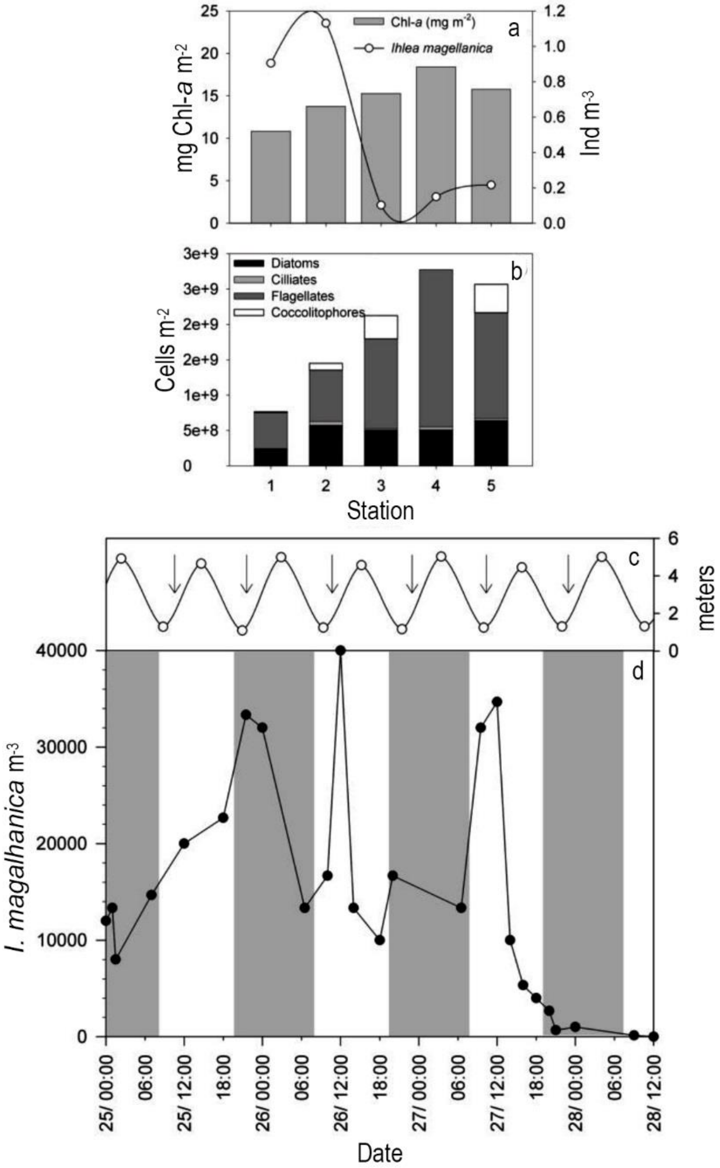

Figure 7. a) *Ihlea magalhanica* abundance (ind m^{-3}) collected at Huelden stations during 5 September 2010, and chlorophyll concentration (mg Chl-*a* m^{-3}), 2.5 km perpendicular to the coast transect, b) abundance of main groups of phytoplankton (cells m^{-3}) along the off shore transect, c) tidal height during massive *I. magalhanica* outbreak in Huelden bay between 25 and 28 September (source http://www.shoa.cl), d) *I. magalhanica* abundance (ind m^{-3}) recorded by salmon farmers between 25 and 28 September. Grey areas indicate night time samplings.

gging of salps in salmon farm nets during the rising tide. While during the ebbing tide, salps were transported towards to the inner sea, reducing abundance significantly close to the farm. This outbreak lasted for almost three days after the first observations, reducing gradually on the afternoon of the third day. By the fourth day no noticeable abundances were recorded by the salmon farmers, therefore sampling was terminated. Potential relationships between the abundance of organisms and the diel cycle were not observed which lead us to discard changes in abundance due to vertical migrations.

Reloncaví Sound

The *I. magalhanica* abundances recorded between July and November 2010 show a clear outbreak event in the Reloncaví Sound. While from July to August no individuals were collected. During September the first appearance of salps were observed with a large predominance of adult and young solitary forms, which are both close to the abundance of aggregate individuals

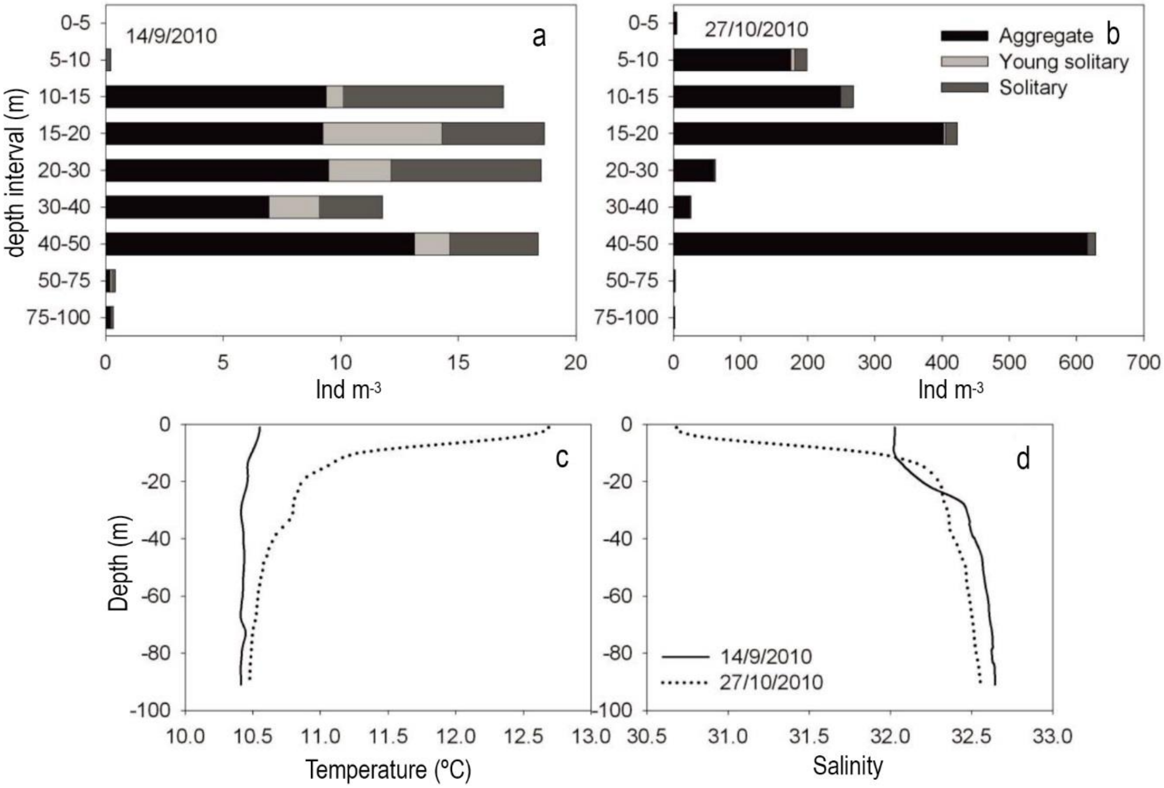

Figure 8. Abundance and vertical distribution of *Ihlea magalhanica* reproductive life stages at the Reloncaví Sound during: a) September and b) October 2010. Vertical distribution of temperature: c) and salinity, d) during both sampling periods.

(aggregate/solitary mean ratio of 2.1) (Fig. 8a). Salps showed low abundance at surface (<0.23 ind m^{-3} in the 0-10 m depth stratum), and increased sharply up to 18.5 ind m^{-3} below a depth of 10 m where salps were distributed almost evenly down to a depth of 50 m (Fig. 8a). Their abundance declined again sharply to less than 0.4 ind m^{-3} below 50 m. One and a half months later (mid November), a new massive outbreak took place (up to 628 ind m^{-3}, Fig. 8b), in which a change to their relative reproductive life cycle phase contribution occurred as depicted by the decrease in the relative abundance of solitary forms to levels similar to those previously recorded in Huelden, and the aggregate phase dominated overall (aggregate/solitary mean ratio of 18.8).

Vertical distribution was uneven with low abundance on the surface and a steady increase from 200 ind m^{-3} at the 5-10 m stratum up to 422 ind m^{-3} at the 15-20 m depth stratum (Fig. 8b). Under this depth range, there was a region (20-40 m depth) that showed a decline in abundance and then an abrupt increase in the 40-50 m stratum, coinciding with the higher abundance recorded at this station (628 ind m^{-3}). Finally, below this stratum abundances decreased down to 0.2 ind m^{-3} from 50 to 100 m depth; following the same pattern observed in September. In parallel with the observed changes in salp abundance, the hydrographic characteristics at the Reloncaví Sound also changed significantly from September to October 2010 (Figs. 8c, 8d). During September, a vertical quasi-homogeneous thermal distribution (10.4ºC) was found (Fig. 8c) with a weak saline gradient, forming a fragile halocline at a depth of 25 m (Fig. 8c). In October, a strong vertical thermal and haline gradient was formed with low salinity (30.6) and a high temperature (12.7ºC) at surface, decreasing sharply at 20 m where the base of the mixed layer is formed (Figs. 8c, 8d).

DISCUSSION

The Patagonian fjord offshore region is influenced by the eastward flow of the SPC, which reaches the coast of South America at ~45ºS were it deflects, forming the Cape Horn Current to the south, and the Humboldt Current to the north. Part of the SAAW near the coast enters at subsurface depths (see below) to the ISCh through a narrow 2 km, 150 m deep channel (Chacao Channel, 42ºS) to the north of Chiloé Island, and the Guafo Passage (43.5ºS), a 37 km wide channel with an entrance at sill *ca.* 150 m depth (Silva *et al.*, 1995). SAAW

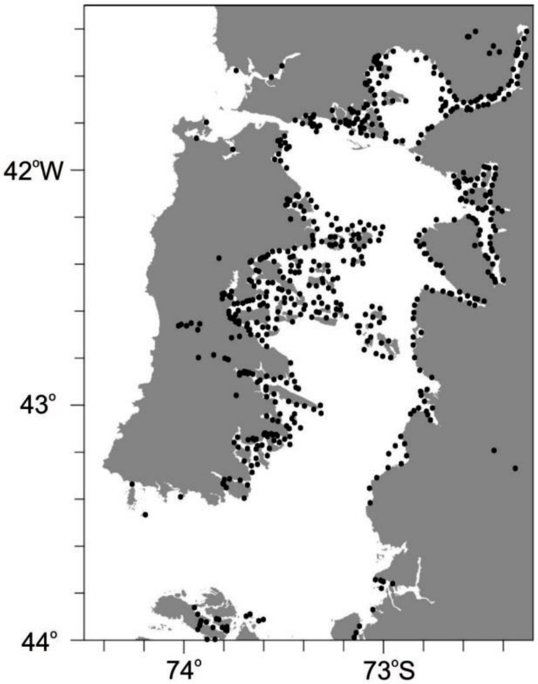

Figure 9. Salmon farm concessions granted until September 2009. (Source: Subsecretaria de Pesca, 2009).

which enters through the Guafo Passage has a low salinity signature (~33, Palma & Silva, 2004), derived from the northward costal transport of fresh water discharges along the fractured coast line from 47 to 43ºS (Dávila *et al.*, 2002). This low salinity water mass, results from the mix of SAAW and Estuarine Water (EW), which forms the Modified Subantarctic Water (MSAAW). The general circulation pattern through the Guafo Passage is an offshore outflow of MSAAW at the surface (upper 25 m) and an inflow of SAAW at depth (25-110 m) (Palma & Silva, 2004). Thus the entrance of subantarctic species into the ISCh under normal conditions should occur at the subsurface. However, during some episodic events such as those observed during January 2010, a change in the circulation pattern associated with the intensification of zonal currents can cause a massive entrance of SAAW into the ISCh, as revealed by a temperature drop in the Guafo Passage and around the ISCh from January to February 2010 (Fig. 4e). This intrusion was most probably responsible for the transport of oceanic subantarctic species, such as *I. magalhanica* into this coastal semi enclosed habitat.

The ISCh is geographically divided into three clearly defined sub-basins (Tello & Rodriguez-Benito, 2009): (1) the northern one being the Reloncaví Sound, a semi enclosed system influenced by a strong silicic-acid-rich freshwater input and strong stratification in the upper 4-7 m. Beneath this layer, a strong nutricline develops isolating the lower SAAW, nutrient-rich (nitrate and orthophosphate) water (Silva *et al.*, 1998; González *et al.*, 2010). The particular geographical structure of the ISCh, *i.e.*, being split into three sub-basins, allows for the development of high numbers of large chain-forming diatom blooms which (see Fig. 6), are not only limited to the austral spring and summer seasons but are also frequent in winter and autumn. (2) The central sub-region (Ancud Sound) is a larger basin with less intense haline stratification and a seasonal production coupled with the light regime, supporting a rich phytoplankton biomass, largely dominated by large chain-forming diatoms (Fig. 6, González *et al.*, 2010). (3) The southernmost basin (Corcovado Gulf) is separated from the middle basin (Ancud Sound) through a string of islands (Desertores Islands). The Corcovado Gulf connects with the Pacific Ocean through the Guafo Passage, where the SAAW mixes with fresh waters coming from rivers, generating a lower salinity water mass (31 to 33, Silva *et al.*, 1998). The entire area between Desertores Islands and up to the Corcovado Channel is less productive than the enclosed northern and central basins, while a clear seasonality is still observed (Fig. 6, Lara *et al.*, 2010).

Proliferation of salps were only recorded in the Reloncaví and Ancud sounds, north of Desertores Islands, while no records were registered in the Corcovado Gulf, despite several salmon farms existing in this region that might have documented the event (*ca.* 170 fish farms, Fig. 9). Why the salp outbreaks developed exclusively in the northern innermost basins is not yet clear. One possible hypothesis is that the Desertores Islands may function as a natural barrier, creating a retention area for planktonic organisms, by limiting the circulation and dispersal of organisms across the central and southern basins while providing a suitable area for aggregation and development, as sugested by Tello & Rodriguez-Benito (2009). Salp outbreaks, such as those observed in this study, occur explosively, facilitated by their direct development and release of progeny at relatively large sizes, high growth rates and short generation times as the reported for other salp species such as *Thalia democratica* (Madin & Purcell, 1992; CIESM, 2001). A drastic increase in abundance was observed in September 2010 at the station located at the Ancud Sound, where tens of solitary forms were collected initially, while at the end of October, six weeks later, abundances reached up to 600 ind m^{-3}, mainly dominated by aggregates, indicating that this species is most likely capable to complete its life cycle in the ISCh. The absence of salps, during the months before or after the outbreaks, are not necessarily a result of a lack of reproduction over the entire area but most likely related to the patchy

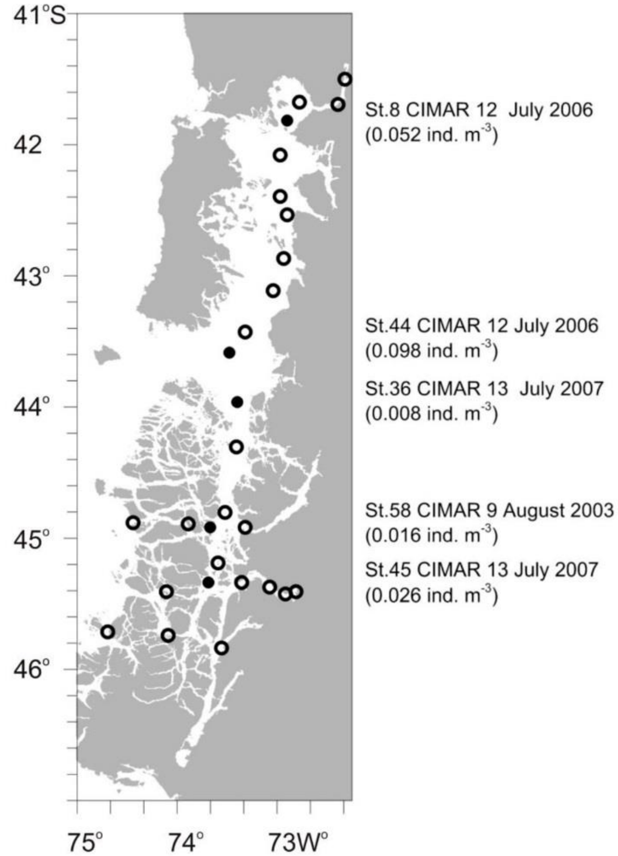

Figure 10. Inner Sea of Chiloé locations where salp abundance was detected. Information was compiled from samplings carried out during CIMAR Cruises 9, 12 and 13. Filled circles show areas where salps were recorded, while open circles represent areas where salps were absent. Numbers in the legends indicate salp density (ind m^{-3}).

distribution of this event. The fast increase and in most cases short persistency of the outbreaks in a particular area makes it extremely difficult to follow and almost impossible to predict. Thus, most of the warnings we received could not be properly investigated and upon our arrival (one to two days after warnings) the salps had already gone.

Reports of salps in Patagonia are scarce and usually include numbers less than 0.052 ind. m^{-3} (Fig. 10). These have only been recorded during winter time and have been absent during spring and summer. Thus, the outbreaks during 2010 are the highest recorded for this group of species to date and occurred in summer and spring. The first large-scale outbreaks were recorded in late February 2010, a situation in which the ISCh offshore and inshore temperature showed strong negative anomalies (-1.5ºC) and a month later accompanied by Chl-*a* concentrations well below the historical averages expected for this region (Fig. 5b). The reason why outbreaks did not developed in the past is unknown, despite of the presence of salps in this region in previous years and that intensive aquaculture established since the 1990´s. Prior recorded abundances of salps in the ISCh were usually low, probably limiting a successful reproduction, which leads to assume that the intrusion of SAAW might have transported an already developed outbreak into the ISCh.

The potential effect on the phytoplankton community in the ISCh might be considerable when taking into account that they filter continuously throughout the day and also that each salp may display very high filtering rates as in the case of *Pegea confoederata* that can exert grazing pressure equivalent to that of several hundreds of large calanoid copepods (Harbison & Gilmer, 1976) considering that the filtration rate is not known for *I. magalhanica*. This is especially relevant given the high concentrations recorded of up to 654,000 salps m^{-3} close to coastal net pens and 600 ind m^{-3} in the more open systems in the Reloncaví Sound.

Accordingly, the effect of the salp outbreaks on the ISCh pelagic food web might be considerable taking into account the drastic decrease in phytoplankton cell abundance and Chl-*a* biomass. If this decrease was mainly result of grazing we also might expect a substantial export of organic carbon out of the photic zone via fecal pellets. Salps are able to filter on a wide size range of particles above 0.1 µm, which results in an aggregation of small particles into large and fast sinking fecal pellets. Sinking rates of salp fecal pellets range from between 59 up to 2238 m d^{-1} (Bruland & Silver, 1981; Madin, 1982), which implies an extremely efficient export of organic matter and nutrients from the upper water column down to the benthos.

Massive sinking events of fecal pellets and senescent bodies during salp outbreaks have been previously reported in other regions (Bathmann, 1988). On that occasion, salps with an abundance more than 700 ind m^{-3} were able to deplete surface nutrients by exporting organic matter and nutrients out of the photic zone off the coast of Ireland. This process could explain why phytoplankton was not able to recover its biomass over several months after the first outbreaks in the ISCh. The only phytoplankton species which showed an unusual increase were small flagellates, which are capable of migrating through the water column to the nutricline and have lower nutrient requirements than diatoms because of their larger surface to volume ratio. On the other hand, the decrease in cell abundances of large, chain-forming diatoms (especially those equipped with long setae and protuberances) throughout 2010 would also favor the development of *I. magalhanica* growth, since large phytoplankton have shown to be deleterious to filtering activity, causing clogging of feeding structures (Harbison *et al.*, 1986).

Gelatinous species with short generation times such as ctenophores (Sullivan *et al.*, 2001) siphonophores (Pagès *et al.*, 2001) and pelagic tunicates (Purcell & Madin, 1991), have the ability to make use of aggregation for reproductive purposes to maintain and/or increase their population density. In this study, field observations indicated that salmon net pens can effectively act as a physical barrier to salp movement, promoting the clogging, increasing local salp aggregations. Thanks to short generation times, these massive aggregations along salmon net pens have the potential to increase reproductive encounter rates, which can result in a highly effective instrument to maximize reproductive success and promote outbreak formation (Heron & Benham, 1985).

Aggregations have generally been described by the presence of geological barriers (*i.e.*, shoreline and seafloor) and hydrographic (*i.e.*, horizontal fronts and vertical discontinuities) (reviewed by Graham *et al.*, 2001) or mesoscale eddies (Everett *et al.*, 2011). However, the effect of man-made barriers is less well documented (Purcell *et al.*, 2007; Doyle *et al.*, 2008; Baxter *et al.*, 2011; Mianzan *et al.*, 2014). The ISCh possess the majority of the country's salmon farms with over 500 fish farms along the ISCh coast (excluding fjords) (Fig. 10), thus the potential use of these structures as aggregation barriers to achieve a high reproductive success is enormous.

Effect on aquaculture

Warnings of high densities of salps close to salmon farms occurred seven times in 2010, while adverse effects were only recorded on one occasion. High salp density inside fish cages hamper normal fish feeding on food pellets, as observed in the guts of dead salmon collected from cages. The stomachs of these fish were entirely filled with salps, while gills were clogged by salp remains. Several salmon biopsies could not reveal the exact cause of death; however, veterinarians suggested that gill damage and the reduction of the oxygen diffusion due to clogging might be the primary cause of death.

Overall, Chl-*a* levels and cell density remained low throughout the entire year, which not only favored the persistence of salps (until the end of October) but also showed serious negative consequences for blue mussel farmers, who experienced decreased growth of adults and little settlement of juveniles in the following season (http://www.mundoacuicola.cl/comun/?modulo-=3&view=1&cat=1&idnews=341). Deleterious effect of gelatinous zooplankton on aquaculture has becoming increased attention in the last decades; which on one hand has being linked to climate-driven variability (Condon *et al.*, 2012) and to the proliferation of settlements and increased human activities in coastal areas (Purcell, 2012). The inner sea of Chiloé is not an exception, where proliferations of the scyphomedusa *Chrysaora plocamia* and *Phacellophora catschatica* have affected salmon farming installations (Palma *et al.*, 2007; Bravo *et al.*, 2011). Unfortunately, and as same as most cases, reports as same as impacts are mainly based on anecdotic information given by local farmers (see Mianzan *et al.*, 2014), and more reliable information based on scientific orientated approaches are extremely scarce. The random nature of the occurrence (spatial and temporal) basically associated to a complex life cycle and "r" strategy (Boero *et al.*, 2008), makes gelatinous zooplankton outbreaks very hard to follow.

Future

There is no clear evidence of which kind of remote forcing might have been involved during the intrusion of oceanic water into the ISCh, and whether it might increase/decrease in frequency in the future. There is however some hints from remote atmospheric anomalies that occurred during the end of 2009 and the beginning of 2010 which might have been partially responsible for the build-up of this scenario which favors the intrusion of SAAW into the northern ISCh.

In the last few decades it has become evident that climate variability in the southern hemisphere is mainly forced by the variability on timescales from intra-seasonal to interannual by the Southern Annular Mode (SAM), which is characterized by a large scale alteration of atmospheric mass between mid and high-latitudes; modifying the latitudinal distribution of the westerly winds. Positive SAM is associated with a significant increase in SST in the Subtropical Zone (STZ) (Lovenduski & Gruber, 2005), while inverse patterns occur during negative anomalies (Hall & Visbeck, 2002).

Positive anomalies usually persist throughout all seasons, but are strongest during the austral summer (Marshall, 2003). During the austral summer 2010, an unusual negative SAM was documented (Fig. 11) coinciding with strong negative SST anomalies at the outer Patagonian region. If this anomaly triggered the entrance of *I. magalhanica* to the ISCh, two processes must have occurred simultaneously to achieve these outbreaks. First we would need a substantial transport of SAAW towards to the coast, which ultimately must carry enough organisms to facilitate a successful reproduction to generate an abundant offspring. The achievement of these two conditions makes these scenario relatively improbable phenomena to occur on

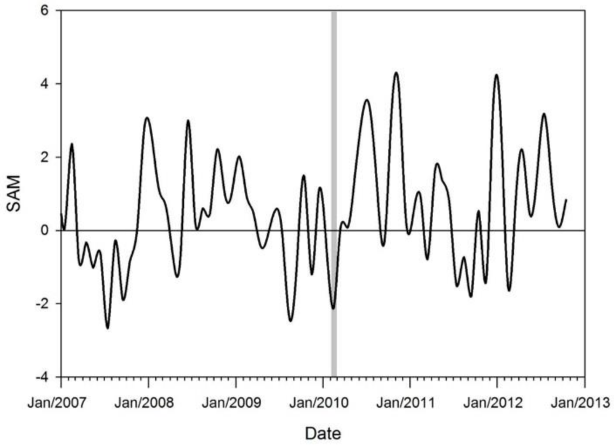

Figure 11. Marshal re-analysis of the Southern Annular Mode (SAM), time series between January 2007 and August 2010. Grey area indicates the month where first outbreaks and negative temperature anomalies were recorded in the fjord region. Data obtained from http://www.nerc-bas.ac.uk/icd/gjma/sam.html.

a regular basis. The exact mechanism controlling the coupling between climate forcing and zooplankton outbreaks needs further study and many questions remain unanswered. Examining the role of the meridional circulation across the Southern Pacific and the advection of oceanic water masses into the ISCh and its relation to remote forcing such as the SAM variability might help to unveil some of these answers. Additional modeling work, both regionally and globally, can help to demonstrate biological and physical coupling and allow potential predictions on changes in productivity and help to anticipate potential invasions.

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