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Variabilidad estacional e interanual de la estructura comunitaria de copépodos y biomasa mesozooplanctónica en la zona de surgencia de Chile centro-sur

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RESUMEN

"Variabilidad estacional e interanual de la estructura comunitaria de copépodos y biomasa mesozooplanctónica en la zona de surgencia de Chile centro-sur"

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La región costera de Chile centro-sur es caracterizado por ser una de las áreas más productivas a nivel mundial, cuya productividad biológica se sustenta principalmente por la surgencia costera. En los últimos años se ha observado que la zona costera ha estado sujeta a una condición esencialmente fría, producto del incremento de la surgencia costera en la zona, lo cual provoca una fuerte variabilidad en las condiciones físicas y químicas de la columna de agua. Estos cambios de largo plazo pueden inducir modificaciones en las comunidades zooplanctónicas, afectando a los ecosistemas marinos en términos de diversidad y productividad. Estudios han revelado que organismos de niveles tróficos inferiores, como el zooplancton, pueden ser utilizados como grupo centinela que reflejan los cambios en ecosistemas marinos y proporcionan los primeros indicios de las respuestas biológicas frente a la variabilidad climática. El zooplancton está compuesto por organismos de ciclos de vida corta, muy sensibles a los cambios ambientales, los cuales pueden responder rápidamente, en términos de abundancia y composición, a cambios de las variables bio-oceanográficas clave tales como, temperatura, cantidad y calidad de alimento, estratificación y oxigenación de la columna de agua y en la circulación de las masas de agua. Esta tesis estudia los cambios estacionales e interanuales de la biomasa zooplanctónica y de la estructura comunitaria de copépodos (diversidad y abundancia) frente a la variabilidad de la surgencia costera en la última década frente a Chile centro-sur. Se plantea como hipótesis de trabajo que el incremento de la surgencia costera inducida por el viento sobre una ventana de tiempo de 10 años ha modificado significativamente la estructura comunitaria del grupo Copepoda en la zona costera de Chile centro-sur. Estas modificaciones se pueden reflejar en cambios en la biomasa total del zooplancton, abundancia de algunas especies, abundancia total, índices de diversidad específica, o cambios en la dominancia.

Los cambios en la estructura comunitaria de copépodos fue estudiada en dos periodos de tiempo, 2002-2004 y 2010-2012 y para el estudio de la biomasa zooplanctónica se consideraron los 10 años de la serie de tiempo, 2002-2012. Se identificaron 74 especies de copépodos de los cuales el Orden Calanoida estuvo representado por un 68% del total de especies. Las especies dominantes fueron *Paracalanus indicus*, *Oithona similis*, *Calanoides patagoniensis*, *Drepanopus forcipatus* y *Acartia tonsa*. Para el primer y segundo periodo, hubo cambios significativos en la abundancia y dominancia de las especies. *P. indicus* fue numéricamente desplazado por *D. forcipatus*, el cual incrementó sus abundancias y dominó en el periodo 2010-2012. También hubo una disminución significativa en la abundancia total de copépodos hacia el periodo más reciente, así como cambios en la estructura de tamaños. La biomasa mesozooplanctónica total (BM) fluctuó entre 0.07 y 60 g peso seco m^{-2}. Se observaron dos máximos anuales en BM, uno en primavera (noviembre) y otro en otoño (mayo) pero no se encontraron diferencias significativas entre periodos de surgencia y no surgencia. Sin embargo, hubo una fuerte variabilidad interanual en la BM, con mayores valores en el periodo 2002-2003, y mucho menos hacia el final de la serie en 2010-2012. También hubo una tendencia lineal negativa significativa en la BM a través del tiempo, la cual puede ser explicado por la disminución en la abundancia de copépodos, los cuales representan el 80-90% de la abundancia total de zooplancton en la zona. Las condiciones oceanográficas revelaron condiciones más frías para la columna de agua y más salinas y densas en la capa superficial para el último periodo (2010-2012) posiblemente causado por el aumento en la duración de la surgencia costera y disminución de la estratificación (ϕ). Nuestro estudio sugiere que las alteraciones en las condiciones de surgencia costera inducido por aumento en intensidad y duración de los vientos meridionales favorables a surgencia es una fuerza impulsora de los cambios observados en la estructura comunitaria de copépodos y biomasa mesozooplanctónica durante una ventana de observación de 10 años. En este contexto, la tesis apoya la hipótesis planteada y concluye que el zooplancton puede reflejar importantes respuestas del ecosistema frente a condiciones alteradas en este sistema de surgencia altamente productivo.

ABSTRACT

"Seasonal and interannual variability of the zooplankton biomass and copepod community structure in the upwelling zone of Central/southern Chile"

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2013
Supervised by Dr. Pamela Hidalgo D.
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The coastal zone of Central/southern Chile is recognized as one of the most productive areas of the world ocean, whose biological production is induced by coastal upwelling. In recent years, some observations show that the coastal zone has been subjected to conditions essentially cool, as a result of increased upwelling. On a long run this increased upwelling can cause strong alterations in the physical and chemical conditions of the water column. Long-term changes in oceanographic conditions can induce modifications in the zooplankton community, affecting the whole marine ecosystem in terms of diversity and productivity. Previous studies have revealed that organisms at lower trophic levels, such as the zooplankton, can be used as sentinels to assess the changes in marine ecosystems and provides the first indications of biological responses to climate change. The zooplankton is comprised by short-lived organisms, highly sensitive to environmental change, and rapid responders to these changes in terms of abundance and composition. They can respond to quantity and quality of food, water column stratification and oxygenation, and circulation and water mass distribution. This thesis focuses on the seasonal and interannual changes in zooplankton biomass and copepod community structure (diversity and abundance) in relation to upwelling variability in the last decade off Central/southern Chile. The working hypothesis states that increased wind-driven during a 10-years window has significantly modified the copepod community structure in the coastal zone. These modifications are reflected in changes in total mesozooplankton biomass, abundance of some dominant species, total copepod abundance, diversity indexes and changes in dominance.

Changes in copepod community structure were studied for two time periods, 2002-2004 and 2010-2012, while zooplankton biomass was examined for the complete 10 years time series 2002-2012. 74 copepod species were identified of which the Calanoid order was represented by 68% of the species. Dominant species were *Paracalanus indicus*, *Oithona similis*, *Calanoides patagoniensis*, *Drepanopus forcipatus* and *Acartia tonsa*. From the first to second period there were significant changes in abundance and species dominance. *P. indicus* was numerically replaced by *D. forcipatus*, which incremented their abundance and dominance during the period 2010-2012. There was also a significant reduction in total copepod abundance in the more recent period and a significant change in community structure. Mesozooplankton biomass (BM) fluctuated between 0.07 and 60 g dry weight m^{-2}. There were two annual peaks in BM, one in spring (November) and another in autumn (May).When temporal variability is divided into upwelling and non-upwelling periods, no significant differences in BM were detected. However, there was a strong and significant interannual variation in BM with higher values in the period 2002-2003, and lower in recent years (2010-2012). Also, a negative, linear trend in BM was significant over the years, which can be explained by decreasing abundance of copepods, as they represent 80-90% of total numerical abundance of zooplankton in this zone. Oceanographic variables revealed a colder condition in the water column and more saline (only in near surface water) for the more recent period (2010-2012), possibly caused by increased in the duration upwelling and decrease of stratification (ϕ). This study suggest that alterations in upwelling conditions triggered by meridional wind have caused the observed changes in copepod community structure and mesozooplankton biomass during 10 years observation window. Therefore, the stated hypothesis is supported and it is concluded that zooplankton can indeed reflect ecosystem responses to an altered environment in this highly productive upwelling ecosystem.

1. INTRODUCCION

Los sistemas de surgencia costera son ecosistemas muy dinámicos y altamente variables en escalas temporales y espaciales (Freón et al. 2009). Se caracterizan por una fuerte variabilidad en las condiciones físicas y químicas (Hill et al. 1998), y en la variabilidad estacional e interanual, como es el caso del Sistema de Corriente de Humboldt (SCH) en el Pacífico Sur Oriental (Barber and Chavez 1986; Alheit and Bernal 1993; Thomas 1999; Hebbeln et al. 2000; Hidalgo and Escribano 2001; Ulloa et al. 2001). Los procesos de surgencia costera están continuamente aportando nuevos nutrientes a las capas superficiales, promoviendo altos niveles de biomasa fitoplanctónica y sustentando importantes pesquerías principalmente de pequeños pelágicos, siendo así, el SCH considerado como una de las áreas más productivas del mundo (Cushing 1990; Alheit and Bernal 1993).

En la región costera de Chile centro-sur (30-40°S) el ambiente es caracterizado por surgencia estacional que comienza en primavera y alcanza su intensidad máxima durante el verano, producto de los vientos predominantemente sur y suroeste. Este proceso promueve el ascenso a Aguas Subsuperficiales Ecuatoriales (ESSW), asociadas con bajas concentraciones de oxígeno disuelto y salinidades más altas que las aguas superficiales (Sobarzo et al. 2007). Junto con la variabilidad estacional, el SCH está sujeto a la variabilidad interanual impulsado principalmente por fases cálidas y frías del ENSO (El Niño Oscilacion del Sur) (Escribano et al. 2004), forzamiento atmosférico local, entradas de aguas continentales y condiciones de temperatura sobre la superficie del océano (Sobarzo et al. 2007). La variabilidad interanual parece estar muy bien conectado a la variación en la intensidad y frecuencia de los eventos de surgencia y a la posible duración de la temporada de surgencia cada año. Esta fuente de variabilidad puede determinar cambios importantes en términos de diversidad y productividad del ecosistema marino (Escribano and Morales 2012).

En los últimos años se ha observado que el ambiente marino ha estado sujeto a una condición esencialmente fría, con surgencia intensa y ausencia de eventos cálidos notables (Escribano et al. 2012). Se ha observado un enfriamiento regional, producto del incremento de la surgencia costera (Falvey and Garreaud 2009), la cual provoca el afloramiento de aguas más frías, más salinas, ricas en nutrientes y pobres en oxígeno a la superficie, provocando también el ascenso gradual del límite superior de la zona mínima de oxígeno (ZMO) (Escribano and

Morales 2012). Estos cambios de largo plazo, sean directos del ambiente físico-químico o indirectos (efectos tipo "top-down" y "bottom-up"), podrían inducir modificaciones en los componentes del zooplancton ya que éstos son fuertemente alterados por el cambio climático (Richardson 2008). Esta preocupación está siendo confirmada por varios estudios de largo plazo en distintas regiones del mundo en relación a la variabilidad climática (Beaugrand et al. 2002; Richardson 2008; Peterson et al. 2009; Mackas et al. 2010).

Los estudios en series de tiempo consideran actualmente al zooplancton como indicadores de gran relevancia para evaluar las respuestas de los ecosistemas marinos frente a la variabilidad climática (Beagraund et al. 2002; Richardson and Schoeman 2004; Richardson 2008; Mackas 2010). El zooplancton está compuesto por organismos de ciclos de vida corta, muy sensibles a los cambios ambientales, pueden responder rápidamente, en términos de abundancia y composición, a alteraciones en algunas de las variables clave, tales como la temperatura (Peterson 2006), cantidad y calidad alimentaria (Vargas et al. 2006), estratificación y oxigenación de la columna de agua (Gewin 2010; Seibel 2011) y en la circulación de las masas de agua (Keister 2009). Todas estas variables pueden verse alteradas por la variabilidad climática debido a la fuerte interacción entre el océano y la dinámica de la atmósfera (Sarmiento et al. 2011).

Consecuentemente, el zooplancton puede ser utilizado como un taxa centinela que refleja los cambios en los ecosistemas marinos, proporcionando los primeros indicios de respuesta biológicas a la variabilidad climática (Richardson and Schoeman 2004; Hays et al. 2005, Mackas et al. 2007). La biomasa y la estructura comunitaria de zooplancton es ciertamente un componente que puede verse afectado por los cambios oceanográficos inducidos por el clima en la zona de surgencia (Escribano et al. 2012). Estas alteraciones pueden afectar particularmente al grupo Copepoda que es reconocido por presentar respuestas rápidas a los cambios climáticos-oceanográficos (Beaugrand et al. 2003, Richardson 2008).

Estas respuestas, tales como cambios en la diversidad, abundancia y biomasa, han sido utilizadas para estudiar cambios de largo plazo en la composición y diversidad de especies (Beaugrand et al. 2000), cambios en biomasa y abundancia (Roemmich and McGowan 1995), y cambios en la estructura de tamaño y fenología (Richardson 2008; Mackas et al. 2012).

Es importante documentar las tendencias en biomasa ya que cualquier cambio ambiental puede impactar negativa o positivamente las especies del zooplancton, tal que la comunidad se modifique a través de cambios en la abundancia, diversidad o tamaño de las especies, esto puede ser muy relevante en el contexto de la productividad del ecosistema, debido a que son un componente clave en la trofodinámica del ecosistema pelágico (Beaugrand 2005) y puede influir en la disponibilidad de alimento para niveles tróficos superiores o al menos para alguna etapa de su ciclo de vida (Cushing 1997), esto además posee implicancias en el reciclamiento de bioelementos (C y N), con consecuencias climáticas también (Roemmich and McGowan 1995; Escribano et al. 2007).

En cuanto a la estructura comunitaria de copépodos, el grupo Copepoda fue utilizado como modelo de estudio ya que son los organismos más abundantes dentro del zooplancton marino en el sistema de surgencia centro-sur de Chile (36°S) (Escribano and Hidalgo 2000; Hidalgo et al. 2010, 2012). El estudio de la estructura comunitaria también puede ser utilizado como indicador de respuestas a los cambios ambientales (Perry et al. 2004), ya que muchas especies de copépodos son conocidas por ser especies indicadoras, cuya presencia o ausencia puede representar la influencia relativa de diferentes tipos de masas de agua (Hooff and Peterson 2006). A su vez, la diversidad es un parámetro biológico clave que influye en múltiples aspectos en la función y estructura del ecosistema (McGowan and Walker 1985; Hooper et al. 2005). La variación de la surgencia costera ha sido considerada un factor clave en la modulación de la diversidad de la comunidad de copépodos en zonas de surgencia (Hidalgo et al. 2012), sin embargo estudios de la composición de sus especies son escasos o se limitan a unas pocas especies, así el conocimiento básico sobre la diversidad de copépodos en esta región podría ser muy relevante para comprender de qué forma responden las distintas especies a los cambios ambientales.

En este estudio, se han examinado los potenciales cambios en la abundancia, diversidad y dominancia de especies de copépodos en respuesta a la variabilidad ambiental, a través de dos periodos de estudio (2002-2004 y 2010-2012), donde cada periodo cubre la variabilidad intraestacional, estacional e interanual del sistema de surgencia centro-sur de Chile, desde la Serie de Tiempo del Centro Oceanográfico del Pacífico Sur Oriental (COPAS) (www.copas.cl). Para el estudio de la biomasa zooplanctónica se consideraron los 10 años de la Serie de Tiempo (2002-2012), para evidenciar tendencias continuas de la variabilidad zooplanctónica a través de su contribución al sistema marino de la zona de estudio.

1.1 Objetivo General

Conocer la variabilidad que presenta el grupo Copepoda en su estructura comunitaria y biomasa mesozooplanctónica frente a los cambios en la variabilidad de la intensidad de la surgencia costera en la última década en Chile centro-sur.

2. HIPOTESIS Y OBJETIVOS ESPECIFICOS

Hipótesis

El incremento de la surgencia costera inducida por el viento sobre una ventana de tiempo de 10 años ha modificado significativamente la estructura comunitaria del grupo Copepoda en la zona costera de Chile centro-sur. Estas modificaciones se pueden reflejar en cambios en la biomasa total del zooplancton, abundancia de algunas especies, abundancia total, índices de diversidad específica, o cambios en la dominancia.

Objetivos Específicos

1. Caracterizar y comparar las condiciones oceanográficas y meteorológicas de dos ventanas de tiempo (2002-2004 y 2010-2012) en la zona centro-sur de Chile.

2. Determinar las variaciones estacionales e interanuales en la biomasa total del mesozooplancton en la Estación 18 de la zona centro-sur de Chile.

3. Comparar y revelar potenciales cambios en la estructura comunitaria del grupo Copepoda durante dos ventanas de tiempo (2002-2004 y 2010-2012) en la zona centro-sur de Chile.

4. Establecer relaciones entre la variabilidad oceanográfica asociada a la surgencia y los descriptores comunitarios del grupo Copepoda en la zona centro-sur de Chile.

3. MATERIALES Y METODOS

3.1 Área de estudio

La región de surgencia costera de Chile centro-sur (30-40°S) comprende la porción sur del Sistema de Corriente de Humboldt en el Pacífico Sur Oriental y exhibe un régimen fuertemente estacional, dominado por surgencia intensa durante primavera-verano y condiciones de hundimiento en otoño-invierno (Sobarzo et al. 2007; Escribano and Schneider 2007). Además presenta una amplia plataforma continental (~ 60 km) que es interrumpida por algunos cañones submarinos, cerca de Concepción (Figueroa and Moffat 2000). Las precipitaciones y ríos son importantes en esta región ya que contribuyen a la variación en la estructura de la columna de agua, con aguas de baja salinidad (< 33.8), las cuales pueden extenderse fuera de la costa (> 30 km) durante invierno y principios de la primavera (Sobarzo et al. 2007). El área costera es mayormente influenciada por las siguientes masas de aguas: Agua Superficial Subantártica (SAAW) y Agua Subsuperficial Ecuatorial (ESSW). Esta última asociada con la zona mínima de oxígeno (Escribano and Morales, 2012). El límite superior de la ZMO (≤ 1 ml O_2 L^{-1}) en esta región se encuentra a > 100 m de profundidad durante el invierno, y en verano puede llegar a < 25 m en la zona costera, asociada a la época de presencia e intensificación de los eventos de surgencia costera (Sobarzo et al. 2007). Esta región de surgencia se caracteriza por presentar una alta producción primaria (10 g C m^{-2} d^{-1}) (Montero et al. 2007), la cual sostiene las grandes pesquerías de peces pelágicos en la región (Arcos et al. 2001).

El Centro Oceanográfico del Pacífico Sur Oriental (COPAS) mantiene un estudio de Serie de Tiempo desde agosto de 2002 a la fecha, en la cual se muestrea mensualmente la Estación 18 (36°30.80'S -73°7.75'W) ubicada a 20 km de Dichato y a una profundidad de ~90 m sobre la plataforma continental (Fig. 1). El presente estudio considera el uso de muestras zooplanctónicas y de datos oceanográficos provenientes de la Serie de Tiempo COPAS (www.copas.cl).

Para el estudio de la biomasa zooplanctónica se analizaron 10 años de la Serie de Tiempo, desde el año 2002 al 2012. Para el estudio de la estructura comunitaria de copépodos la Serie de Tiempo fue analizada comparando dos periodos de tiempo, de dos años consecutivos cada uno; el periodo 1, comprende el periodo desde agosto 2002 hasta agosto de 2004 y periodo 2, comprende el periodo desde agosto 2010 hasta agosto 2012.

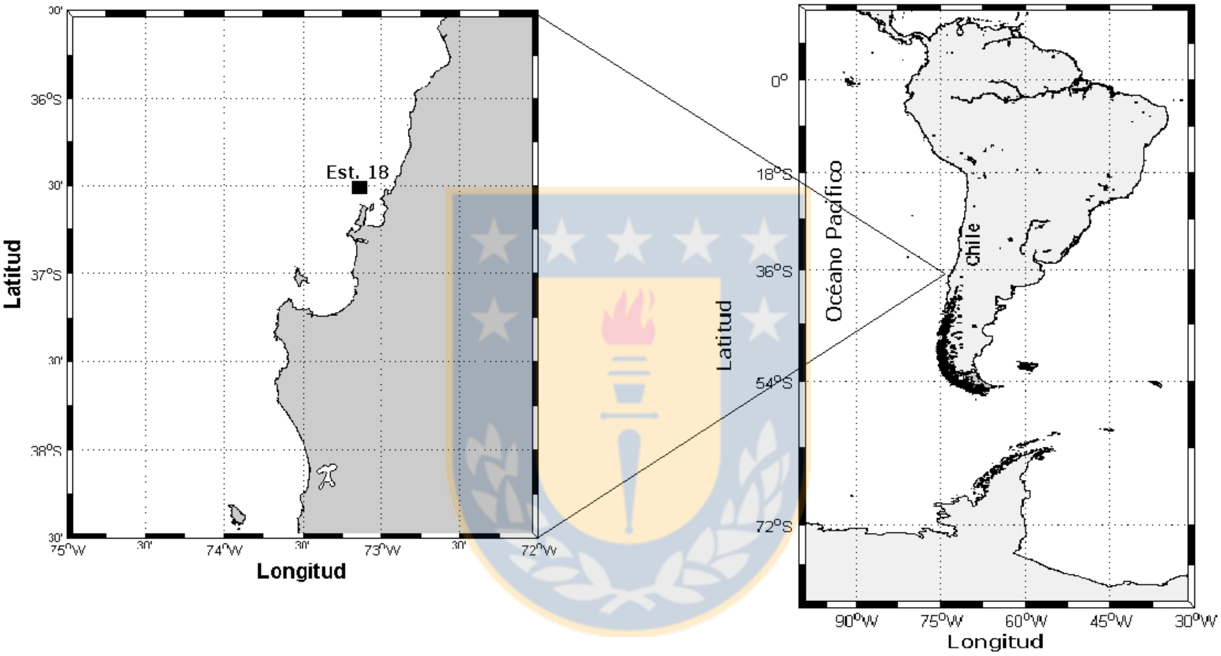

Figura 1. Región de surgencia costera frente a Concepción y estación de muestreo Estación 18 de la Serie de Tiempo COPAS, de la cual fueron obtenidos los datos oceanográficos y las muestras zooplanctónicas.

3.2 Obtención de datos bio-oceanográficos y muestras zooplanctónicas

La información de las condiciones de las variables bio-oceanográficas de la columna de agua fue obtenida durante los muestreos de la Estación 18, utilizando perfiladores autónomos tipo CTD SBE-25 o SBE-19 Plus, los cuales recolectan información de temperatura, conductividad, presión; además, están equipados con sensores de oxígeno y fluorescencia para obtener información del contenido de oxígeno disuelto y pigmentos fotosintéticos, respectivamente. Adicionalmente, agua de mar fue obtenida desde 9 profundidades (0-5-10-15-20-30-40-50-y 80 m) con una Roseta Oceanográfica o con botellas oceanográficas tipo Niskin de 10 L para estimaciones de concentración de clorofila-*a* por el método fluorométrico.

Las muestras de zooplancton fueron obtenidas mediante lances oblicuos diurno-nocturnos y estratificados (80-0 m, 80-50 m y 50–0 m), usando red Tucker Trawl de 1 m^2 de área de boca, provista con malla de 200 µm, equipada con un flujómetro para estimar el volumen filtrado por la red durante la recolección de los organismos. Las muestras de zooplancton fueron inmediatamente divididas a bordo, una fracción (1/4 o 1/2 de la muestra original) fue separada y congelada (-20°C) para estimar biomasa en peso seco y el resto de la muestra fue preservada en una solución de formalina neutralizada al 4% para el posterior análisis de composición. Para obtener el peso seco, las muestras fueron descongeladas y filtradas en filtros de fibra de vidrio GF/C previamente pesado, luego son secadas por 24 h a 60°C y pesados nuevamente, para obtener la biomasa zooplanctónica en unidades de gramos de peso seco en un metro cuadrado (g Peso Seco m^{-2}).

Para el análisis de composición de especies se identificaron y contabilizaron en detalle las especies del grupo Copepoda de las muestras recolectadas durante el día desde los 80 a 0 m. La identificación de especies se realizó con el apoyo de referencias bibliográficas especializadas (Rose 1933, Bradford-Gieve et al. 1999, Razouls et al. 2005).

3.3 Análisis de datos

Los datos oceanográficos obtenidos fueron procesados para describir las condiciones de surgencia y los patrones físicos y químicos sobre la escala temporal de la columna de agua de la Estación 18.

Se determinó el Índice de Surgencia para analizar la variabilidad temporal de la intensidad de la surgencia. Para esto, se utilizaron los índices mensuales de surgencia estimados por la National Oceanic and Atmospheric Administration (NOAA), del proyecto Reanalysis NCEP/NCAR de la Physical Sciences Division (www.esrl.noaa.gov/ psd/data/reanalysis), derivados desde los cambios en los campos de presión atmosférica sobre el nivel del mar, a través del Índice de Bakun (Bakun 1973).

Se estimó la Estratificación de la columna de agua (ϕ), utilizando los valores mensuales de temperatura y salinidad, para determinar los perfiles de densidad (Sigma-T), utilizando la ecuación de estado del agua de mar de UNESCO 1980. Este índice fue estimado para la capa de los primeros 50 m de profundidad, de acuerdo a la estimación de Anomalía de la Energía Geopotencial (ϕ), descrita por Bowden (1983).

Para complementar los datos oceanográficos, se adicionaron las mediciones diarias de temperatura superficial del mar (TSM) obtenidas desde un sitio costero en la Estación de Biología Marina en Dichato de la Universidad de Concepción.

La climatología de las variables oceanográficas fue derivada a partir de la serie temporal de 10 años para analizar su ciclo anual.

En cuanto al análisis de muestras zooplanctónicas, la abundancia numérica de cada especie fue estandarizada a individuos por metro cúbico (ind m^{-3}) para cada una de las muestras analizadas en los dos periodos de estudio. Para examinar cambios en la comunidad de copépodos se utilizaron descriptores comunitarios, tales como, riqueza de especies, abundancias, dominancia e índices de diversidad. La riqueza de especies está dado por el número de especies presentes en la muestra; la abundancia es el número de individuos de cada especies. La dominancia fue evaluada como la abundancia relativa (%) de una especie dada, con respecto al total; la diversidad de especies fue estimada a través del índice de diversidad de Shannon-Wiener (MacArthur and MacArthur 1961).

Todos los descriptores comunitarios estimados y las variables oceanográficas fueron analizados comparando los dos periodos de tiempo, para evidenciar posibles cambios en la escala decadal de la Estación 18 entre los periodos I (2002-2004) y II (2010-2012). Los análisis estadísticos consistieron en evaluar potenciales diferencias entre los periodos de estudios y su asociación con la variabilidad oceanográfica.

Para el análisis de biomasa zooplanctónica, la variabilidad interanual de las condiciones oceanográficas fueron divididas en dos periodos: condiciones de surgencia (Octubre-Marzo) y condiciones de hundimiento (Abril-Septiembre), debido a que el régimen anual de surgencia costera está dominado por un patrón estacional en la zona de estudio. De esta forma de analizó el efecto de la estacionalidad de la surgencia sobre la variabilidad oceanográfica (temperatura, salinidad, oxígeno disuelto, profundidad de la ZMO, anomalía de la energía geopotencial, clorofila-a) y biomasa mesozooplanctónica.

Para examinar los efectos diurnos-nocturnos sobre cambios en la biomasa mesozooplanctónica derivados de cualquier desplazamiento vertical de migradores y la evasión de la luz del día se analizaron los datos disponibles de muestreos diurnos y nocturnos.

La variabilidad en la distribución vertical de la biomasa zooplanctónica también se examinó, a causa de la fuerte gradiente en la concentración de oxígeno principalmente durante el periodo de surgencia. Para esto, se comparó la biomasa zooplanctónica de las capas 0-50 m y 50-80 m.

4. RESULTADOS

Capítulo 1: Manuscrito enviado a la revista Marine Ecology Progress Series

"Respuestas de la comunidad de copépodos a la variabilidad en las condiciones de surgencia en la Estación 18 en Chile centro-sur (2002-2012)"

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Resumen

La estructura comunitaria de copépodos pelágicos que habitan en la zona de surgencia de Chile centro-sur fue comparado entre los periodos 2002-2004 y 2002-2012. En ambos periodos, se identificaron 74 especies de copépodos entre ellos el Orden Calanoida estuvo representado por un 68% de la abundancia total. Las especies numéricamente dominantes (ca.80% de la abundancia total) fueron *Paracalanus indicus*, *Oithona similis*, *Calanoides patagoniensis*, *Drepanopus forcipatus* y *Acartia tonsa*. Del primer periodo (2002-2004) al segundo (2010-2012), hubo cambios significativos en la abundancia de algunas especies, orden de dominancia, estructura de tamaño de la comunidad y agrupación de las especies, aunque no hubo cambios significativos en la riqueza de especies ni en los índices de diversidad. La especie dominante, *Paracalanus indicus* fue desplazado numéricamente por *Drepanopus forcipatus* hacia el periodo 2010-2012. También hubo una disminución significativa en la abundancia total de copépodos en los años recientes 2010-2012. La evaluación de las variables oceanográficas reveló que condiciones más frías y más salinas (solo en la capa superficial) prevalecieron durante el 2010-2012, posiblemente causado por el incremento de la surgencia costera. Estos hallazgos sugieren que las alteraciones en las condiciones de surgencia costera, posiblemente impulsados por el cambio climático en el Pacífico Sur Oriental, en un factor importante para originar los cambios observados en la estructura comunitaria de copépodos durante los últimos 10 años. Estos cambios pueden reflejar una respuesta ecosistémica importante a las condiciones alteradas en la zona de surgencia costera.

Palabras claves: coastal upwelling, copepods, community structure, climate change

Responses of the copepod community to variable upwelling conditions at Station 18 off central/southern Chile (2002-2012)

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SHORTENED TITLE: Copepods responses to upwelling

Abstract

The community structure of pelagic copepods inhabiting the coastal upwelling zone of central-southern Chile was compared between the periods 2002-2004 and 2010-2012. For both periods, 74 copepod species were identified among which those belonging to the Order Calanoida accounted for 68% of total abundance. The numerically dominant species (ca. 80% of total abundance) were *Paracalanus indicus*, *Oithona similis*, *Calanoides patagoniensis*, *Drepanopus forcipatus* and *Acartia tonsa*. From the first (2002-2004) to the second (2010-2012) period, there were significant changes in abundance of some species, order of dominance, community size structure, and grouping of species, although no significant changes in species richness and diversity indexes were detected. The dominant, *Paracalanus indicus*, were numerically displaced by *Drepanopus forcipatus* towards the period 2010-12. There was also a significant decrease in total abundance of copepods in the more recent years 2010-2012. The assessment of oceanographic variables revealed that colder and saltier conditions (near surface layer only) prevailed during 2010-2012, due to increased upwelling activity. These findings suggest that altered upwelling conditions, possibly driven by climate changes in the eastern South Pacific, is an important factor for causing changes in the copepod community structure during the more recent 10 years. These changes can reflect a major ecosystem response to modified conditions of the coastal upwelling zone.

KEY WORDS: coastal upwelling, copepods, community structure, climate change

INTRODUCTION

Eastern boundary currents (EBC's) are considered highly dynamic ecosystems which can strongly vary in their physical and chemical properties over all temporal and spatial scales (Freón et al. 2009). EBC's usually cover extensive latitudinal gradients, exhibit strong seasonal and interannual variability, and can be subjected to large-scale multidecadal variability, regime shifts, and ENSO (El Niño Southern Oscillation) variability (Chavez et al. 2003, Cahuin et al. 2009).

In the eastern South Pacific, the EBC is represented by the Humboldt Current System (HCS). This is a Large Marine Ecosystem with an extensive coastal upwelling zone (ca. 40 degrees) and directly influenced by the high pressure center of the Pacific anticyclone, which causes strong South-West (SW) winds, inducing persistent coastal upwelling along Chile, Peru and Ecuador coastal waters (Thomas 1999).

EBC's systems are being affected by anthropogenic-induced global warming (Garreaud & Falvey 2009). In the HCS, increased coastal upwelling, due to the intensification of S and SW winds, may be causing the prevalence of colder conditions, as it has also been described for the Benguela system (Santos et al. 2012). The HCS is also characterized by a subsurface Oxygen Minimum Zone (OMZ) (Paulmier & Ruiz-Pino 2009), and this hypoxic layer may become shallower upon increased upwelling. These long-term changes in the physical-chemical environment of the ocean and in the HCS can greatly affect the marine ecosystems, both in terms of diversity and productivity (Hoegh-Guldberg & Bruno 2010).

At lower trophic levels, zooplankton is a group that may be affected by climate change (Richardson 2008). This concern has been confirmed by several studies showing long-term changes in community structure, diversity and abundance of various zooplankton groups from different regions of the world. These changes have been related to climate variability (Beaugrand et al. 2002, Richardson 2008, Mackas & Beaugrand 2010). Therefore, zooplankton can be used as a sentinel group reflecting changes in the marine ecosystem and providing the first evidence of biological response to climate variability (Hays et al. 2005).

A previous study suggested that community structure of zooplankton in the HCS may be affected by climate-induced oceanographic changes in the upwelling zone (Escribano et al. 2012). These oceanographic alterations may affect particularly the group Copepoda, which is known to be a rapid responder to climatic/oceanographic changes (Richardson 2008). Additional works also suggested that variation in upwelling intensity, causing changes in vertical distribution of the oxygen minimum zone, might be a key factor in modulating species diversity of copepods in upwelling areas (Hidalgo et al. 2012).

Other studies have shown that biomass and abundance of copepods appear correlated to upwelling variation in the HCS (Ayón et al. 2008, Escribano et al. 2012), but it is unclear how this group will respond to gradually increasing upwelling. Although more upwelling may promote more primary production by increasing nutrients inputs to surface water (Bakun et al. 2010), copepods might not be able to utilize the surplus of phytoplankton biomass if food spectra has been modified. Also the complexity of the food web dynamics in the upwelling zone, characterized by a seasonal interplay between a microbial food web and classical phytoplankton-herbivores C-transfer (Vargas et al. 2007) may not assure more secondary production. Increased upwelling may have further implications, such as increased offshore advection and more hypoxic condition, both of which can negatively impact copepod populations (Peterson 1998, Donoso & Escribano 2013, Wishner et al. 2013). All these factors may affect the copepod community and alterations may be reflected in changes in abundance of some species, in total abundance, in diversity indices, or in changes in the order of dominance.

In this study, we compared the abundance, diversity and dominance of copepod species in an upwelling zone off Chile between two periods: 2002-2004 and 2010-2012. These two periods represent conditions for potential changes taking place after a decade of sampling in the coastal upwelling zone off central/southern through the COPAS Time Series Study of Concepción at Station 18 (Escribano & Morales, 2012). Our study aimed at examining the consequences for the copepod community after colder conditions in more recent years as a result of increased wind-driven upwelling.

METHODS

2.1 Zooplankton sampling and oceanographic measurements

The upwelling region of southern-central Chile (30-40 ° S) corresponds to the southern portion of the Humboldt Current System in the eastern South Pacific (Fig. 1). Off Concepción (36°30'), the COPAS Center maintains a time series study since August 2002 to present date at Station 18 (ST St-18) (36°30.80'S, 73°7.75'W), which was initially sampled every 15 days (2002-2003), and thereafter it has been sampled monthly (Escribano & Morales 2012). This fixed station is located over the continental shelf at about 20 km from the coastline at a depth of ~ 90 m (Fig. 1).

At Station 18, chemical, physical and biological conditions of the water column are surveyed with autonomous profilers, CTD SBE-25 and SBE-19 Plus, attached to a SeaBird SC-32 Rosette for water sampling. Collected data are temperature, salinity and pressure. CTD's are also equipped with calibrated oxygen sensors and fluorometers. CTD casts are averaged at a 1 m resolution from surface to 85 m. Water samples, either with the Rosette or with 10 L Niskin bottles, are obtained at 9 depths from surface to 85 m and they are used to measure Chlorophyll-a (Chla) by fluorometric methods, as described in Anabalón et al. (2007), and dissolved oxygen by microwinkler technique as described by Montero et al. (2007).

Since 2002, zooplankton samples have been collected by oblique hauls for three depth strata: 80-0 m, 80-50 m and 50-0 m. For this, a 1 m^2 Tucker Trawl net fitted with 200 µm mesh size, and equipped with a calibrated flowmeter has been used. On occasions, day and night samples have been carried out on the same sampling day, and some samples (0-80 m) were also obtained with a 200 µm 0.5 m opening WP2 during rough weather conditions. For this study, we have used integrated samples of the 0-80 m stratum and for daylight conditions.

After collection, zooplankton samples were immediately preserved onboard with a solution of 4% neutralized formalin for later analysis. We identified and counted all species of copepods. Highly concentrated samples were fractionated up to a maximum of 25% of the total sample for taxonomic analysis. Identification of species was performed with stereomicroscopes Nikon SMZ 1000 and Leica DM500.

2.2 Data Analysis

For this study, we used copepod data from two distinct periods for two consecutive years each, after 10 years of the COPAS Time Series Study. Period 1 is from August 2002 to August 2004. Detailed analyses of copepod species for this period were available because they had been performed before the 27F tsunami destruction of the Marine Biology Station-Dichato in 2010 (Escribano & Poulet 2010). This event caused the loss of many zooplankton samples of the time series. The second period included samples from August 2010 to August 2012 for which detailed analysis of the copepod community has recently been carried out. Monthly data for each study period (1 and 2) cover intra-seasonal, seasonal and interannual variation in the upwelling zone.

Oceanographic conditions between periods were compared mostly by considering changes in temperature, salinity and density at 10 m depth. This depth appears as suitably representing the temperature with which most dominant copepods seem associated (Escribano et al. 2007), it is the depth at which the phytoplankton and microzooplankton can provide the nutritional environment for copepods (Iriarte et al. 2000, Anabalòn et al. 2007), and it may also represent most of the environmental variation occurring in the mixing layer. Oxygen conditions and Chlorophyll-a concentration of the water column were also considered at 10 m depth, but also by estimating the upper boundary of the oxygen minimum zone (OMZ), as defined by depth of 1 mL O_2 L^{-1}. All these variables were assessed in terms of their seasonal annual cycle by averaging each month. In addition, CTD data were also used to estimate annual vertical profiles of temperature, salinity and density from 3-months moving averages for each study period.

Water column stratification was estimated to assess the physical structure of the water column. The monthly Stratification Index (ϕ) of the water column was derived from temperature and salinity and density (Sigma-T). ϕ was estimated for the upper 50 m layer by estimating the geopotential energy anomaly as described by Bowden (1983), such that:

$$\Phi = \int_{-H}^{0} (\rho m - \rho)\, gz\, dz \qquad (1)$$

Where ϕ is the stratification index (J m^{-2}), g is the acceleration of gravity (9.8 m s^{-2}), H is the depth of the water column (50 m), ρ is water density (kg m^{-3}) at depth z (m) and ρm is the average density of the water column (0-50 m).

Upwelling variability in the region was examined from monthly upwelling indices estimated by the National Oceanic and Atmospheric Administration (NOAA) from the Project NCEP/NCAR Division of Physical Sciences, derived for 36° S off the Chilean coast as the Bakun index (Bakun 1973). We complemented this information with meridional winds computed from two data assimilating type NCEP/FNMOC (NOAA) near Station 18.

Analysis of copepod data involved the calculation of numerical abundance of species standardized to individuals per cubic meter (ind. m^{-3}), and relative abundance and occurrence were estimated as percentages. Changes in the copepod community were assessed using the descriptors: species richness (R), numerical abundance (N), dominance (relative abundance), and diversity indices. Species diversity was estimated with Shannon-Wiener diversity index (H '), defined as:

$$H' = - \Sigma\, pi \ln (pi) \qquad (2)$$

Where pi is the proportion of individuals of a species i to the total of individuals (ni / N), ni is the number of individuals of the species i and N is the total number of individuals in the sample. In order to incorporate a copepod size effect on the diversity index, a modified H' index was also calculated. For this, an H's index was standardized by the average size of adult stages of the species present in the corresponding sample. This size-weighed H's index has been suggested as to better represent copepod diversity in highly advective ecosystems (Hidalgo et al. 2012). Size structure of the copepod community was also examined by distinguishing size classes and their abundances. Four size classes were distinguished: <1 mm 1- 2 mm, 2- 3 mm and > 3 mm, using total body length. We obtained direct measurements of body length of at least 30 adult female individuals, and also complemented copepod sizes from the literature for rare species.

Statistical analyzes were focused on potential differences between study periods, and their association with oceanographic changes from one period to the other. Differences in oceanographic variables between periods were assessed by mean comparisons (t-test) and the non-parametric Kruskal-Wallis test. The latter was also applied to compare species abundances between periods and community descriptors. General linear models (GLM) were also applied on log-transformed variables to test eventual relationships between species and oceanographic variables. Finally, as to explore changes in community structure using the complete species assemblages, we applied a cluster analysis using the Pearson correlation matrix as a measure of distance.

RESULTS

3.1 Oceanographic Conditions

Seasonality of upwelling became clear from CTD data and it was reflected in all oceanographic variables. Fig. 2 summarizes monthly variability of oceanographic conditions at Station 18 for the two study periods: 2002-2004 and 2010-2012. Near surface temperature (10 m depth) shows the differences between upwelling (spring-summer) and non-upwelling seasons (autumn-winter). The annual mean temperature at 10 m depth was 12.87 ± 0.925 (mean± SD) and 12.68 ± 1.202 (mean± SD) for Periods 1 and 2, respectively. Maximal temperature at 10 m was 15.67 °C during March for Period 1, whereas in Period 2 the greatest temperature was 15.77 °C observed in January. The coldest conditions were also found during the spring-summer months upon increased upwelling with temperatures <11.5 °C at 10 m depth in both periods. Mean temperatures of the water column were 11.59 ± 0.573 (mean± SD) for Period 1 and 11.39 ± 0.708 (mean± SD) for Period 2, where the lowest mean temperatures were also found in the spring-summer season in both periods (Fig. 2a).

By examining the annual cycles, for most months temperature was lower in the more recent Period 2. Colder conditions in Period 2 were confirmed by statistical comparisons. Annual means were significantly different after t-test. At 10 m depth differences were significant with $\alpha=0.05$ ($t_{(2),\,42} = 2.52$, $P<0.05$), whereas differences in the whole water column (0-80 m) means were highly significant at $\alpha=0.01$ ($t_{(2),\,42} = 6.17$, $P<0.05$).

Salinity showed a similar annual cycle for both periods, with much lower salinity in winter associated with the rainy season and increased river discharge, contrasting with higher salinity occurring in periods of active upwelling (Fig 2b). Mean salinity at 10 m depth was considerably different between periods with 33.818± 0.7372 (mean± SD) and 34.014± 0.6184 (mean± SD) for Periods 1 and 2, respectively. A highly significant greater salinity at 10 m in Period 2 was confirmed by t-test ($t_{(2), 42} = 8.86$, $P<0.01$). Mean salinity for the entire water column (0-80 m) was 34.321± 0.2105 (mean± SD) and 34.363± 0.2346 (mean± SD) for Periods 1 and 2, respectively. These means also differ significantly ($t_{(2), 41} = 6.68$, $P<0.01$).

Dissolved oxygen (DO) also exhibited a seasonal patterns (Fig 2c), characterized by sharp decreases during the spring-summer after nearly saturated conditions (5-6 mL O_2 L^{-1}) during the winter. At 10 m depth, annual mean of DO was 5.41 ± 1.122 mL O_2 L^{-1} (mean ± SD) and 5.22 ± 0.956 (mean ± SD) for Periods 1 and 2, respectively. These values of DO did not differ significantly between periods (($t_{(2), 42} < 1.86$, $P>0.05$).

Concentration of chlorophyll-a (Chla) showed a marked seasonal pattern, characterized by a maximum concentration in the spring-summer seasons, but also with marked changes between periods (Fig. 2d). During the upwelling season (spring-summer) the mean Chla at 10 m depth was 4.86 ± 6.661 mg Chla m^{-3} for Period 1, and 4.85 ± 5.791 (mean± SD) for Period 2. By contrast, in the non-upwelling season (autumn-winter) Chla was 1.93 ± 2.803 mg m^{-3} and 1.455 ± 2.142 mg m^{-3} at 10 m depth for Periods 1 and 2, respectively. Chla values did not differ significantly between periods (($t_{(2), 42} < 1.86$, $P>0.05$).

From CTD data it can be shown that the complete water column was subjected to significant changes from Period 1 to Period 2. Moving averages (3 months) of annual vertical profiles clearly showed that the entire water column of Period 2 was colder, saltier and denser (Fig. 3). Significant differences are illustrated by standard deviations of the profiles (Fig. 3).

When comparing the annual cycle of upwelling condition for both periods through the regional upwelling index of Bakun (1973), the seasonal regime of upwelling intensity became clear, although there were no apparent differences between periods (Fig. 4a). In the water column at Station 18 however, water column stratification was clearly different between periods, revealing that during the most recent period (2010-12) mixed, less-stratified conditions prevailed as compared to the period 2002-04 (Fig. 4b). The seasonal pattern of ϕ also showed that stratification was greater during the winter and this is caused by low salinity water at surface after rainfall and river runoff. Meantime, the annual cycle of depth of the OMZ also shows a clear seasonal pattern characterized by a very shallow (<50 m) OMZ in the spring-summer in both periods and apparently the OMZ was much shallower during the more recent 2010-12 period (Fig. 4c).

3.2 Species Composition

The copepod community for both study periods was represented by 74 species belonging to 4 orders, 29 families and 41 Genera. The Order Calanoida was the most representative with 67.6% of total species, followed by the Order Cyclopoida with 16.2%, and the Orders Harpacticoida 8.1% and Poecilostomatoida with 8.1%. The complete list of species is provided as complementary material.

Numerically dominant species, representing >1% of total abundances in either period, are shown in Table 1. These species were also present throughout the year in the upwelling zone with frequency of occurrence greater than 60% (Table 1). During Period 1 (2002-2004) there was a total number of 58 species of copepods, of which 53 were identified to species level and 5 to Genera (see Supplementary Material). In this period, *Paracalanus indicus*, *Calanoides patagoniensis*, *Oithona similis* and *Acartia tonsa* were the dominant species, representing more than 90% of the total copepod community. *Paracalanus indicus* was the most abundant species (Table 1) representing 60% of the abundance of copepods in this period. During Period 2 (2010-2012), a total number of 55 species were found, all of them identified to species level. In this case, *Drepanopus forcipatus*, *Oithona similis*, *Calanoides patagoniensis*, *Paracalanus indicus*, *Clausocalanus arcuicornis*, *Acartia tonsa*, *Microcalanus pygmaeus* and *Microsetella norvegica* were the dominant species (>1%), making up more than 90% of total copepod abundances. During this second period there was a sharp decrease in the abundance of *Paracalanus indicus*, which in this case represented only 8% of the whole community and with an abundances one order of magnitude lower (Table 1). In this period, the species *Drepanopus forcipatus* dominated the community, being the most abundant one (Table 1) and accounting for 28% of the total copepod community.

When comparing the copepod composition between periods in terms of their contribution to the entire community, there were clear changes as illustrated by their relative abundances (Fig. 5). First, *Paracalanus indicus* notoriously prevailed in the first period, whereas the second period was markedly dominated by *Drepanopus forcipatus*. In addition, *Calanoides patagoniensis*, *Acartia tonsa* and *Oithona similis* had higher abundances during the first period, whereas *Clausocalanus arcuicornis*, *Microcalanus pygmaeus* and *Pleuromamma gracilis* increased over 50% in their abundances during Period 2 (Fig. 5).

The annual cycle of dominant species, in terms of their abundances and occurrences, is shown in Fig. 6. The highly dominant *P. indicus* in Period 1 seem to increase during the spring-summer as compared to winter months, but such pattern is not clear during Period 2.

Instead, there was an abrupt decrease of this species by the spring season (Fig. 6a). *C. patagoniensis* showed the same pattern in both periods with a slight tendency to decrease by mid-winter (Fig. 6b). *O. similis* appear were present during all seasons with similar levels of abundance and no clear seasonal pattern (Fig. 6c). *A. tonsa* also decreased by the winter, but exhibited strong variation in other months (Fig. 6d). Finally, *D. forcipatus* clearly increased in abundance during the autumn and early spring of Period 2, whereas in Period 1 this species varied sharply with no clear seasonality (Fig. 6e). The nonparametric Kruskal-Wallis test showed that *Paracalanus indicus* significantly differed between periods (Table 3), as a resulted of their greatly decreased abundances in the second period, whereas the abundances of *Calanoides patagoniensis*, *Oithona similis*, *Acartia tonsa* and *Drepanopus forcipatus* did not significantly differ between periods (Kruskal-Wallis test, $P>0.05$).

The community descriptors, R, H', H's and N, were examined by looking at their annual cycles (climatologies), and also compared between periods. The annual cycle of species richness (R) for both periods, show the highest values during May for the first period and in August for the second period, in both cases under non- upwelling conditions (downwelling), whereas much lower values were found during the spring-summer seasons (Fig . 7a). The annual cycle of the diversity index (H ') was unclear, although with a slight tendency to increase in the winter and decrease in early spring (Fig. 7b), whereas the diversity index standardized by copepod size (H's) was more variable throughout the year, with a slight decrease in the spring and greater values by mid winter (Fig. 7c). Meantime, total copepod abundance (N) shows two major peaks in the spring and in the autumn in both periods and marked low values during the winter (Fig. 7d).

When analyzing the interannual variability of community of R, H 'and H's, the Kruskal-Wallis test revealed that apparent differences were not statistically significant ($p > 0.05$). By contrast, the annual cycle of the total number of individuals (N) differed significantly between the two periods studied (Table 3), and this resulted from the abundances recorded during February-March-April and November for Period 1, and May abundances in Period 2 (Fig. 7d).

Eventual changes in community size structure were examined by grouping copepod abundances in four size classes (<1mm, 1-2mm, 2-3mm and >3 mm). This analysis revealed that during the first study period the small size class (<1 mm) was numerically dominant , contributing with 72% to total abundance (Fig. 8a). Species belonging to this size class were *Paracalanus indicus*, *Oithona similis*, *Microcalanus pygmaeus* and *Oncaea media*. By contrast, in the second study period the mid-size class 2-3mm dominated and small copepods notoriously decreased in their abundance (Fig. 8b). This mid-size class was mostly represented by *Drepanopus forcipatus*.

A cluster analysis, used to compare the community structure based on all species, was applied separately for each period. Cluster analysis for Period 1 revealed the grouping of 5 species assemblages (Fig. 9a). In order to characterize these groups we looked at the seasonal cycles of their abundances, and we also considered their distributions from previous studies. Clustering of Period 1 resulted in a first group (g1) represented by two species of which *A. tonsa* has a stable abundance during the year along with the rare species, *Scaphocalanus echinatus*, which showed up only when *A. tonsa* had sudden increases. The second group g2 was represented by species having more oceanic distribution and which occasionally approach the coastal zone. g3 is the group with most species, and it was represented by spring-summer species, i.e. upwelling condition species. g4 mostly grouped winter species, whereas g5 was represented by two highly abundant species in the coastal zone, present year-round, and only one rare species.

Cluster analysis in Period 2 (Fig. 9b) resulted in a very different grouping of species assemblages, although it also suggested 5 distinct groups. In this case, g1 and g2 represented rare species, mainly present during the winter time, except by one species, *Nannocalanus minor*, which was more abundant and became associated with rare species by exhibiting peaks of abundance coinciding with rare species. In this period, g3 was the group of most abundant species throughout the year, although these species were not the same as in g5 of Period 1 (abundant all year). In this Period 2, there were two separate groups for spring-summer species, g4 and g5. Group g4 contained abundant species, whereas g5 was comprised by rare ones (Fig. 9b).

In order to assess the influence of oceanographic conditions on abundance of dominant species, a GLM analysis was applied on log-transformed data of species abundances as dependent variable, and oceanographic variables as dependent ones. GLM analysis for the five most abundant species showed that for Period 1 only two species had significant correlations with oceanographic variables. In this Period 1 *Oithona similis* were significantly correlated to temperature, salinity, the Upwelling Index, and to water column stratification, whereas *Drepanopus forcipatus* were significantly associated with Chla, temperature, and OMZ depth. For Period 2, only *Paracalanus indicus* showed a significant association with mean temperature 0-80 m ($p = 0.045$) (Table 4). Community descriptors, R, H ', H's and N were also related to oceanographic variables by GLM, although no significant correlations were found ($p > 0.05$).

DISCUSSION

For central/southern Chile, the evidence suggests that major changes in the water column have occurred in the last 10 years resulting in a colder and saltier condition. This condition has been induced by increased upwelling promoted by stronger southerly winds in the eastern South Pacific region in the last decades (Garreaud & Falvey 2009, Bakun et al. 2010). However, the comparison of the NOAA regional upwelling index showed no differences between periods. This lack of differences in the Bakun index might be explained in terms of spatial effects. Bakun index is derived from geostrophic winds which cannot have sufficient resolution in the coastal area (Bakun 1973), such as it may occur at Station 18, where increasing upwelling might be taking place. Therefore, a higher resolution analysis of wind data might be necessary. In fact, wind data for both periods at two points near Station 18 derived from NCEP/FNMOC models show clear differences in meridional winds when comparing periods, suggesting much increased upwelling during the 2010-12 period (Fig. 10).

This study conducts the first analysis of the copepod community in relation to oceanographic variability over a decadal scale in central/southern Chile. Previous studies could only assess seasonal variability of few or single species (Castro et al. 2007, Escribano et al. 2007), or covered a few years only (Hidalgo et al. 2010, Escribano et al. 2012). These previous studies described shown strong seasonal variation of copepod abundances, but whether such patterns can repeat every year remained uncertain. Indeed our study shows that interannual variability can be larger than seasonal one. We have also shown that over a few years, changing environmental conditions in terms of temperature, salinity and stratification, in this case driven by changes in upwelling intensity, may affect the structure of copepod communities, as it has been shown in other regions of the world ocean. For example, in the northern California current, a change from warm to colder conditions can affect the species richness and the composition of the copepod community (Peterson et al. 2006). In the northern HCS the zooplankton community, including copepods can also respond to changing warm-cold conditions driven by El Niño/La Niña fluctuations (Aronéz et al. 2009), and in the north Atlantic region, several works have shown the strong influence of changing hydrographic conditions on copepod diversity and abundance (Beaugrand et al. 2002).

Changes in the community structure of copepods from Period 1 to Period 2 were mainly reflected in species abundance. Some species increased towards the Period 2 (example *Drepanopus forcipatus*), other reduced their abundance (e.g. *Paracalanus indicus*), and other species were maintained in similar abundances (*Oithona similis*) (Fig. 5 and Table 2). The dominance of some species also changed between periods. *Paracalanus indicus* was displaced by *Drepanopus forcipatus*. The latter is a species found in colder waters originated in the subantarctic or Antarctic regions. Therefore, this species could be signaling an increase in the proportion of sub-Antarctic waters in the study area. This region is recognized by been subjected to the influence of subantarctic waters, equatorial and subtropical water in different proportions in the surface layer (<100 m), where copepods can be indicators of different water masses (Morales et al. 2010). This mixing of waters of different origins can be affected by changes associated with ENSO (El Niño Southern Oscillation) conditions, i.e. from a cold to a warm phase (El Niño and La Niña, respectively) (Escribano et al. 2004). However, NOAA data show that both study periods mainly represent either neutral or La Niña ENSO conditions, therefore, the observed changes in abundance and species replacement cannot be attributed to ENSO variability and most likely they have been induced by longer term changes in upwelling intensity (Bakun et al. 2010).

All species found in this study have been previously described for this region (Hidalgo et al. 2010, Hidalgo et al. 2012, Morales et al. 2010, Escribano et al. 2012). It should be noted that names of three species have been modified in recent years, such as *Pseudoamallothrix ovata*, *Pseudoamallothrix profunda* and *Scolecithricella bradyi*. Therefore, our review of the species represents the current taxonomic status, and the species names have been validated in the Global Registry of scientific names of marine species (WoRMS) (www.marinespecies.org). This analysis is essential to avoid confusion of synonyms or names assigned errors for studies of diversity and abundance of species.

We also found a decrease in total abundance of copepods for the more recent period, which is consistent with the decrease in *Paracalanus indicus*. Previous studies have shown that over 46% of total abundance of pelagic copepods in the HCS corresponds to *P. indicus* (Hidalgo et al. 2010, Hidalgo et al. 2012). This species could therefore account for a reduction of total abundance of copepods in the central-southern Chile observed during the period 2002-2008 (Escribano et al. 2012). Declines of zooplankton have been observed in other time series in coastal upwelling areas (Roemmich & McGowan 1995), and these are suggested to be caused by physical forcing, such as changes in winds, thermocline depth, heat flux and temperature (Clarke & Lebedev 1999), although other work postulate that pelagic fish predation on zooplankton can explain their decline (Carrasco & Lozano 1989).

There are limitations when assessing zooplankton variability from fixed stations. Distribution of zooplankton is strongly variable over time and space, and in upwelling waters zooplankton distribution is highly aggregated (Peterson 1998, Morales et al. 2010). This strong aggregation can affect temporal observations of the water column when based on fixed stations. Despite these potential sources of errors for sampling, long-term studies based on fixed stations, have proven useful to examine temporal trends in zooplankton (Mackas & Beaugrand 2010).

Although underlying mechanisms explaining the changes in community structure of copepods as a response to changing conditions are unclear, the evidence shows that alterations in water mass distribution and circulation patterns may be an important factor (Peterson et al. 2006). However, changes in abundances of particular species can also be induced by direct influence of oceanographic factors of which temperature (e.g. Ulloa et al. 2001) and probably food conditions must be considered as key ones. Certainly, there are top-down and bottom-up factors acting on copepod communities, forcing their composition, size-structure, and species diversity and abundance (Mackas & Beaugrand 2010). However, both types of community control can be altered by modifications of the physical environment. In this regard, alterations of water mass distribution and circulation should be important processes altering the physical, chemical and biological environment (Peterson et al. 2006). In any case, it seems that increased coastal upwelling in the HCS induced by global warming may gradually and substantially modify the zooplankton community, and this can have a major impact at the ecosystem level, including potential alterations in community structure of higher trophic levels.

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Table 1

Numerically dominant species (>1% of total abundance) of copepods found at Station 18 in the coastal upwelling zone off Central/southern Chile during the COPAS Time Series study 2002-2012. Data are from monthly samples for two periods, August 2002 to August 2004 (Period 1) and August 2010 to August 2012 (Period 2). The complete list of identified species and their abundances is provided as Supplementary Material. N is the mean abundance and f represents the frequency of occurrence.

	Period 1 (2002-04)		Period 2 (2010-12)	
Species	N (Number m^{-3})	f (%)	N (Number m^{-3})	f (%)
P. indicus	755.6	100.0	41.7	95.2
C. patagoniensis	220.2	95.7	68.4	76.2
O. similis	151.5	100.0	115.4	90.5
A. tonsa	58.1	100.0	24.9	85.7
D. forcipatus	34.5	100.0	138.2	90.5
O. setigera	16.7	100.0	7.7	81.0
C. arcuicornis	7.3	82.6	29.6	71.4
M. pygmaeus	7.0	82.6	16.2	66.7
P. gracilis	3.0	78.3	6.4	71.4

Table 2

The non-parametric Kruskal-Wallis test to compare the abundance of a dominant copepod species, and total copepod abundance between two sampling periods: Period 1: 2002-2004 and Period 2: 2010-2012). Zooplankton data are from the COPAS Time Series Study at Station 18 in the coastal upwelling zone off Central/southern Chile.

Variable	Period 1 Rank Sum	Period 2 Rank Sum	df	P
Paracalanus indicus	211.00	89.00	1	<0.01
Total abundance (N)	187.00	113.00	1	0.03

Table 3

Generalized Linear Model (GLM) analysis to test the influence of oceanographic variables on abundance of dominant copepod species found in the upwelling zone off Central/southern Chile during two sampling periods 2002-04 and 2010-12. GLM analysis was applied on log-transformed data of copepod abundances and only significant correlations are shown.

Dependent variable	Independent variables	Coefficient	P
Oithona similis	Temperature 10m	670.3	0.045
	Salinity 10m	823.4	0.049
	Upwelling Index	14.9	0.048
	Stratification	19.2	0.038
Drepanopus forcipatus	Chlorophyll-a 10m	-116.9	0.024
	Chlorophyll-a 80m	218.2	0.026
	Temperature 80m	599.0	0.047
	OMZ depth	-14.4	0.049
Paracalanus indicus	Temperature 80m	162.4	0.045

FIGURE CAPTIONS

Figure 1. The eastern South Pacific region and the coastal upwelling zone off Central/southern Chile, illustrating the location of Station 18 where the COPAS time series study has been carried out since 2002 to present date.

Figure 2. Annual cycles of near surface (10 m depth): a) temperature, b) salinity, c) dissolved oxygen, and d) Chlorophyll-a at Station 18 in the Central/southern upwelling region off Chile for two sampling periods: Period 1 (2002-04) and Period 2 (2010-12). Data are from monthly means.

Figure 3. Annual means of water column conditions after 3-months moving averages of vertical profiles of temperature, salinity and density at Station 18 in the Central/southern upwelling region off Chile for two sampling periods: Period 1 (2002-04) and Period 2 (2010-12). Data are from monthly CTD casts. std=standard deviation.

Figure 4. The seasonal pattern of a) the Bakun upwelling index at the Central/southern region off Chile for two periods: Period 1 (2002-04) and Period 2 (2010-12). Data are from monthly means as obtained from geotrophic winds by NOAA. b) Water column stratification at Station 18 estimated as the potential energy anomaly from density profiles of the water column. c) Depth of the upper boundary of the oxygen minimum zone (OMZ) from monthly profiles of dissolved oxygen at Station 18.

Figure 5. Relative abundance of dominant copepod species at Station 18 in the coastal upwelling zone off central/southern Chile for two comparative periods: Period 1 (20012-04) and Period 2 (2010-12). Data are from monthly samplings.

Figure 6. Annual cycles of numerical abundance (log-scale) of dominant copepod species at Station 18 in the coastal upwelling zone off central/southern Chile for two comparative periods: Period 1 (20012-04) and Period 2 (2010-12). Data are means from monthly samplings.

Figure 7. Annual cycles of community descriptors of the copepod community a) species richnees (R), b) Shannon-Wiener index (H'), c) Size-weighed Shannon-Wiener index (H's), d) copepod total abundance (N), at Station 18 in the coastal upwelling zone off central/southern Chile for two comparative periods: Period 1 (20012-04) and Period 2 (2010-12). Data are means from monthly samplings.

Figure 8. Changes in size structure of the copepod community at Station 18 in the coastal upwelling zone off central/southern Chile for two comparative periods: Period 1 (20012-04) and Period 2 (2010-12) after comparing relative abundance (a) and numerical abundance in log-scale (b). Data are means from monthly samplings. The four copepod size classes were assigned on the basis of adult total length of females.

Figure 9. Cluster analysis of the copepod community at Station 18 off Central/southern Chile after monthly zooplankton samples for two periods. a) Period 2002-2004, b) Period 2010-2012

The grouping (g1 to g5) was based on significant differences between groups from the Pearson correlation distances.

Figure 10. Meridional winds at two points near Station 18 in the coastal upwelling zone off central/southern Chile for two comparative periods: Period 1 (20012-04) and Period 2 (2010-12). Data are from monthly values of FNMOC and NCEP forecasting models of NOAA.

Figure 1

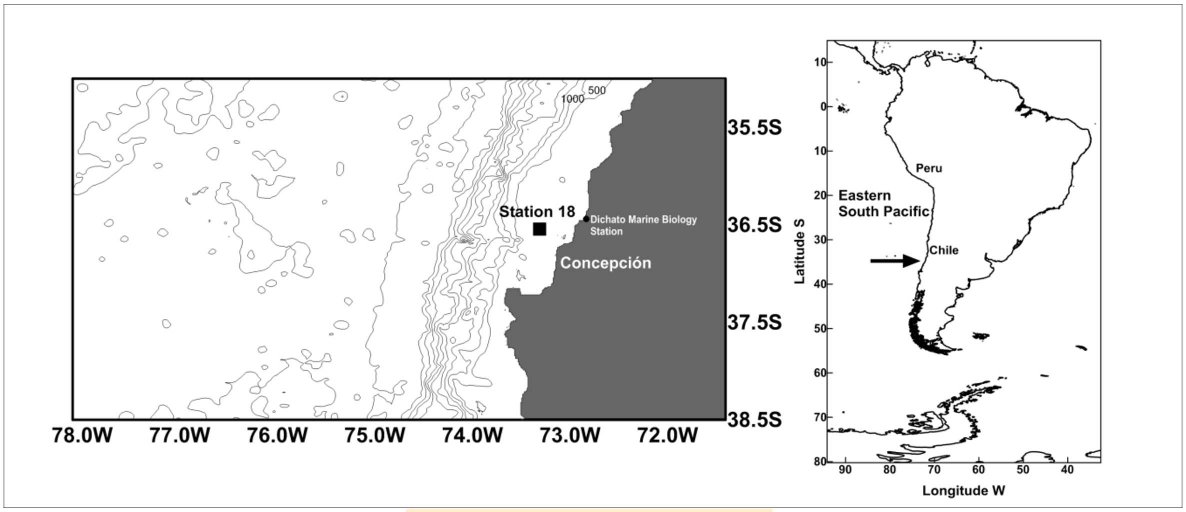

500
1000
Station 18
Dichato Marine Biology Station
Concepción
35.5S
36.5S
37.5S
38.5S
78.0W
77.0W
76.0W
75.0W
74.0W
73.0W
72.0W
Peru
Eastern South Pacific
Chile
Latitude S
Longitude W
10
0
10
20
30
40
50
60
70
80
90
80
70
60
50
40

Figure 2

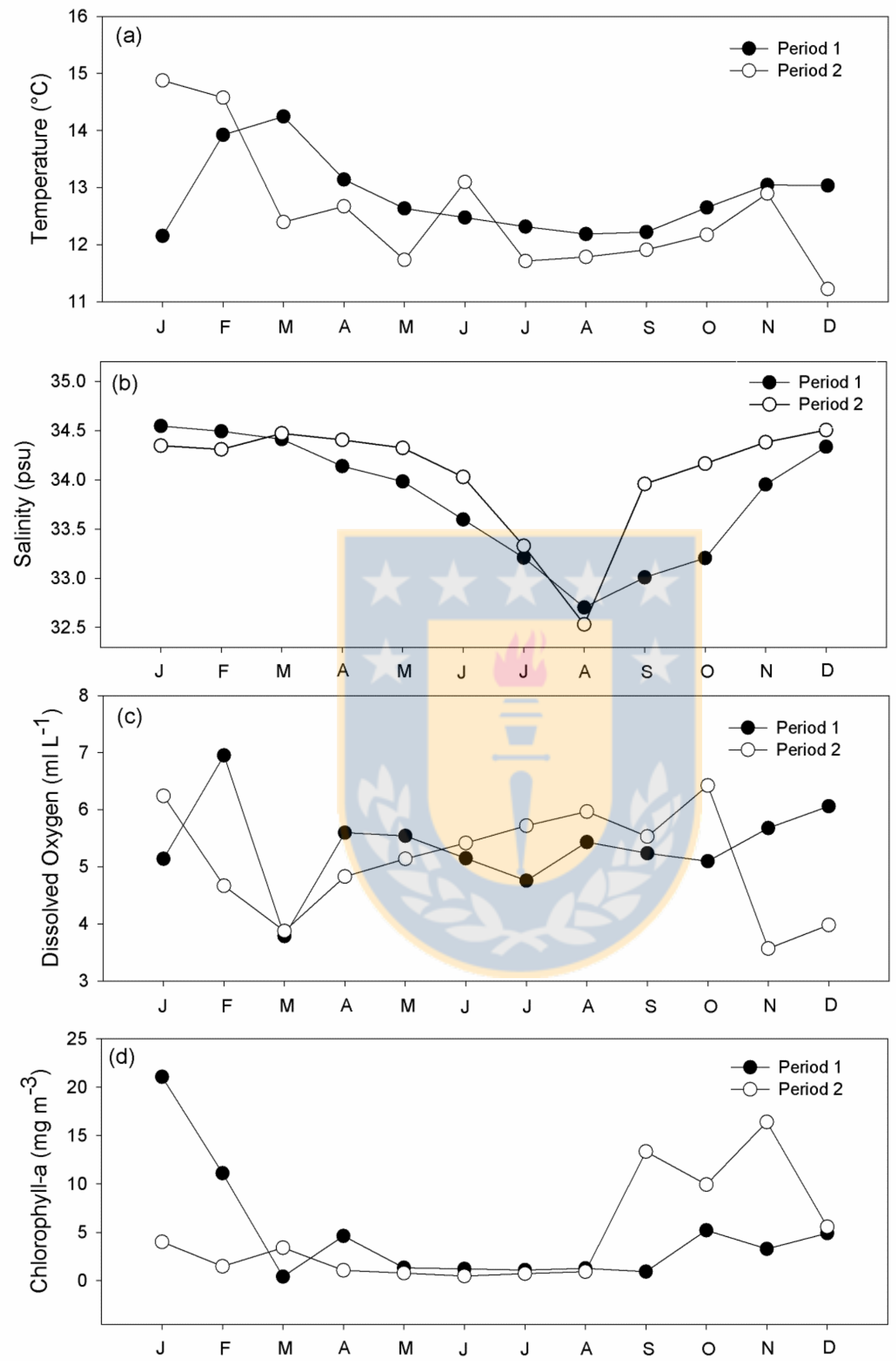

(a)
Temperature (°C)
16
15
14
13
12
11
Period 1
Period 2
J
F
M
A
M
J
J
A
S
O
N
D
(b)
Salinity (psu)
35.0
34.5
34.0
33.5
33.0
32.5
Period 1
Period 2
J
F
M
A
M
J
J
A
S
O
N
D
(c)
Dissolved Oxygen (ml L-1)
8
7
6
5
4
3
Period 1
Period 2
J
F
M
A
M
J
J
A
S
O
N
D
(d)
Chlorophyll-a (mg m-3)
25
20
15
10
5
0
Period 1
Period 2
J
F
M
A
M
J
J
A
S
O
N
D

Figure 3

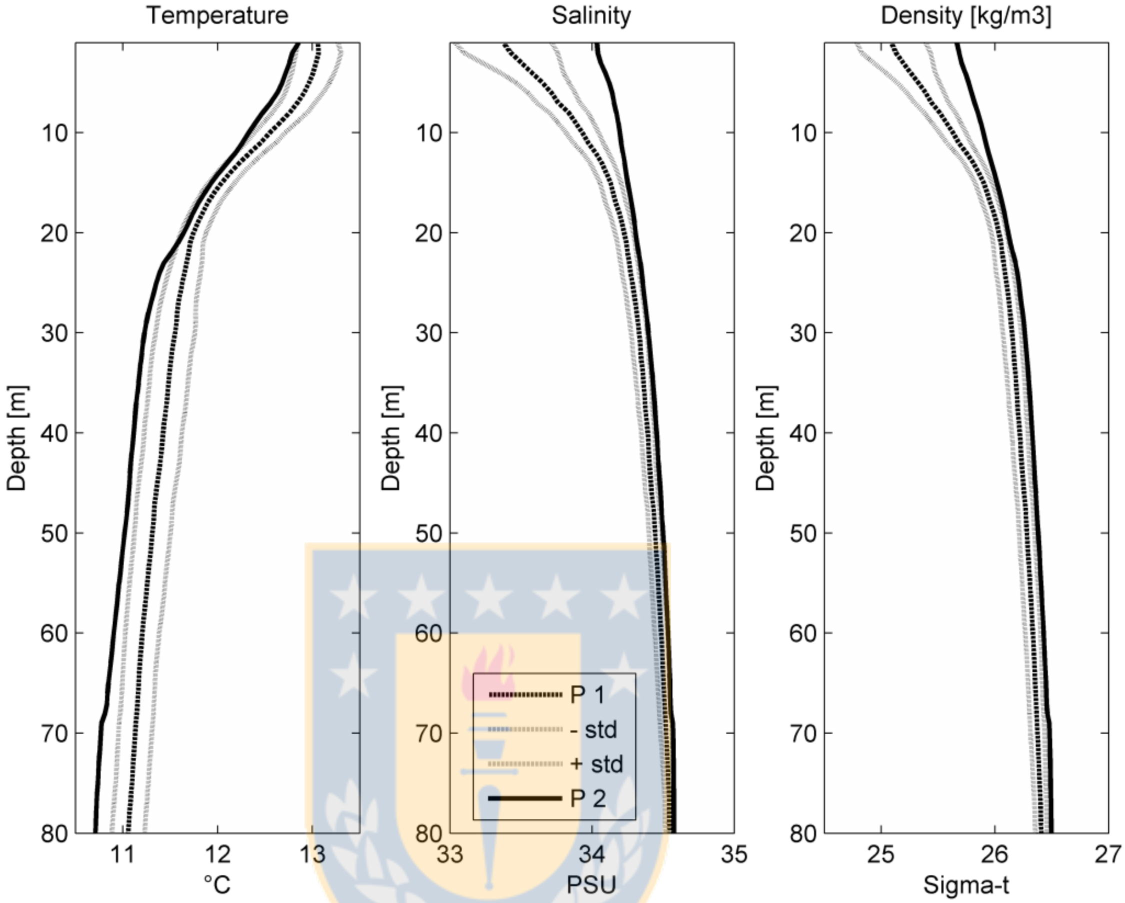

Temperature
Salinity
Density [kg/m3]
Depth [m]
10
20
30
40
50
60
70
80
11
12
13
°C
33
34
35
PSU
25
26
27
Sigma-t
P 1
- std
+ std
P 2

Figure 4

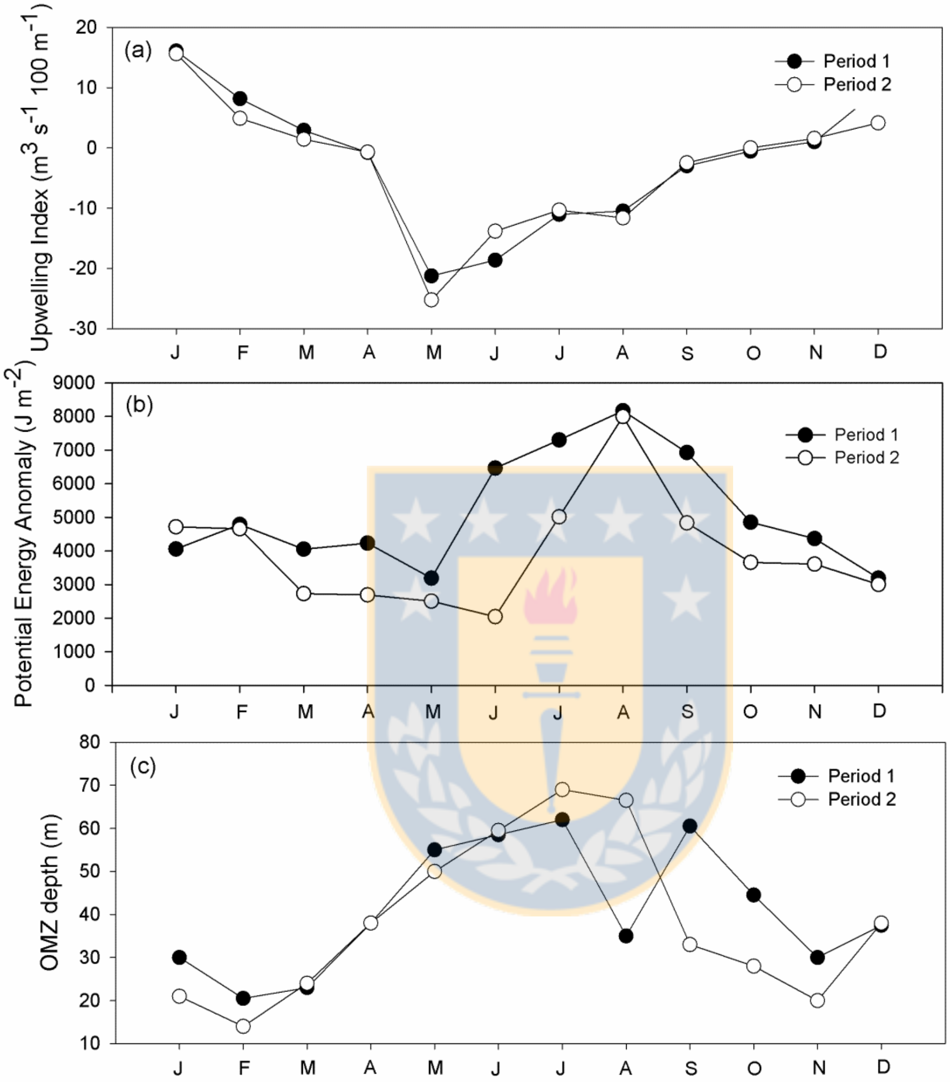

(a)
Upwelling Index ($m^3 s^{-1} 100 m^{-1}$)
20
10
0
-10
-20
-30
Period 1
Period 2
J F M A M J J A S O N D
(b)
Potential Energy Anomaly ($J m^{-2}$)
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
Period 1
Period 2
J F M A M J J A S O N D
(c)
OMZ depth (m)
80
70
60
50
40
30
20
10
Period 1
Period 2
J F M A M J J A S O N D

Figure 5

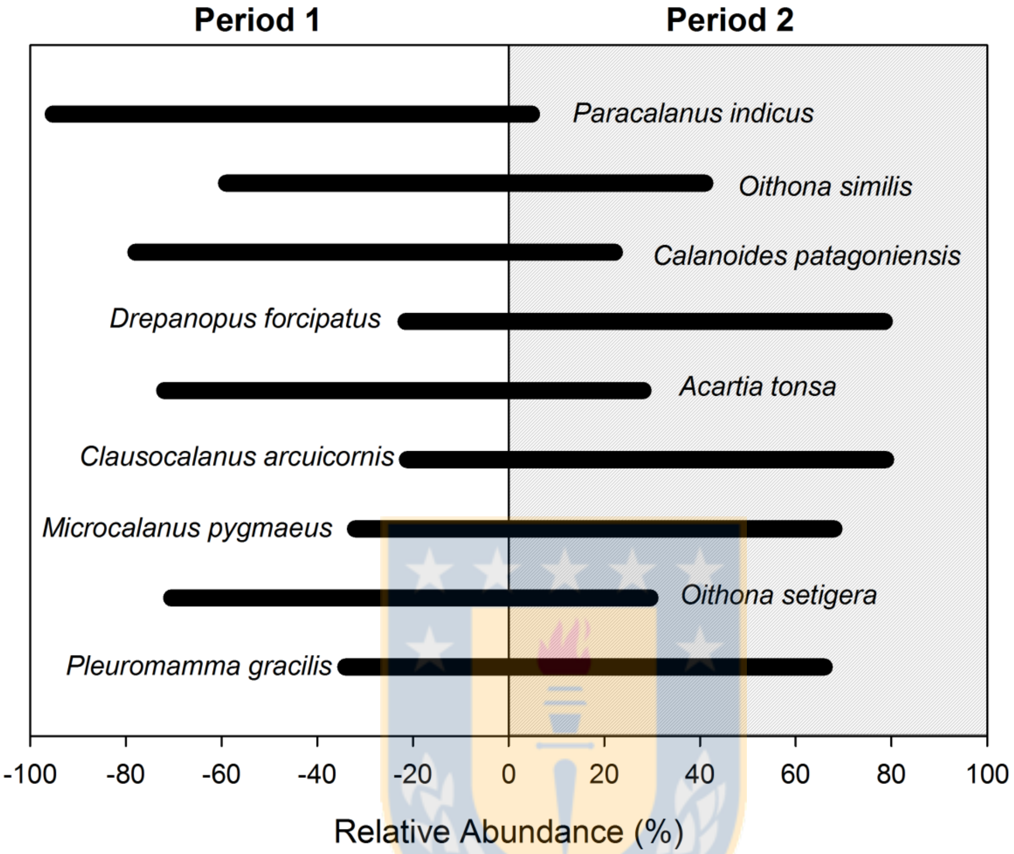
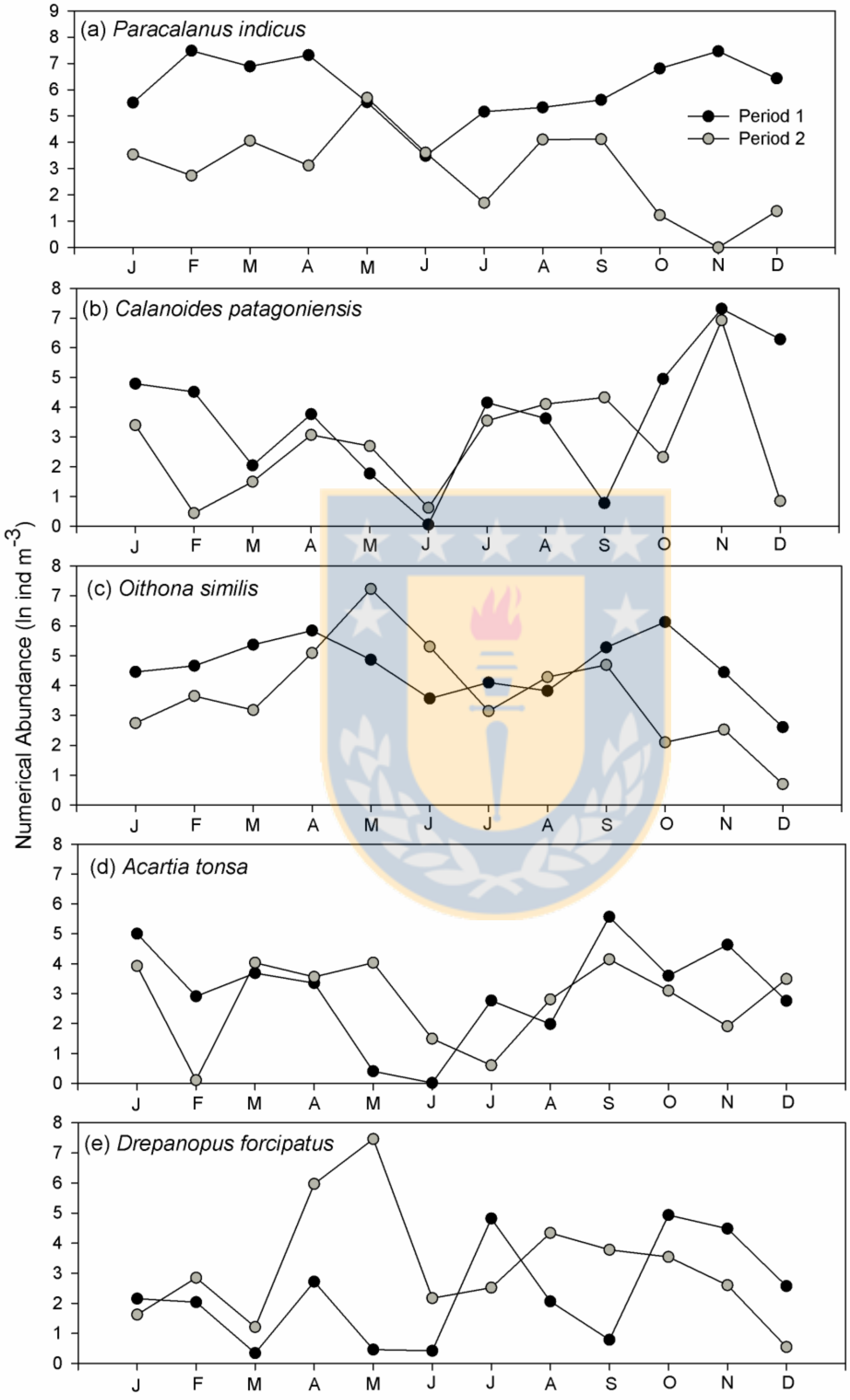

Period 1
Period 2
Paracalanus indicus
Oithona similis
Calanoides patagoniensis
Drepanopus forcipatus
Acartia tonsa
Clausocalanus arcuicornis
Microcalanus pygmaeus
Oithona setigera
Pleuromamma gracilis
-100
-80
-60
-40
-20
0
20
40
60
80
100
Relative Abundance (%)

Figure 6



(a) *Paracalanus indicus*
(b) *Calanoides patagoniensis*
(c) *Oithona similis*
(d) *Acartia tonsa*
(e) *Drepanopus forcipatus*
Period 1
Period 2
Numerical Abundance (ln ind m-3)
J
F
M
A
M
J
J
A
S
O
N
D
0
1
2
3
4
5
6
7
8
9

Figure 7

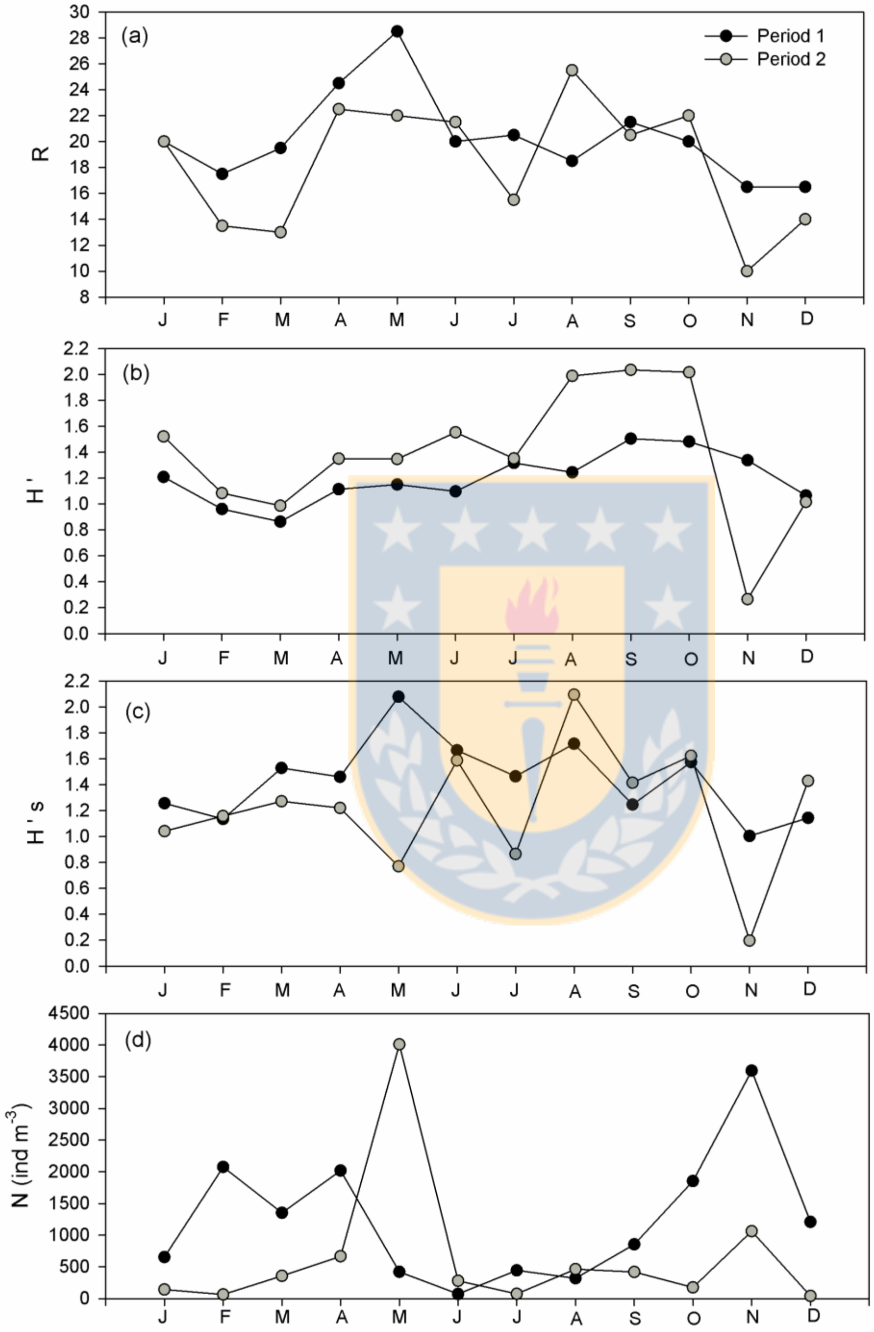

(a)
R
Period 1
Period 2
30
28
26
24
22
20
18
16
14
12
10
8
J
F
M
A
M
J
J
A
S
O
N
D
(b)
H '
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
(c)
H ' s
(d)
N (ind m^{-3})
4500
4000
3500
3000
2500
2000
1500
1000
500
0

Figure 8

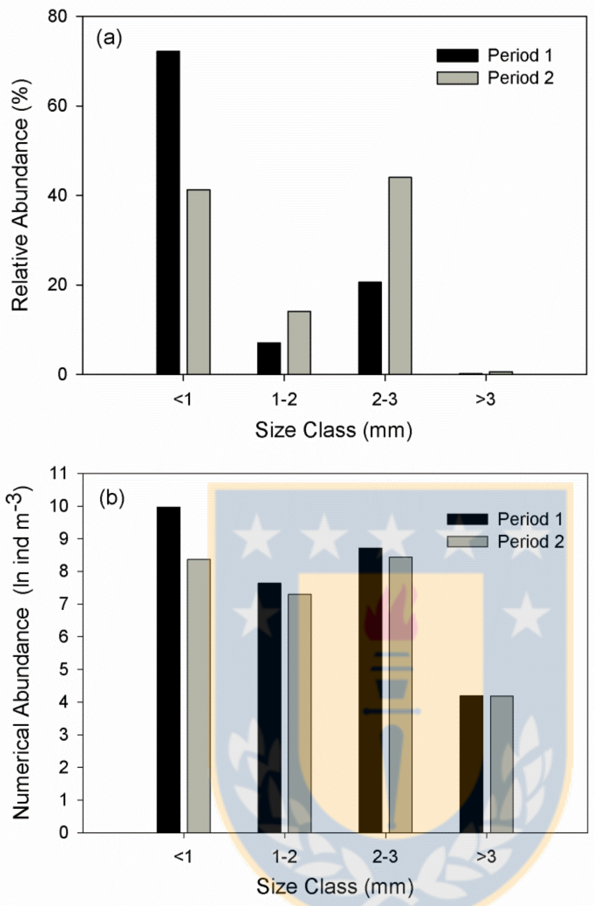

(a)
Period 1
Period 2
Relative Abundance (%)
0
20
40
60
80
<1
1-2
2-3
>3
Size Class (mm)
(b)
Period 1
Period 2
Numerical Abundance (ln ind m^{-3})
0
1
2
3
4
5
6
7
8
9
10
11
<1
1-2
2-3
>3
Size Class (mm)

Figure 9

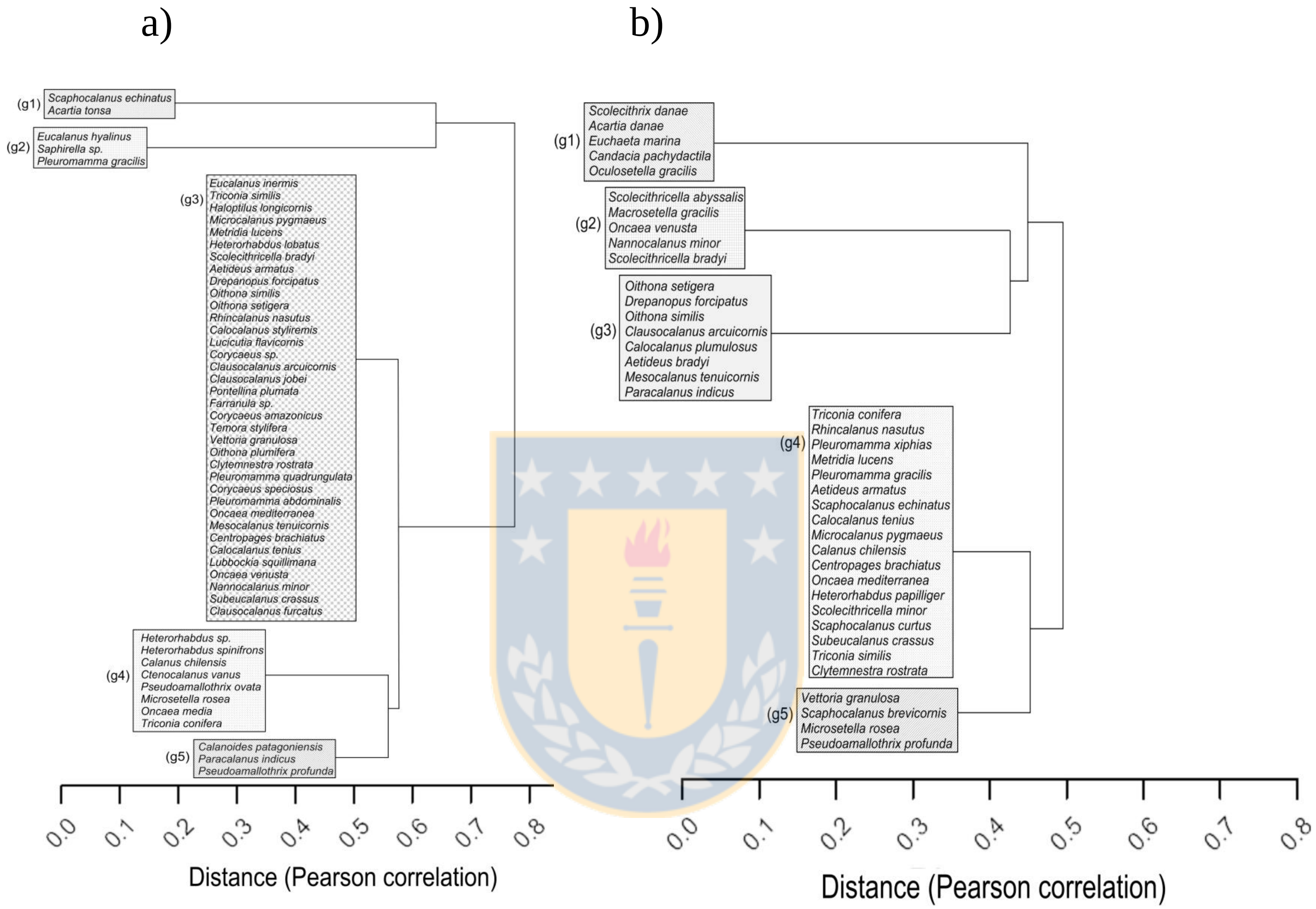
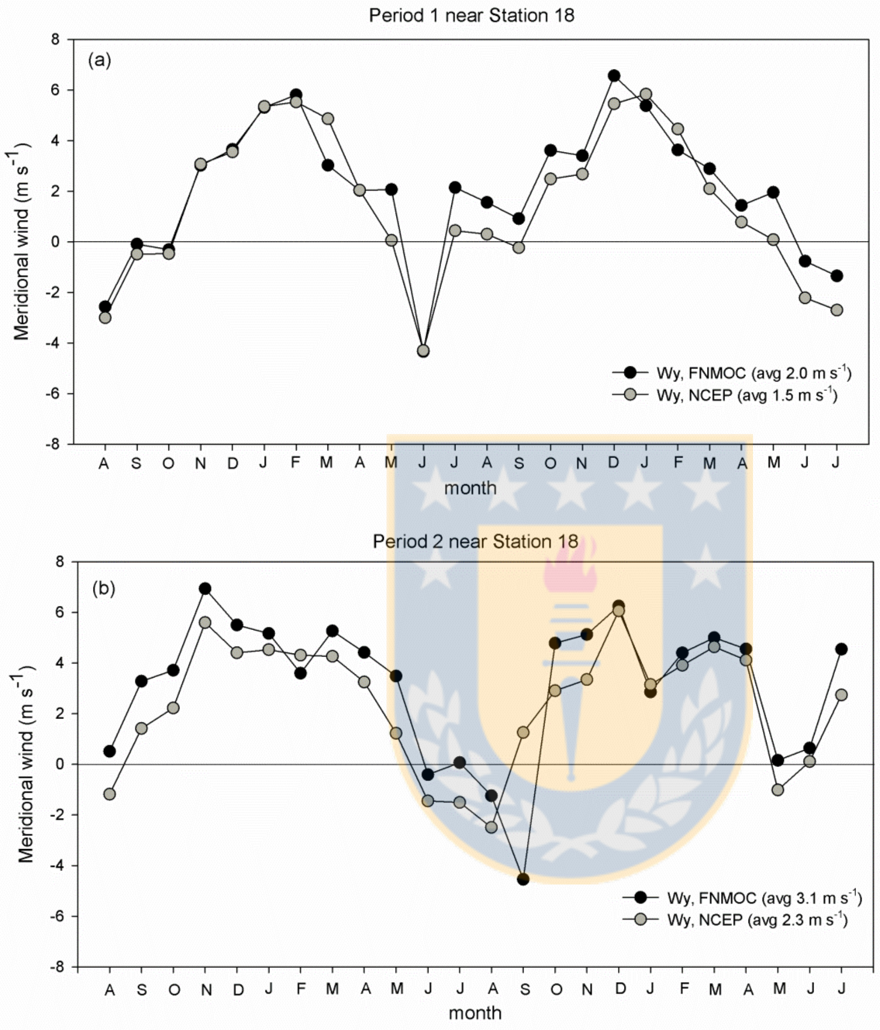

a)
(g1)
Scaphocalanus echinatus
Acartia tonsa
(g2)
Eucalanus hyalinus
Saphirella sp.
Pleuromamma gracilis
(g3)
Eucalanus inermis
Triconia similis
Haloptilus longicornis
Microcalanus pygmaeus
Metridia lucens
Heterorhabdus lobatus
Scolecithricella bradyi
Aetideus armatus
Drepanopus forcipatus
Oithona similis
Oithona setigera
Rhincalanus nasutus
Calocalanus styliremis
Lucicutia flavicornis
Corycaeus sp.
Clausocalanus arcuicornis
Clausocalanus jobei
Pontellina plumata
Farranula sp.
Corycaeus amazonicus
Temora stylifera
Vettoria granulosa
Oithona plumifera
Clytemnestra rostrata
Pleuromamma quadrungulata
Corycaeus speciosus
Pleuromamma abdominalis
Oncaea mediterranea
Mesocalanus tenuicornis
Centropages brachiatus
Calocalanus tenius
Lubbockia squillimana
Oncaea venusta
Nannocalanus minor
Subeucalanus crassus
Clausocalanus furcatus
(g4)
Heterorhabdus sp.
Heterorhabdus spinifrons
Calanus chilensis
Ctenocalanus vanus
Pseudoamallothrix ovata
Microsetella rosea
Oncaea media
Triconia conifera
(g5)
Calanoides patagoniensis
Paracalanus indicus
Pseudoamallothrix profunda
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Distance (Pearson correlation)
b)
(g1)
Scolecithrix danae
Acartia danae
Euchaeta marina
Candacia pachydactila
Oculosetella gracilis
(g2)
Scolecithricella abyssalis
Macrosetella gracilis
Oncaea venusta
Nannocalanus minor
Scolecithricella bradyi
(g3)
Oithona setigera
Drepanopus forcipatus
Oithona similis
Clausocalanus arcuicornis
Calocalanus plumulosus
Aetideus bradyi
Mesocalanus tenuicornis
Paracalanus indicus
(g4)
Triconia conifera
Rhincalanus nasutus
Pleuromamma xiphias
Metridia lucens
Pleuromamma gracilis
Aetideus armatus
Scaphocalanus echinatus
Calocalanus tenius
Microcalanus pygmaeus
Calanus chilensis
Centropages brachiatus
Oncaea mediterranea
Heterorhabdus papilliger
Scolecithricella minor
Scaphocalanus curtus
Subeucalanus crassus
Triconia similis
Clytemnestra rostrata
(g5)
Vettoria granulosa
Scaphocalanus brevicornis
Microsetella rosea
Pseudoamallothrix profunda
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Distance (Pearson correlation)

Figure 10


Period 1 near Station 18
(a)
Meridional wind (m s^{-1})
8
6
4
2
0
-2
-4
-6
-8
A S O N D J F M A M J J A S O N D J F M A M J J
month
Wy, FNMOC (avg 2.0 m s^{-1})
Wy, NCEP (avg 1.5 m s^{-1})
Period 2 near Station 18
(b)
Meridional wind (m s^{-1})
8
6
4
2
0
-2
-4
-6
-8
A S O N D J F M A M J J A S O N D J F M A M J J
month
Wy, FNMOC (avg 3.1 m s^{-1})
Wy, NCEP (avg 2.3 m s^{-1})

Capitulo 2: Manuscrito en preparación

"Variabilidad estacional e interanual de la biomasa mesozooplanctónica de la Estación 18 en la zona de surgencia costera de Chile centro-sur"

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Resumen

Se evalúo la variabilidad estacional e interanual de la biomasa mesozooplanctónica de la serie de tiempo COPAS en la estación 18 en el sistema de surgencia costera de Chile centro-sur para el periodo 2002-2012. La biomasa mesozooplanctónica total (BM) fluctuó entre 0.07 y 60 g peso seco m^{-2} en el estrato de 0-80 m. Se observaron dos máximos anuales, uno en primavera (noviembre) y otro en otoño (mayo). El patrón estacional no estuvo relacionado con el ciclo anual de clorofila-a, a excepción del máximo de primavera que coincide con el florecimiento de fitoplancton. Las condiciones oceanográficas durante la serie de tiempo muestran una fuerte estacionalidad que se repiten año tras año, caracterizándose por un periodo de surgencia activa en primavera-verano, y un periodo de no surgencia en otoño-invierno. Cuando la variabilidad temporal de la BM fue divida en periodos de no surgencia y surgencia, no se encontraron diferencias significativas en la BM. Sin embargo, hubo una fuerte variabilidad interanual en la BM altamente significativo, con mayores valores en el periodo 2002-2003, y mucho menos hacia el final de la serie de tiempo en 2010-2012. También hubo una tendencia lineal negativa y significativa en la BM a través del tiempo. Estudios anteriores proporcionan evidencia de una tendencia en el aumento de la surgencia en la zona costera. La tendencia negativa en la biomasa parece relacionada con este incremento gradual de la intensidad de la surgencia. Aunque la correlación de múltiples factores puede afectar a la comunidad zooplanctónica, nuestro estudio sugiere el uso de la BM como un indicador simple y fácil de medir las respuestas de los ecosistemas marinos al cambio climático-oceanográfico, ya que estos pueden reflejar rápidamente las presiones bottom-up y top-down que actúan sobre los niveles tróficos inferiores.

Seasonal and interannual variation of mesozooplankton biomass at Station 18 in the coastal upwelling zone off Central-southern Chile

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ABSTRACT

We assessed seasonal and interannual variability of mesozooplankton biomass at Station 18 from the COPAS Time Series Study in the coastal upwelling system of central/southern Chile for the period 2002-2012. Zooplankton biomass (ZB) ranged between 60.13 and 0.067 g dry weight m^{-2} in the upper 0-80 m. Two annual peaks were observed in the spring (November) and in the autumn (May). The seasonal pattern was not related to the annual cycle of Chlorophyll-a, except for the spring peak that coincided with the spring phytoplankton bloom. Oceanographic conditions were strongly seasonal, characterized by a spring-summer active upwelling period, and a non-upwelling or downwelling (autumn-winter) period. When temporal variation of ZB is divided into upwelling (spring-summer) and non-upwelling (autumn-winter) periods, there were no significant differences in ZB. By contrast, there was a strong and highly significant interannual variability in ZB, with greater values in 2002-2003 and much lower to the end of the time series 2010-12. There was also a significant negative linear trend in ZB through time. Evidence for a long trend of increasing upwelling in this coastal region suggests that the negative trend in biomass may relate to a negative impact of increased upwelling on zooplankton production and biomass. Although multiple-correlated factors can affect ZB in the ocean, our study suggests the use of ZB as a simple and easy-to-measure proxy of ecosystem response to climate-oceanographic variability, as it can readily reflect both bottom-up and top-down pressures acting on lower trophic levels.

1. Introduction

Long-term observations of zooplankton are currently considered as a valuable tool to assess the responses of marine ecosystem to climate variability (Perry et al. 2004, Richardson and Schoeman, 2004; Beaugrand et al., 2002; Richardson, 2008; Mackas and Beaugrand, 2010). Zooplankton is comprised by short-lived organisms, highly sensitive to environmental change, and considered as rapid responders in abundance and composition to alterations in some key oceanographic variables, such as temperature (Huntley and Lopes 1992, Escribano et al. 2013), food quantity and quality (Bonnet et al. 2002, Hirst and Bunker 2003, Vargas et al. 2010), stratification of the water column (Richardson 2008), oxygenation (Seibel 2011, Dam 2013, Wishner et al. 2013, Donoso and Escribano 2013), and changes in circulation of water masses (Peterson and Mendelson 2009, Chiba et al. 2010). All these variables may be altered by climatic variability due to the strong interaction between ocean and atmosphere dynamics (Reid et al. 2009, Belkin 2009, Bakun et al. 2010).

Most works dealing with zooplankton studies have considered that changes in community structure can be used as indicators of responses of the marine ecosystem to environmental change (Beaugrand et al. 2002, Hays et al. 2005, Reid et al. 2009). However, taxonomic and size structure analyses of zooplankton, is a time-demanding work, and therefore results take time to become available. The bulk of zooplankton biomass has been less used in the context of climate change, in spite of some findings that show correlation between biomass and long-term environmental changes (Rommich and McGowan 1995, Ayon et al., 2004). Studies have revealed long-term trends associated with low frequency fluctuations in oceanography conditions (Perry et al. 2004, Mackas et al. 2010), suggesting that climate variability may regulate the whole zooplankton community with probable consequences for higher trophic levels and most likely affecting ecosystem productivity.

In the context of climate change, in the coastal upwelling zone of the eastern south Pacific there are very few long-term observations of zooplankton biomass. The longest time series involving zooplankton biomass comes from IMARPE off Peru, and started by 1960 (Ayón et al. 2004, 2008). At northern Chile, a zooplankton time series initiated in 1988 has been focused only on copepod species and biomass (Escribano et al. 2012). In central/southern Chile, the COPAS time series (Escribano and Morales 2012) started by mid 2002 includes zooplankton biomass and composition. Preliminary observations on seasonal zooplankton biomass (2002-2005) are described in Escribano et al. (2007), and also seasonal and interannual variation in copepod biomass is examined by Escribano et al. (2012).

In central/southern Chile the most important source of variation for oceanographic conditions over seasonal and interannual scales come from changes in upwelling intensity (Strub et al. 1998). Upwelling conditions prevail during the spring-summer and downwelling or non-upwelling conditions dominate in the autumn and winter (Sobarzo et al. 2007). Copepod species and biomass seem to respond to upwelling variation, at least for dominant species (Hidalgo and Escribano, 2007; Escribano et al., 2012). Although copepods can greatly contribute to total zooplankton biomass, at times larger-sized euphausiids may also dominate the zooplankton community. It is not known whether the bulk of zooplankton biomass fluctuates in association with the strongly seasonal upwelling, and if eventual longer-term changes in upwelling can affect the magnitude of the entire zooplankton community.

In this work, we assess seasonal and interannual variation of total mesozooplankton biomass from the COPAS Time Series at Station 18 for the period 2002-2012. We aim at testing the hypothesis that upwelling intensity is the key driver for seasonal and interannual variability in plankton production, and that such response can be reflected in the bulk of mesozooplankton biomass.

2. Methods

2.1. Sampling and data collection procedures

The COPAS Time Series studies was initiated in August 2002 at Station 18 off Concepción (36°30') (Fig. 1), and it was intended as an integrated research initiative of COPAS Center to assess physical, chemical and biological variability at the coastal upwelling zone off Central/southern Chile (Escribano and Schneider 2007). The study also included some biogeochemical processes, such as primary production rate and nutrient recycling upon seasonal and interannual variability (Escribano and Morales 2012).

Zooplankton sampling at Station 18 Started with the Time Series (August 2002) and it has been maintained since then, roughly on a monthly basis. Sampling methods were described in detail in Escribano et al. (2007). Briefly, a 1 m^2 Tucker Trawl net equipped with a 200 µm mesh-size and a calibrated flowmeter is vertically deployed down to 80 m. The Tucker Trawl is equipped with three opening/closing nets with which we sampled three depth strata: 0-80 m, 80-50 m and 50-0 m. The net is trawled at about 1 m s^{-1} for ca. 20 minutes, and during 2011 and 2012 night-time and daytime samples were obtained in a 12 h interval at same station 18. Samples of zooplankton were immediately split onboard and a fraction (1/4 or 1/2) is frozen for dry weight and the rest preserved in 4% formalin for later analysis. Zooplankton biomass as dry weight is obtained after drying samples for 24 h at 60 °C, as described in Escribano et al. (2007).

Along with zooplankton sampling, the water column conditions at Station 18 are assessed with vertical profiles of a SeaBird SBE-25 or SBE-19 plus CTD's equipped with oxygen sensors and fluorometer. Additionally, water samples are obtained at 9 depths with an Oceanographic Rosette and Niskin bottles for analysis of Chlorophyll-a (Chla) by fluorometric methods. Oceanographic variability has also been complemented with daily measurements of SST at a coastal site at the Dichato Marine Biology Station (Fig. 1).

2.2. Data analyses

Because upwelling is strongly seasonal, and it becomes mostly active during the spring-summer seasons, we divided the oceanographic data into upwelling (October-March) and non-upwelling (April- September) periods, and also compared and examined zooplankton biomass (ZB) between these two periods. The following hydrographic variables were considered: temperature, salinity, dissolved oxygen, depth of the oxygen minimum zone (OMZ), defined as depth at 1 mL O_2 L^{-1}, water column stratification and Chlorophyll-a. Additionally, we used an upwelling index estimated from geostrophic winds for the region and available at the NOAA Center (www.NOAA.gov). This upwelling index has been estimated through the NCEP/NCAR Reanalysis Project at the NOAA/ESRL Physical Sciences Division (Kalnay et al. 1996).

The monthly Stratification Index (ϕ) of the water column was derived from temperature, salinity and density (Sigma-T). ϕ was estimated for the upper 50 m layer by calculating the geopotential energy anomaly, as described by Bowden (1983), such that:

$$\Phi = \int_{-H}^{0} (\rho m - \rho)\ gz\ dz \qquad (1)$$

where ϕ is the stratification index (J m^{-2}), g is the acceleration of gravity (9.8 m s^{-2}), H is the depth of the water column (50 m), ρ is water density (kg m^{-3}) at depth z (m) and ρm is the average density of the water column (0-50 m).

From hydrographic variables, time series of contours were constructed for the 0-80 m layer and also the annuals cycles (climatology) for each variable were derived along with the annual cycle of ZB. Annual means for each variable were derived separately for upwelling and non-upwelling periods. Statistical comparisons of ZB between day and night conditions, between vertical strata and among years were performed with ANOVA after testing normality of data with the Kolmogorov-Smirnov (K-S) test. ZB data were previously log-transformed. Linear trends of the time series were assessed by least-square linear regression, whereas correlations between ZB and oceanographic variables were examined with stepwise multiple regressions.

3. Results

3.1. Oceanographic variability at Station 18

Hydrographic variables at Station 18 describe the general conditions of the upwelling zone off central/southern Chile for the last 10 years (2002-2012). A summary of descriptive statistics for these hydrographic variables is shown in Table 1. SST statistics is derived from the near-shore daily measurements. The almost 7 °C difference in SST reflects the temperature variation in surface water between summer and winter at the near-shore. The other variables are from Station 18. Salinity showed minimal values during the winter upon runoff and river discharges, and greater values during the summer when upwelling becomes active. The dissolved oxygen range at the surface in Station 18 can also be an expression of seasonality and upwelling variability from a highly mixed and possibly oxygen-saturated water in the winter to lower surface oxygenation (<3 mL O_2 L^{-1}) in the summer condition. The assumed upper boundary of the OMZ (1 mL O_2 L^{-1}) may also vary depending on seasonal upwelling conditions from a deep OMZ in the winter to a much shallower one (<15 m) in the summer.

Associated with seasonal upwelling surface Chla exhibits a wide range from very high (>30 mg m^{-3}) in the spring-summer to very low (<1 mg m^{-3}) during downwelling condition in the winter (Table 1).

The strong seasonality of upwelling is clearly reflected in the hydrographic conditions of the water column (Fig. 2). Surface warming occurs subsequently to the subsurface ascent of colder water due to upwelling in late spring and early summer (Fig. 2a). Variability of salinity occurs mainly in the upper 20 m layer and it characterizes by sudden decreases in the winter, as related to increased freshwater inputs (Fig. 2b). Dissolved oxygen also showed a strong seasonal pattern characterized by spring-summer incursions of the OMZ into the upper 20 m (Fig. 2c). Meantime, Chla variation exhibits important increases during the upwelling season in the upper 20 m layer, although this pattern does not show much regularity from year to year (Fig. 2d).

Using data from the entire time series, climatology was derived for all hydrographic variables (Fig. 3). Despite the inflow of colder water during upwelling in the spring-summer season, surface warming during the austral summer is a clear pattern for SST, and the lowest temperatures occur in the middle of winter (Fig. 3a). The climatology of salinity also shows a minimal surface salinity in the middle of winter (Fig. 3b). Meantime, the annual cycle of dissolved oxygen follows a seasonal pattern also related to the upwelling season, although in this case exhibiting a minimal surface oxygen level by the end of the summer, and over-saturated levels in the summer, possibly related to high photosynthesis in near-surface water (Fig. 3c). By contrast, the OMZ depth clearly reflects seasonal upwelling from a deep OMZ in the winter to a shallow one in the spring-summer (Fig. 3d). The seasonal climatology of water column stratification shows maximal stratification during the winter (Fig. 3e), and this is related to decreased surface salinity (Fig. 2b) in this period causing a much lower density in surface, although there is also a secondary peak in stratification during the summer upon surface warming (Fig. 3e). All these seasonal patterns in hydrographic conditions are greatly caused by the strong seasonality of the upwelling process, as shown by the annual regime of upwelling reflected in the climatology of the NOAA upwelling index for this region (Fig. 3f).

Since the annual regime is dominated by a clear pattern of upwelling and downwelling seasons, the time series data were divided into these two periods (Fig. 4). Downwelling and upwelling differences are reflected in SST variation (Fig. 4a), surface salinity (Fig. 4b), whereas in surface oxygen conditions differences are unclear (Fig. 4c), but remarkable in depth of the OMZ (Fig. 4d). Water column stratification seems greater during downwelling, although with much variability (Fig. 4e), and Chla is strongly variable but clearly higher during the upwelling period (Fig. 4f).

The oceanographic variables also exhibited strong interannual fluctuations (Fig. 4). The results from a two-ways ANOVA to test the effect of upwelling and interannual variation on oceanographic variables are shown in Table 3. Significant differences in upwelling vs downwelling conditions were found in the Upwelling Index, SST, OMZ depth and surface Chla, whereas interannual variation was not significant in the oceanographic variables shown in Fig. 4.

3.2. Variability of zooplankton biomass

Potential diurnal effects on zooplankton biomass derived from either, vertical displacement of migrators or net avoidance during daylight conditions, were tested using data available from daytime and nighttime sampling. Water column integrated biomass (0-80 m) was used, and because of small sample size (n=13), a non-parametric Kolgomorov-Smirnov (K-S) test was applied. Diurnal biomass (mean= 5339.7 mg DW m^{-2}) was not significantly different from night biomass (mean=5444.1 mg DW m^{-2}) ($K\text{-}S_{1,12}$= 0.23, $P>0.05$).

Variability in vertical distribution of biomass was also examined, because of the strong gradient in oxygen concentration mainly during the upwelling period (September-March). Zooplankton biomass between the 0-50 m and 50-80 m layers were compared and biomass was expressed as mg DW m^{-3}. Data (n=65) were log-transformed and a one-way ANOVA was applied. The 0-50 m biomass (mean=41.2 ± 60.12 mg DW m^{-3}) was not significantly different from that in the 50-80 m layer (mean=33.1 ± 51.37 mg DW m^{-3}) ($F_{1,128}$ =0.27, $P>0.05$).

Separate time series of zooplankton biomass (water column integrated) by strata and diurnal conditions are shown in Fig. 5, as expressed in a log-scale for comparison purposes. The integrated 0-80 m biomass exhibited strong interannual variation and had a significant negative trend ($F_{1,119}$ =8.28, $P<0.01$) from 2002 to 2012 (Fig. 5a). Biomass in the layer 0-50 m (Fig. 5b) and 50-80 m (Fig. 5c) showed the same patterns as the integrated one.

The annual cycle of zooplankton biomass (Fig. 6) revealed two major peaks. The first peak occurred during late spring (November) and a secondary peak takes place in the autumn (May). This pattern is clearly shown in 0-80 m integrated biomass, but not clearly reflected in stratified estimates of biomass. This annual cycle does not seem related to the annual cycle of Chla, except for the spring peak that coincides with the spring phytoplankton bloom (Fig. 6).

When analyzing interannual variability of biomass, as divided into upwelling and downwelling conditions, there appear not to be major differences between upwelling vs downwelling conditions (Fig. 7), and in fact the apparent differences are non-significant (Table 3). Meantime, ANOVA showed highly significant differences among years (Table 3). A multiple comparison a posterior test (LS means) showed that year-to-year differences in biomass occurred after significant higher biomasses in 2002 and 2003, and a significantly lower biomass at the end of the series in 2010. All these differences are consistent with the negative linear trend towards the end of the series as shown in Fig. 4a.

It was thought that interannual variability in biomass could be related to some of the oceanographic changes occurring year to year. However, a stepwise-multiple regression, between log-transformed data of biomass and oceanographic variables, showed the absence of any significant correlation (P>0.05).

4. Discussion

When studying the dynamics of zooplankton, the bulk of zooplankton biomass (ZB) is a relatively simple measurement of the plankton community, and it can be suggested as an alternative approach to the time-consuming analysis of composition of taxonomic groups, or even species composition. A. ZB can be estimated as volume, wet or dry weight, C and N (Harris et al. 2000), and it can provide a rapid low-cost and synoptic assessment of ecosystem state. In fact, in several regions of the world ocean time series of zooplankton have served to assess ecosystem responses to climate variability (Atkinson et al. 1974, McGowan and Rommich, 2005; Ayón et al. 2004).

Variability in ZB might reflect changes in plankton production which can be driven by bottom-up processes (Huggett et al. 2009). However, there are many sources of forcing for ZB in the ocean, acting as both bottom-up and top-down processes. Over the spatial domain, advection and mixing are processes can strongly affect horizontal and vertical distribution of plankton (Peterson 1998), whereas temporal changes can obey to multiple factors acting from short-term to long-term scales. From the viewpoint of climate variability, long-term changes and trends are relevant, since they can indeed reflect the effects of persistent altered conditions. It is thus expected that gradual responses would take place for biological components as an adjustment to new conditions (Richardson, 2007; Beagraund et al. 2002). Certainly, lower trophic levels are likely to reflect such changes more rapidly than higher ones. Therefore, plankton variability itself has been used as indicator of ecosystem change to climate variability.

Our study shows that ZB can respond to upwelling variation over a long (interannual/decadal) time scale. Upwelling variation can impose several constraints to plankton production through bottom-up processes, but it can also promote top-down control of plankton populations through biological interactions (Thiel et al. 2007, Escribano et al. 2012). It also seems that dominant zooplankton species, such as copepods and euphausiids can couple their annual cycles to the upwelling regime (Hidalgo and Escribano 2008, Riquelme-Bugueño et al. 2012). Synchronizing life cycles with upwelling pulses seems an advantage in terms of reproductive success, because pulses of upwelling promote phytoplankton flourishing and subsequent food chains to increase zooplankton production and hence ZB. Even although, both type of food, autotrophic and heterotrophic may be sufficient year round to sustain population growth of dominant zooplankton in the upwelling zone (Vargas et al. 2006; Escribano et al. 2009), egg spawning to initiate new cohorts may substantially depend on pulses of phytoplankton growth which can be upwelling-dependent.

In a 20 year time series study of copepods, the dominant group in the zooplankton of the upwelling zone, performed in northern Chile, it was found that copepod biomass exhibited interannual variation closely related to upwelling intensity, and that gradually increased upwelling in late years (2000-2010) was associated with a negative trend of biomass (Escribano et al. 2012). It was therefore suggested that extremely increased upwelling may negatively impact zooplankton populations (Escribano et al. 2012), and perhaps productivity of the entire upwelling system might decrease as a consequence of abnormally high upwelling, as suggested by Bakun et al. (2010).

Acknowledgements

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Table 1. Oceanographic variability at Station 18 during 2002-2012 from the monthly time series. SST= Sea Surface Temperature (°C), SAL = Surface Salinity, O_2= Surface Dissolved Oxygen (mL L^{-1}), OMZ= Oxygen Minimum Zone depth (m), Chla=Surface Chlorophyll-a (mg m^{-3}). SE= Standard error, C.V= Coefficient of Variation, n= Sample size.

Variable	Mean ± SE	Range	C.V.	n
SST	13.03 ± 0.121	10.78-17.290	0.009	116
SAL	33.74 ± 0.095	29.47-34.592	0.003	104
O_2	4.97 ± 0.102	2.55-7.316	0.021	97
OMZ	-38.64 ± 1.976	13.00-80.000	0.051	84
Chl-a	5.21 ± 0.698	0.20-41.242	0.134	104

Table 2. Zooplankton biomass (g DW m^{-2}) from the time series at Station 18 off Concepción in three depth strata and for daytime and nighttime conditions. SE= standard error, C.V= Coefficient of Variation, n= Sample size.

Depth strata	Mean ± SE	Range	C.V.	n
0-80 m	5.42 ± 0.795	0.07-60.126	0.147	108
0-80 m (night)	5.44 ± 1.550	0.08-18.892	0.285	13
50-0 m	2.06 ± 0.373	0.11-15.962	0.181	65
80-50 m	0.98 ± 0.188	0.03-8.840	0.192	66

Table 3 Two-way ANOVA to test the effect of upwelling condition (upwelling vs downwelling period) and interannual variation on oceanographic variables and zooplankton biomass, during the time series study off Concepcion (2002-2012).

Variable	Source of variation					
	Upwelling condition			Interannual		
	df	F-ratio	p-value	df	F-ratio	p-value
Upwelling Index	1	55.14	0.000**	10	0.142	0.999
SST	1	67.972	0.000**	10	1.168	0.320
Salinity	1	0.213	0.645	10	1.114	0.360
OMZ depth	1	55.409	0.000**	10	0.512	0.877
Stratification	1	1.190	0.278	10	1.040	0.417
Chla	1	23.871	0.000**	10	1.197	0.301
Zoo Biomass	1	1.396	0.240	10	3.175	0.001**

**p<0.01

Figure Captions

Figure 1. The coastal upwelling region of central-southern Chile, illustrating location of Station 18 where the COPAS Time Series Study takes place since 2002 to present.

Figure 2. Time series of profiles of temperature (°C), salinity (psu) and dissolved oxygen (ml L^{-1}) at Station 18 from August 2002 to September 2012 and Chlorophyll-a (mg m^{-3}) from August 2002 to March 2012.

Figure 3. Annual cycle of a) Sea surface temperature (SST) (°C), b) salinity, c) dissolved oxygen (ml L^{-1}), d) OMZ depth (m), e) potential energy anomaly (J m^{-3}), and f) Upwelling Index (m^3 s^{-1} 100 m^{-1}), at Station 18 in the coastal upwelling zone off central/southern Chile 2002-2012.

Figure 4. Oceanographic conditions during upwelling and downwelling periods at Station 18 (2002-2012). a) SST (°C), b) salinity, c) dissolved oxygen (ml L^{-1}), d) OMZ depth (m), e) potential energy anomaly (J m^{-3}), and f) Chlorophyll-a (mg m^{-3}).

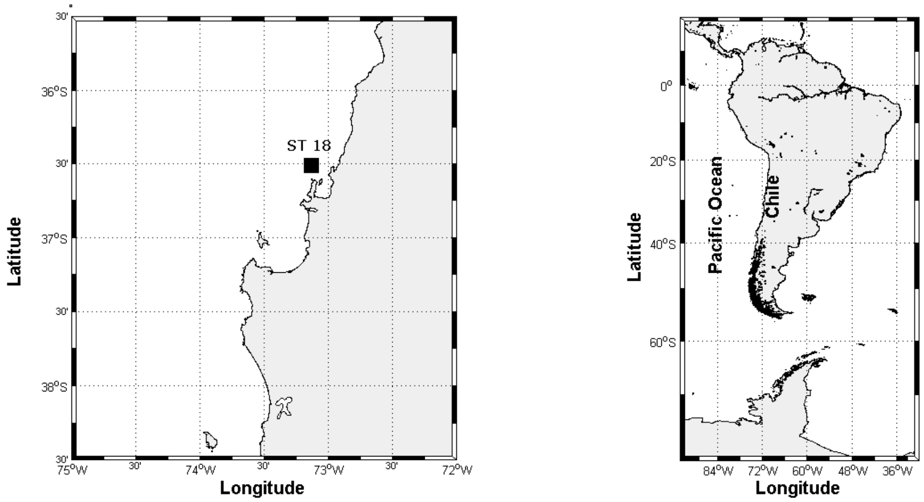
Figure 5. Mesozooplankton biomass (ZB) (log-scale) in the depth strata 0-80 m (day and night conditions), 50-0 m and 80-50 m, at Station 18 during 2002-2012

Figure 6. Annual cycle (climatology) of zooplankton biomass (ZB) (g DW m^{-2}) in three depth strata 0-80 m, 50-0 m, and 80-50 m and Chlorophyll-a (mg m^{-3}) at Station 18 during 2002-2012 in the upwelling zone of Central/southern Chile.

Figure 7. Zooplankton biomass (ZB) (g DW m^{-2}) for upwelling (October to March) and downwelling (April to September) conditions at Station 18 during 2002-2012.

Figure 8. Time series of ZB (log-scale) and upwelling index at Station 18 in the coastal upwelling zone off Central/southern Chile.

Figure 1



ST 18
Latitude
Longitude
30'
36°S
30'
37°S
30'
38°S
30'
75°W
30'
74°W
30'
73°W
30'
72°W
Pacific Ocean
Chile
Latitude
Longitude
0°
20°S
40°S
60°S
84°W
72°W
60°W
48°W
36°W

Figure 2

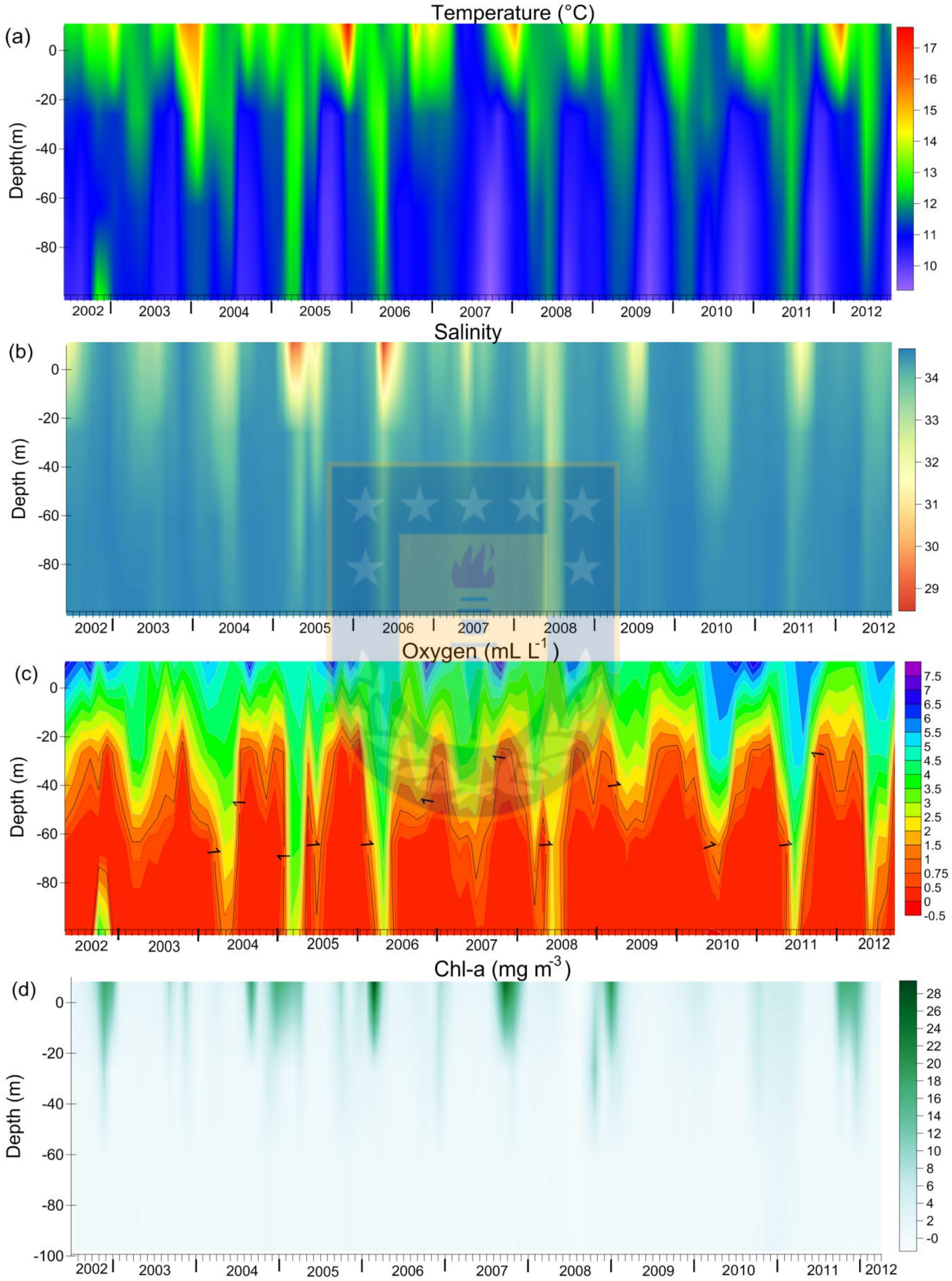

Temperature (°C)
(a)
Depth(m)
0
-20
-40
-60
-80
17
16
15
14
13
12
11
10
Salinity
(b)
Depth (m)
0
-20
-40
-60
-80
34
33
32
31
30
29
Oxygen (mL L^{-1})
(c)
Depth (m)
0
-20
-40
-60
-80
7.5
7
6.5
6
5.5
5
4.5
4
3.5
3
2.5
2
1.5
1
0.75
0.5
0
-0.5
Chl-a (mg m^{-3})
(d)
Depth (m)
0
-20
-40
-60
-80
-100
28
26
24
22
20
18
16
14
12
10
8
6
4
2
-0
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012

Figure 3

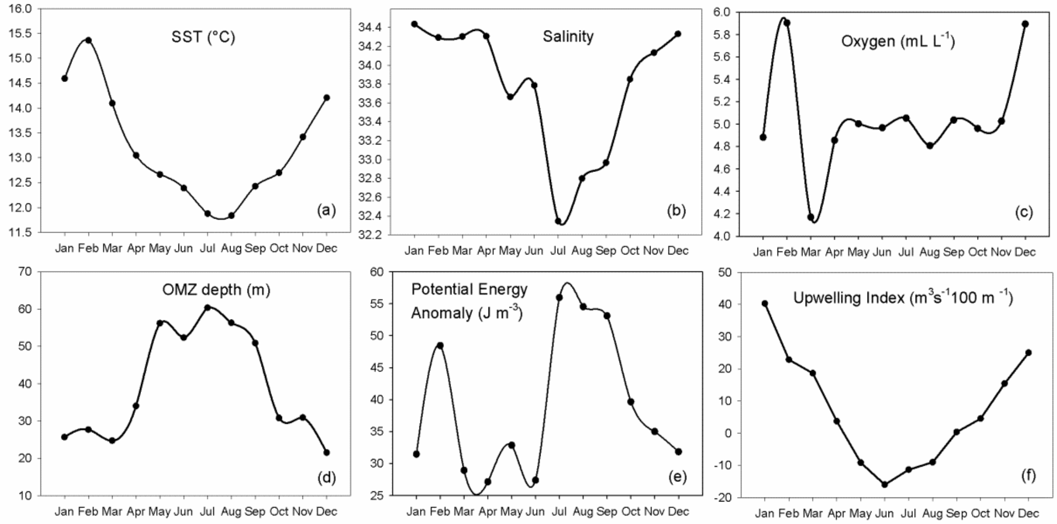

SST (°C)
(a)
16.0
15.5
15.0
14.5
14.0
13.5
13.0
12.5
12.0
11.5
Salinity
(b)
34.4
34.2
34.0
33.8
33.6
33.4
33.2
33.0
32.8
32.6
32.4
32.2
Oxygen (mL L^{-1})
(c)
6.0
5.8
5.6
5.4
5.2
5.0
4.8
4.6
4.4
4.2
4.0
OMZ depth (m)
(d)
70
60
50
40
30
20
10
Potential Energy Anomaly (J m^{-3})
(e)
60
55
50
45
40
35
30
25
Upwelling Index (m^{3}s^{-1}100 m $^{-1}$)
(f)
50
40
30
20
10
0
-10
-20
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec

Figure 4

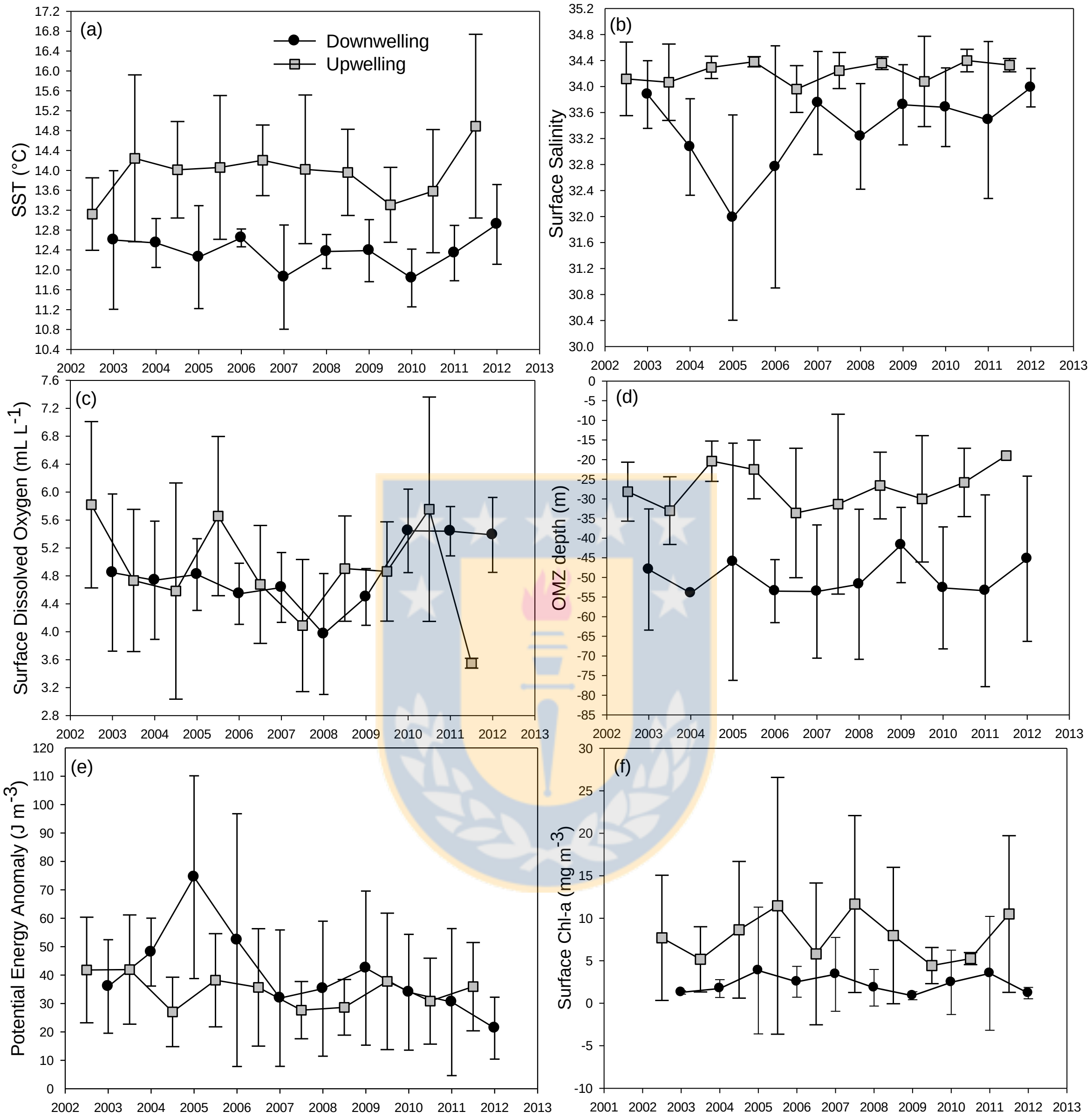

(a)
Downwelling
Upwelling
SST (°C)
17.2
16.8
16.4
16.0
15.6
15.2
14.8
14.4
14.0
13.6
13.2
12.8
12.4
12.0
11.6
11.2
10.8
10.4
2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013
(b)
Surface Salinity
35.2
34.8
34.4
34.0
33.6
33.2
32.8
32.4
32.0
31.6
31.2
30.8
30.4
30.0
2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013
(c)
Surface Dissolved Oxygen (mL L^{-1})
7.6
7.2
6.8
6.4
6.0
5.6
5.2
4.8
4.4
4.0
3.6
3.2
2.8
2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013
(d)
OMZ depth (m)
0
-5
-10
-15
-20
-25
-30
-35
-40
-45
-50
-55
-60
-65
-70
-75
-80
-85
2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013
(e)
Potential Energy Anomaly (J m^{-3})
120
110
100
90
80
70
60
50
40
30
20
10
0
2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013
(f)
Surface Chl-a (mg m^{-3})
30
25
20
15
10
5
0
-5
-10
2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013

Figure 5

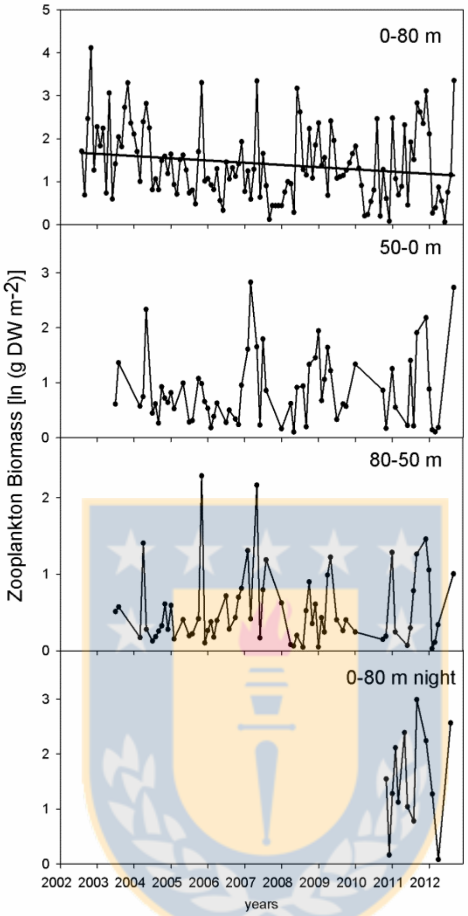
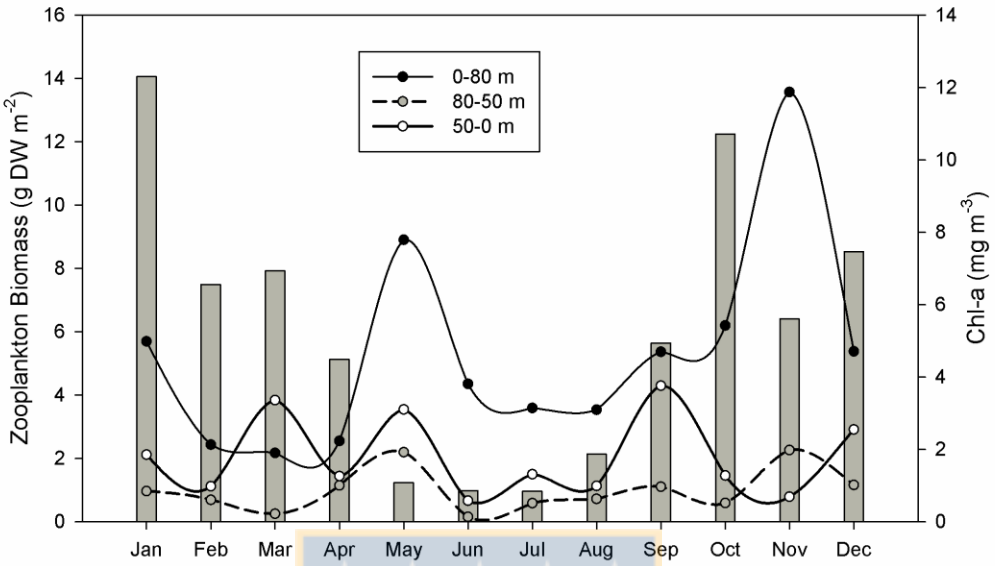
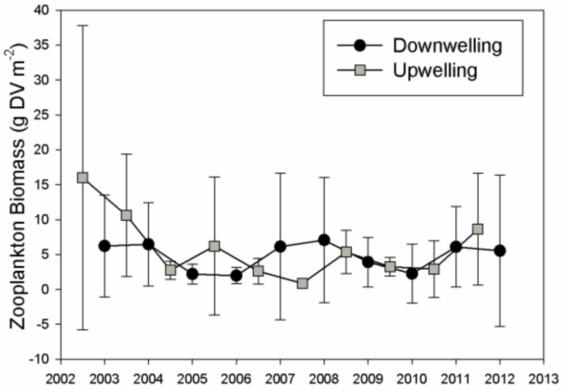

0-80 m
50-0 m
80-50 m
0-80 m night
Zooplankton Biomass [ln (g DW m-2)]
0
1
2
3
4
5
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
years

Figure 6



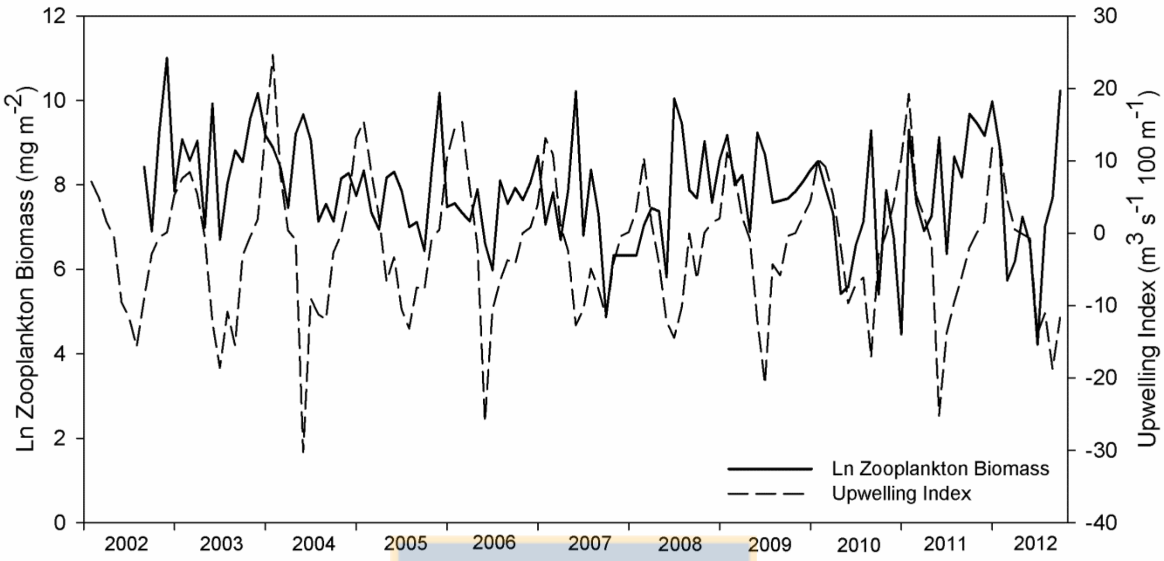
Zooplankton Biomass (g DW m^{-2})
Chl-a (mg m^{-3})
0-80 m
80-50 m
50-0 m
0
2
4
6
8
10
12
14
16
0
2
4
6
8
10
12
14
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 7



Zooplankton Biomass (g DV m^{-2})
40
35
30
25
20
15
10
5
0
-5
-10
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
Downwelling
Upwelling

Figure 8


12
10
8
6
4
2
0
Ln Zooplankton Biomass (mg m^{-2})
30
20
10
0
-10
-20
-30
-40
Upwelling Index (m^3 s^{-1} 100 m^{-1})
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
Ln Zooplankton Biomass
Upwelling Index

5. DISCUSIÓN

Este estudio aborda el primer análisis de los cambios en la estructura comunitaria de copépodos, biomasa mesozooplanctónica y variabilidad oceanográfica en una escala decadal (2002-2012) en la zona centro-sur de Chile. A pesar que 10 años es un periodo relativamente breve y las tendencias podrían corresponder a una oscilación natural de más largo plazo, es la serie de tiempo más extensa que existe en la zona centro-sur de Chile.

Fue posible evidenciar cambios importantes en la biomasa mesozooplanctónica y en la estructura comunitaria de copépodos posiblemente en respuesta a los cambios oceanográficos observados durante los últimos 10 años. En este estudio un punto importante a destacar fueron los cambios en la columna de agua, presentándose más fría y más densa y más salina en la capa superficial. Esto principalmente derivado del aumento en la duración de la surgencia costera producto de la intensificación y duración de los vientos meridionales favorables a surgencia. A pesar de observar intensificación de los vientos meridionales hacia el Periodo 2, el Índice de Surgencia no presentó cambios, esto puede explicarse por efectos espaciales, ya que el Índice de Surgencia es derivado de vientos geostróficos que pueden no tener suficiente resolución en la zona costera donde se ubica la estación 18, de hecho los datos de vientos meridionales de alta resolución en un punto cercano a la estación 18 mostraron diferencias claras entre los dos periodos de estudio, lo que sugiere una mayor duración de surgencia costera en el Periodo 2. Los cambios en la estratificación de la columna de agua (ϕ) podrían confirmar esta condición ya que el Periodo 2 presentó menor estratificación, sugiriendo mayor mezcla vertical.

Los cambios en las condiciones ambientales de temperatura, salinidad y estratificación pueden afectar la estructura de las comunidades zooplanctónicas, como se ha demostrado en otras regiones del mundo (Peterson et al. 2006; Aronés et al. 2009; Beaugrand 2002, 2003; Richardson and Schoeman 2004), reflejando los efectos de las condiciones ambientales alteradas en el tiempo.

Nuestro estudio revela que el zooplancton puede variar y responder a variaciones de la surgencia y que la variabilidad interanual puede ser mayor que la variabilidad estacional. Por ejemplo las especies de copépodos dominantes a lo largo de la serie de tiempo, no presentaron un patrón estacional en sus abundancias asociado a la época de surgencia (primavera-verano), lo cual puede resultar del ciclo de vida que tienen los copépodos en zonas de surgencia costera, donde su reproducción es continua, durante todo el año, al menos para las especies dominantes (Peterson 1998; Escribano et al. 2007; Hidalgo and Escribano 2007). Sin embargo, en la escala interanual fue posible observar cambios en la estructura comunitaria de copépodos, los cuales se vieron reflejados en cambios en la distribución de las abundancias de las especies principales, mientras que algunas especies aumentaron hacia fines de la serie 2010-2012 (*D. forcipatus*) otras especies disminuyeron (*P. indicus*) y otras especies se mantuvieron constantes (*O. similis*). La dominancia de algunas especies también tuvo cambios en el tiempo. Se observó una disminución en la abundancia total de copépodos en el tiempo, lo cual es consistente con la disminución de *P. indicus*. Estudios previos han demostrado que más del 46 % de la abundancia total de copépodos pelágicos en el SCH corresponde a *P. indicus* (Escribano and Hidalgo 2001; Escribano et al. 2001; Hidalgo et al. 2010; Hidalgo et al. 2012). Por lo tanto, esta especie podría ser responsable de la reducción de la abundancia total de copépodos observada durante el período 2002-2008 (Escribano et al. 2012).

La región centro-sur de Chile se caracteriza por estar sometida a la influencia de aguas subantárticas, ecuatoriales y subtropicales en diferentes proporciones en la capa superficial (< 100 m), la mezcla de aguas de diferentes orígenes puede verse afectado por los cambios asociados al ENSO (El Niño Oscilación del Sur). Los datos del Índice Multivariado ENSO (MEI) de la NOAA muestran condiciones principalmente neutrales para el Periodo 1 y condición La Niña principalmente para el Periodo 2 en el Pacífico Ecuatorial. Sin embargo los datos de TSM de la estación 18 no muestran cambios importantes entre ambos periodos, por lo tanto los cambios observados en la abundancia y dominancia de las especies no pueden ser atribuidas a la variabilidad del ENSO, probablemente los cambios han sido inducidos por la duración de la surgencia costera (Bakun et al. 2010).

Todas las especies encontradas en este estudio se han descrito previamente para esta región (Hidalgo et al. 2010, Hidalgo et al. 2012, Morales et al. 2010, Escribano et al. 2012). Cabe señalar que los nombres de tres especies se han modificado en los últimos años. Por lo tanto, esta revisión de especies representa el estado taxonómico actual, que han sido validados en el registro mundial de nombres científicos de especies marinas (WoRMS) (www.marinespecies.org). Este análisis es fundamental para evitar la confusión de sinonimias o errores en la asignación de nombres, para los estudios de diversidad de especies.

La biomasa mesozooplanctónica (BM) por su parte, también presentó mayor variabilidad interanual. Cuando la variabilidad temporal de la BM fue divida en periodos surgencia y no surgencia, no se encontraron diferencias significativas. Sin embargo, hubo una fuerte variabilidad interanual en la BM altamente significativo, con mayores valores en el periodo 2002-2003, y mucho menos hacia el final de la serie de tiempo en 2010-2012. También presentó una tendencia lineal negativa significativa a través del tiempo. Esto puede ser atribuido a la disminución de abundancia de copépodos, los cuales contribuyen con un 80-90% del total de abundancia del mesozooplancton (Hidalgo et al. 2012; Escribano et al. 2012). Nuestro estudio sugiere a la BM como un enfoque alternativo, complementario a la diversidad y abundancia de especies, para medir las respuestas de largo plazo de los ecosistemas marinos, ya que es indicador simple y económico de estudiar la dinámica del zooplancton.

Existen algunas limitaciones al evaluar la variabilidad del zooplancton de las estaciones fijas, ya que la distribución del zooplancton es muy variable en el tiempo y en el espacio, y en aguas de surgencia la distribución del zooplancton es muy agregada (Peterson 1998; Escribano et al. 2002; Hutchings et al . 2006; Morales et al. 2010). Esta fuerte agregación puede afectar las observaciones temporales de la columna de agua cuando se basan en estaciones fijas . A pesar de estos posibles errores de muestreo, estudios de largo plazo realizados sobre la base de las estaciones fijas, han demostrado ser útiles para examinar las tendencias temporales de zooplancton (Perry et al. 2004; Mackas et al. 2010).

Es indudable que existen otros factores que pueden influir en las comunidades del mesozooplancton, como por ejemplo interacciones tróficas (control top-down) u otros forzantes ambientales (control bottom-up), forzando cambios en la composición, tamaño, diversidad y abundancia de las especies (Mackas et al. 2010). Sin embargo, ambos tipos de control de la comunidad pueden ser alterados por modificaciones del entorno físico. En este sentido, las alteraciones de la distribución de la masa de agua y circulación deben ser considerados procesos importantes que alteran el entorno físico, químico y biológico (Chiba et al. 2010). En cualquier caso, parece ser que el aumento en la duración de la surgencia costera en el SCH puede modificar gradualmente y de forma sustancial la comunidad zooplanctónica, esto puede tener un impacto importante a nivel ecosistémico, incluidas posibles modificaciones en la estructura comunitaria en los niveles tróficos superiores, tales como comunidades de peces, aves y mamíferos marinos.

6. CONCLUSIONES

Esta tesis demuestra que el zooplancton y en especial el grupo Copepoda pueden ser utilizados como modelo de estudio para evaluar los potenciales cambios ambientales que ocurren a través del tiempo, actuando como sensores del clima, proporcionando los primeros indicios de alteraciones en el ecosistema marino.

Los cambios en la estructura comunitaria de copépodos estuvieron dados principalmente por la disminución en la abundancia total de copépodos, cambios en la dominancia de las especies, y cambios en la estructura de tamaños.

La tendencia lineal negativa de la biomasa mesozooplanctónica puede ser atribuida a la disminución de copépodos, los cuales contribuyen con un 80-90% del total de mesozooplancton en la zona de estudio.

Las tendencias de las condiciones oceanográficas en la zona costera frente a Concepción revelaron condiciones más frías para la columna de agua y más salinas para la capa superficial del océano desde el año 2002 al 2012, causado por el aumento en la duración de la surgencia costera producto de la intensificación de los vientos meridionales favorables a la surgencia.

Los resultados demuestran la importancia de series de tiempo de zooplancton y confirman la idea de que cambios oceanográficos importantes pueden ser observados en una escala decadal, en la estación 18. Ciertamente son necesarias más investigaciones y una serie de tiempo más larga para comprender en mejor medida las interacciones físicas, químicas y biológicas.

El estudio sugiere que las alteraciones en las condiciones de surgencia costera impulsado por el cambio climático es una fuerza impulsora de los cambios observados en la biomasa mesozooplanctónica y en la abundancia, diversidad y riqueza de especies de copépodos, luego de una ventana de observación de 10 años. En este contexto, la tesis apoya la hipótesis planteada, ya que el incremento de la surgencia costera ha modificado significativamente la estructura comunitaria del grupo Copepoda en la última década.

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ANEXOS

1. SUPPLEMENTAL MATERIAL

Copepod species from the upwelling zone off Central/southern Chile at Station 18, for two sampling periods: 1) August 2002-August 2004 and 2) August 2010-August 2012. N= total abundance (ind. m^{-3}), %= relative abundance (%), StD= standard deviation, mean size= total body length (mm).

Species	N	%	mean	StD	mean size
Period 1 (2002-2004)					(mm)
Paracalanus indicus	17379.77	58.55	755.64	987.19	0.95
Calanoides patagoniensis	5065.43	17.07	230.25	604.69	2.415
Oithona similis	3484.55	11.74	151.50	188.98	0.94
Acartia tonsa	1336.01	4.50	58.09	121.39	1.345
Drepanopus forcipatus	793.54	2.67	36.07	75.42	2.065
Oithona setigera	383.45	1.29	17.43	33.06	1.58
Oncaea media	266.43	0.76	14.15	30.88	0.565
Clausocalanus arcuicornis	166.92	0.56	8.79	27.68	1.36
Microcalanus pygmaeus	160.27	0.54	8.44	10.75	0.86
Centropages brachiatus	102.22	0.34	5.11	5.86	2.25
Calocalanus styliremis	88.59	0.30	4.66	6.59	0.725
Triconia similis	74.53	0.25	14.91	30.06	1.49
Pleuromamma gracilis	69.80	0.24	3.88	6.38	2.025
Rhincalanus nasutus	53.61	0.18	3.57	5.59	5.8
Aetideus armatus	35.98	0.12	2.25	3.38	1.79
Heterorhabdus lobatus	29.61	0.10	1.97	3.24	2.32
Calocalanus tenuis	26.13	0.09	2.90	7.54	1.13
Metridia lucens	25.16	0.08	2.52	4.07	2.95
Oncaea venusta	24.80	0.08	4.96	9.61	1.27
Clytemnestra rostrata	18.17	0.06	1.51	3.42	1.00
Corycaeus sp.	14.65	0.05	1.63	3.29	-
Oncaea mediterranea	14.41	0.05	7.20	6.07	1.225
Clausocalanus furcatus	12.07	0.04	2.41	3.80	1.275
Triconia conifera	11.27	0.04	0.87	1.20	1.11
Nannocalanus minor	8.68	0.03	0.79	0.73	1.925
Lucicutia flavicornis	8.24	0.03	0.82	1.27	1.88
Ctenocalanus vanus	7.97	0.03	0.80	1.56	1.255
Corycaeus speciosus	7.10	0.02	1.42	0.80	1.96
Eucalanus inermis	6.71	0.02	1.34	2.59	6.09
Farranula sp.	6.12	0.02	6.12	-	-
Vettoria granulosa	5.15	0.02	0.74	1.48	0.765
Scolecithricella bradyi	4.94	0.02	0.99	1.56	1.345
Clausocalanus jobei	4.20	0.01	2.10	2.80	1.285
Microsetella rosea	4.20	0.01	1.05	1.30	0.83

Heterorhabdus sp.	2.33	0.01	2.33	-	-
Corycaeus amazonicus	2.04	0.01	2.04	-	0.97
Temora stylifera	2.04	0.01	2.04	-	1.62
Heterorhabdus spinifrons	1.68	0.01	0.84	0.13	3.05
Oithona plumifera	1.58	0.01	0.79	0.81	1.12
Calanus chilensis	1.52	0.01	0.30	0.30	3.1
Oithona nana	1.44	<0.01	1.44	-	0.685
Pontellina plumata	1.36	<0.01	1.36	-	1.485
Pseudoamallothrix profunda	1.31	<0.01	0.65	0.48	2.00
Mesocalanus tenuicornis	0.91	<0.01	0.18	0.10	2.45
Ctenocalanus citer	0.83	<0.01	0.28	0.23	1.125
Eucalanus hyalinus	0.77	<0.01	0.19	0.16	6.325
Pseudoamallothrix ovata	0.74	<0.01	0.74	-	2.2
Saphirella sp.	0.52	<0.01	0.52	-	-
Pleuromamma abdominalis	0.47	<0.01	0.23	0.15	3.45
Scaphocalanus echinatus	0.45	<0.01	0.23	0.29	2.08
Lubbockia squillimana	0.22	<0.01	0.22	-	1.475
Euchirella pulchra	0.19	<0.01	0.19	-	3.64
Pleuromamma quadrungulata	0.16	<0.01	0.05	0.06	4.00
Haloptilus longicornis	0.16	<0.01	0.16	-	2.175
Subeucalanus crassus	0.08	<0.01	0.04	0.03	3.35
Euchirella sp.	0.06	<0.01	0.06	-	-
Oculosetella gracilis	0.03	<0.01	0.03	-	1.045
Acartia danae	0.02	<0.01	0.02	-	1.12

Species Period 2 (2010-2012)	N	%	mean	StD	mean size (mm)
Drepanopus forcipatus	2903.01	27.88	152.79	422.37	2.07
Oithona similis	2423.19	23.27	134.62	320.90	0.94
Calanoides patagoniensis	1436.99	13.80	89.81	250.91	2.42
Paracalanus indicus	876.39	8.42	43.82	70.02	0.95
Clausocalanus arcuicornis	621.19	5.97	41.41	111.25	1.36
Acartia tonsa	522.18	5.01	29.01	37.27	1.35
Microsetella norvegica	445.34	4.28	89.07	198.20	0.56
Microcalanus pygmaeus	340.34	3.27	24.31	44.14	0.86
Oithona setigera	160.97	1.55	9.47	18.50	1.58
Pleuromamma gracilis	135.16	1.30	9.01	22.17	2.03
Corycaeus amazonicus	122.48	1.18	13.61	35.45	0.97
Metridia lucens	78.74	0.76	6.06	14.10	2.95
Oithona nana	78.16	0.75	13.03	9.97	0.69
Triconia similis	63.98	0.61	4.57	11.34	1.49
Rhincalanus nasutus	40.66	0.39	2.71	5.16	5.80

Nannocalanus minor	24.39	0.23	2.03	4.03	1.93
Triconia conifera	22.95	0.22	1.27	2.59	1.11
Pleuromamma xiphias	21.53	0.21	7.18	11.97	4.69
Centropages brachiatus	18.42	0.18	1.23	1.62	2.25
Aetideus armatus	14.76	0.14	1.23	2.17	1.79
Oncaea mediterranea	14.07	0.14	2.81	2.23	1.23
Calocalanus tenuis	11.34	0.11	1.03	1.67	1.13
Triconia minuta	5.67	0.05	1.89	2.79	0.61
Oncaea media	4.97	0.05	1.24	1.75	0.57
Lucicutia flavicornis	4.80	0.05	0.69	1.11	1.88
Mesocalanus tenuicornis	4.59	0.04	0.66	0.80	2.45
Heterorhabdus papilliger	4.23	0.04	0.35	0.62	2.14
Clytemnestra rostrata	3.04	0.03	0.28	0.40	1.00
Oncaea venusta	1.79	0.02	0.45	0.68	1.27
Subeucalanus crassus	1.48	0.01	1.48	-	3.35
Scolecithricella bradyi	1.26	0.01	0.25	0.27	1.35
Vettoria granulosa	0.70	0.01	0.10	0.15	0.77
Scaphocalanus echinatus	0.65	0.01	0.22	0.16	2.08
Aetideus bradyi	0.55	0.01	0.18	0.27	1.61
Pleuromamma abdominalis	0.51	<0.01	0.26	0.31	3.45
Calanus chilensis	0.38	<0.01	0.10	0.14	3.10
Oculosetella gracilis	0.38	<0.01	0.13	0.11	1.05
Clausocalanus pergens	0.31	<0.01	0.31	-	0.90
Scolecithricella minor	0.26	<0.01	0.13	0.09	1.39
Scaphocalanus curtus	0.26	<0.01	0.13	0.16	1.35
Macrosetella gracilis	0.22	<0.01	0.22	-	1.34
Euterpina acutifrons	0.15	<0.01	0.03	0.01	0.64
Candacia pachydactyla	0.14	<0.01	0.07	0.04	2.60
Calocalanus plumulosus	0.06	<0.01	0.06	-	1.11
Pseudoamallothrix profunda	0.06	<0.01	0.06	0.06	2.00
Scaphocalanus brevicornis	0.05	<0.01	0.05	-	2.28
Euchaeta marina	0.05	<0.01	0.02	0.02	3.08
Microsetella rosea	0.04	<0.01	0.02	0.00	0.83
Sapphirina gemma	0.03	<0.01	0.03	-	2.46
Pleuromamma quadrungulata	0.02	<0.01	0.02	-	4.00
Ctenocalanus vanus	0.02	<0.01	0.02	-	1.26
Acartia danae	0.02	<0.01	0.02	-	1.12
Scolecithrix danae	0.02	<0.01	0.02	-	2.16
Scolecithricella abyssalis	0.01	<0.01	0.01	-	1.96
Calocalanus styliremis	0.01	<0.01	0.01	-	0.73