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**Distribución de larvas de invertebrados bentónicos en
el fiordo del río Baker, Patagonia Chilena: factores
biológicos e hidrodinámicos.**

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La Tesis de “*Doctorado en Oceanografía*” titulada “Distribución de larvas de invertebrados bentónicos en el fiordo del río Baker, Patagonia Chilena: factores biológicos e hidrodinámicos”, de la Srta. “*Erika Inge Meerhoff del Rey*” y realizada bajo la Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, ha sido aprobada por la siguiente Comisión de Evaluación:

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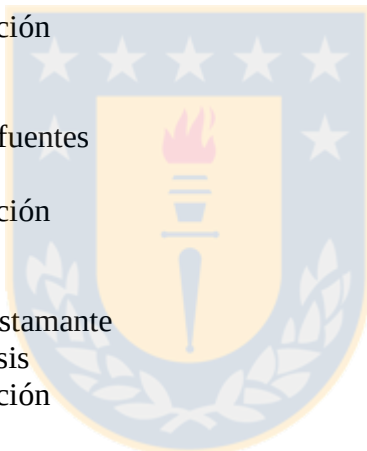
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PATAGONIA

A la Patagonia llaman
sus hijos la Madre Blanca.
Dicen que Dios no la quiso
por lo yerta y lo lejana,
y la noche que es su aurora
y su grito en la venteada
por el grito de su viento,
por su hierba arrodillada
y porque la puebla un río
de gentes aforesteradas.

Hablan demás los que nunca
tuvieron Madre tan blanca,
y nunca la verde Gea
fue así de angélica y blanca
ni así de sustentadora
y misteriosa y callada.
¡Qué Madre dulce te dieron,
Patagonia, la lejana!
Sólo sabida del Padre
Polo Sur, que te declara,
que te hizo, y que te mira
de eterna y mansa mirada.

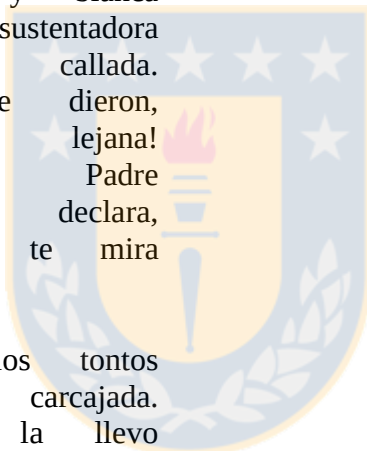
Oye mentir a los tontos
y suelta tu carcajada.
Yo me la viví y la llevo
en potencias y en mirada.

-Cuenta, cuenta, mama mía
¿es que era cosa tan rara?
Cuéntala aunque sea yerta
y del viento castigada.

Te voy a contar su hierba
que no se cansa ni acaba,
tendida como una madre
de cabellera soltada
y ondulando silenciosa,
aunque llena de palabras.
La brisa la regodea
y el loco viento la alza.
No hay niña como la hierba

en abajar bulto y hablas
cuando va llegando el puelche
como gente amotinada,
y silba y grita y aúlla,
vuelto solamente su alma.

Gabriela Mistral.



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Esta tesis y Doctorado son dedicados a mi madre, mis hermanas y toda mi familia, por su apoyo y amor para el logro de mis objetivos profesionales y personales.

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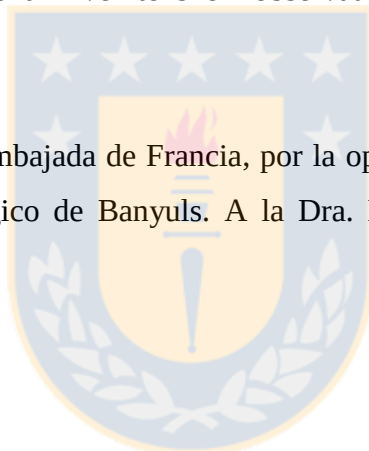
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“La verdadera educación le ayuda al hombre a alcanzar éxito en el proceso de autodomínio. La educación promueve la humildad y por medio de ella uno llega a adquirir el derecho de obtener una profesión, y esa autoridad confiere prosperidad. Una persona próspera posee la capacidad de dedicarse a la caridad y ejercer rectitud en su vida. Y la rectitud en la vida confiere felicidad, tanto aquí como en el más allá”. Sai Baba

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Distribución de larvas de invertebrados bentónicos en el fiordo del río Baker, Patagonia Chilena: factores biológicos e hidrodinámicos.

RESUMEN

Los ambientes estuarinos representan un hábitat crítico para etapas tempranas del ciclo de vida en muchas especies costeras, incluyendo crustáceos bentónicos y peces de importancia económica. La circulación estuarina y su interacción con flujos mareales puede promover la retención o exportación de estadios tempranos y determinar patrones de reclutamiento larval y renovación de las poblaciones. Cambios en los factores físicos con mayor influencia en la circulación estuarina (ej. aportes de agua dulce), podrían tener efectos profundos sobre la estructura y dinámica poblacional de especies costeras cuyos ciclos de vida incluyen estadios tempranos de vida planctónica. En este trabajo se caracterizó la composición y estructura espacial del meroplancton a lo largo del fiordo del río Baker, y se evaluó su asociación con cambios espaciales y estacionales en la estructura hidrográfica. Además, se evaluó el rol del río Baker como regulador del flujo larval de invertebrados bentónicos en el fiordo del río del mismo nombre, en particular en larvas y juveniles del langostino *Munida gregaria*.

La comunidad de meroplancton presentó un cambio en su estructura entre los meses de mínimo y máximo caudal del río (octubre y febrero, respectivamente) explicado por un cambio en el grupo dominante desde larvas de cirripedios a larvas de bivalvos. Este cambio fue consistente con cambios en la estructura hidrográfica a lo largo del fiordo, principalmente asociado con cambios estacionales en la descarga del río Baker. No se encontró un patrón espacial significativo que pudiera dar cuenta de la variación en el meroplancton a lo largo del Canal Martínez en el fiordo del río Baker, en tanto que la variabilidad temporal y las variables ambientales dieron cuenta de 36,6% y 27,6% de la varianza, respectivamente. Los estadios larvales tempranos (nauplios) y avanzados (cipris) de cirripedios fueron más abundantes en agua con menor temperatura, mayor oxígeno disuelto y mayor concentración de clorofila-a; las larvas de bivalvos estuvieron asociadas con aguas más cálidas. El cambio estacional en la dominancia numérica, de larvas de cirripedios en primavera a larvas de bivalvos en verano, sugiere que la reproducción de estos grupos es gatillada por condiciones diferentes, en términos de hidrografía y disponibilidad de alimento.

Además, se caracterizaron los patrones estacional y diurno-nocturno en la abundancia de larvas y juveniles de *Munida gregaria* en esta área. Las larvas zoea fueron más abundantes a fines de invierno y en primavera, coincidiendo con la estación de menor transporte de sedimento y mayor producción primaria en la región. La ocurrencia de juveniles fue exclusivamente en verano. Los patrones de más corto plazo (24 h) en la abundancia y distribución vertical, indicaron que las zoeas fueron significativamente más abundantes en la profundidad de 10-25 m ($p=0,039$), y cambios en la abundancia integrada en profundidad de zoeas y megalopas estuvieron fuertemente asociados con el ciclo mareal. Estos resultados sugieren que la estructura espacial de *M. gregaria* en esta región podría responder al forzamiento combinado de cambios estacionales en aportes de agua dulce, procesos dirigidos por comportamiento de migración y marea como transporte lateral de larvas y juveniles, y cambios en las condiciones locales mediados por ondas internas.

Finalmente, durante la estación de máxima descarga del río se caracterizó la circulación en el fiordo y se determinó el flujo de larvas. Cerca de la desembocadura del río Baker se encontraron asimetrías transversales en la corriente a lo largo del fiordo, la circulación lateral o secundaria también fue importante. Los estadios tardíos de nauplios de cirripedios y las cypis aumentaron su abundancia desde la estación más oceánica hacia una estación próxima a la desembocadura. Cerca de la desembocadura del río Baker, el flujo instantáneo cerca de la superficie (0-25 m) mostró que los nauplios son transportados hacia la cabecera del fiordo mientras que las cypis son advectadas hacia el océano. Las zoeas de *M. gregaria* son exportadas del fiordo al océano, patrón que es consistente con la literatura. Diferentes taxa y estadios de larvas de crustáceos responden de manera diferencial a variaciones espaciales de pequeña escala en flujos a lo largo del fiordo durante la estación de máxima descarga del río. Dadas las tendencias actuales de cambio climático y el aumento del derretimiento de glaciares en los campos de hielo de Patagonia (Glasser *et al.* 2011), los cambios en la descarga de agua dulce podrían fortalecer la circulación estuarina al aumentar el gradiente de densidad (Chua & Xu 2014). Sin embargo, no es posible determinar como el cambio climático afectaría el comportamiento, transporte y retención de larvas, así como los patrones de conectividad entre las poblaciones.

Benthic invertebrate larvae distribution in the Baker River fjord, Chilean Patagonia: biological and hydrodynamic factors.

ABSTRACT

Estuarine environments represent a critical habitat for early life stages in the life cycle of many coastal species, including benthic crustaceans and economically important fishes. Estuarine circulation and its interaction with tidal fluxes can promote the retention or export of early stages and determine patterns of larval recruitment and population renewal. Changes in physical factors that strongly influence estuarine circulation (e.g. freshwater inputs), could affect the structure and population dynamics of coastal species whose life cycles include early stages of planktonic life. In this work, the composition and spatial structure of meroplankton in Baker fjord (Chilean Patagonia) were characterized, together with the association with spatial and seasonal changes in hydrographic structure. Additionally, the role of Baker river as modulator of the hydrodynamics and larval fluxes of benthic invertebrate larvae in the fjord was evaluated, in particular for larvae and juveniles of the squatlobster *Munida gregaria*.

The meroplankton community presented a structure change between the months of minimum and maximum river outflow (October and February, respectively), explained by a switch in the numerically dominant group from barnacle to bivalve larvae. This change in community structure was consistent with changes in hydrographic structure along the fjord, which are mainly associated with seasonal changes in the Baker river outflow. A variance partition analysis showed no significant spatial trend that could account for the variation in meroplankton along the Martinez channel, whereas temporal variability and environmental variables accounted for 36.6% and 27.6% of the variance, respectively. When comparing meroplankton among the Baker and Martinez channels in October, changes in environmental variables explained 44.9% of total variance, whereas spatial variability accounted for 23.5%. Early and late-stage barnacle larvae (i.e. nauplii and cyprids) were more abundant in water with lower temperature, and higher dissolved oxygen and chlorophyll-a concentration, whereas bivalve larvae were more strongly associated to warmer waters. The seasonal shift in numerical dominance, from barnacle larvae in early spring to bivalve larvae in late summer, suggests that reproduction of these groups is triggered by substantially different sets of conditions, both in terms of hydrography and food availability.

To characterize seasonal and diel patterns in the abundance of *Munida gregaria* larvae and juveniles in the Baker river fjord, zooplankton time series collected with different temporal resolution and coverage were examined. Zoeae were more abundant in late winter and spring, coinciding with the season of lower sediment transport and higher primary production in the region. Juveniles occurred exclusively in summer. To characterize shorter-term patterns in larval abundance and vertical distribution, stratified samples were collected every 3 h over a full late-spring day (November 2008) near one of the monitoring stations. Zoeae were significantly more abundant at 10–25 m depth ($p=0.039$), and changes in depth-integrated abundance of both zoea and megalopae were strongly associated with the tidal cycle. Together, these results suggest that the spatial structure and population dynamics of *M. gregaria* in this region may respond to the combined forcing of seasonal changes in freshwater inputs, behavior coupled to tidally-driven processes such as lateral transport of larvae and juveniles, and internal-wave mediated changes in local conditions.

Finally, the larval flux in this estuary was determined during the season of maximum river outflow. Barnacle nauplii late stages and cyprids increased their abundance from a station closer to the ocean towards the inner station, indicating that they are transported towards the head of the fjord. Near the Baker river mouth, the net flux estimates showed that barnacle nauplii are advected landwards and cyprids seawards, respectively, whereas zoeae of the squat lobster *Munida gregaria* are exported from the fjord, consistently with previous findings. This may explain how different taxa and life stages within the meroplankton community respond differently to small scale spatial variations in flow along the fjord during the season of maximum river discharge. Given the current trends of climate change and increase of glacier melting in Patagonian Ice fields (Glasser *et al.* 2011), changes in freshwater discharge could strengthen the estuarine circulation by increasing the density gradient (Chua & Xu 2014). However, it is not possible to determine how the climate change could affect larval behavior, transport and retention in the fjord, as well as the connectivity among populations.

1. INTRODUCCIÓN

1.1 Variabilidad del plancton en sistemas estuarinos

Según Attrill y Rundle (2002) un ecotono es definido como un área de transición/gradiente entre dos sistemas. En este marco, los estuarios pueden verse como compuestos por varios ecotonos (ej. hacia el estuario desde cuencas fluviales o lacustres adyacentes, fuera del estuario hacia el área costera, Elliot & Whitfield 2011). Los estuarios son más variables que otros sistemas acuáticos desde el punto de vista físico-químico (Elliot & Whitfield 2011) y esta variabilidad se refleja en la dinámica de las poblaciones biológicas, en particular de las planctónicas.

La variación espacio-temporal del hábitat y los tipos de hábitats están entre los factores más importantes que afectan los patrones de abundancia, composición y estructura de tamaños del plancton estuarino (Kennish 1990). El zooplancton estuarino con frecuencia manifiesta zonaciones horizontales cuyos límites varían de acuerdo a la marea y descarga de agua dulce (Benfield 2013). En fiordos, la estructura de la columna de agua tiene un fuerte impacto en la estructura comunitaria del zooplancton, y se observan marcadas diferencias verticales y horizontales en biomasa y composición de especies a lo largo de un gradiente salino (Nielsen & Andersen 2002). Se ha propuesto un vínculo entre el aporte de agua dulce a estuarios y un aumento en diversidad de nichos y fuentes de alimento disponibles para los animales en estos sistemas (Whitfield & Bruton 1989, Ter *et al.* 1994).

La salinidad es en general un factor clave en regular por limitaciones osmóticas la distribución espacial y estructura del zooplancton estuarino (Benfield 2013), dado que la mayoría de las especies son capaces de tolerar un cierto rango de salinidades. La temperatura también puede influenciar el zooplancton estuarino sobre un rango de escalas temporales, debido a su efecto en las tasas metabólicas y el comportamiento natatorio (O'Connor *et al.* 2007, Benfield 2013). Además, la disponibilidad de alimento (Toumi *et al.* 2005) y presión de depredación (Williams 1998), ambas afectadas por gradientes de salinidad y temperatura, pueden alterar significativamente la estructura de las comunidades de zooplancton en ambientes estuarinos.

Gradientes salinos horizontales debidos a aportes de agua dulce modifican las corrientes mareales y producen patrones de circulación estuarina, éstos con frecuencia resultan en un transporte neto de agua sub-superficial salina hacia la boca del río y transporte de agua

dulce superficial hacia el océano (Pritchard 1953). Se ha propuesto que este tipo de circulación podría promover la retención de ciertos grupos del zooplankton dentro de un estuario (Dyer 1997), y se sabe que tiene impacto sobre la productividad, composición de la comunidad, estructura de edades, biomasa y distribución del zooplankton en sistemas de fiordos (Basedow *et al.* 2004).

1.2 Estrategias de vida de invertebrados bentónicos estuarinos

La macrofauna bentónica es un componente importante en ecosistemas estuarinos. Estos organismos son fuente de alimento para niveles tróficos superiores incluyendo peces, jaibas (Virnstein 1977, Holland *et al.* 1980) y aves (Botton 1984). Además, la macrofauna bentónica afecta las propiedades físicas y químicas del sedimento y de la columna de agua (ej. Rhoads & Young 1970, Rhoads 1973).

Muchos invertebrados bentónicos estuarinos tiene ciclos de vida que incluyen larvas planctónicas (Strathmann 1987). Larvas planctónicas de especies estuarinas pueden ser retenidas en el mismo (Bousfield 1955), o completar su desarrollo en aguas de la plataforma continental y reingresar al estuario para asentarse (ej. *Callinectes sapidus*). Las larvas que regresan desde la plataforma a los estuarios no solo deben migrar a la costa, también deben migrar a través del límite estuario/océano (Boehlert & Mundy 1988). Por otro lado, el retorno de las larvas del ambiente pelágico al bentónico es un factor determinante de las tasas de reclutamiento y estructura poblacional (Connell 1985, Roughgarden *et al.* 1988, Ólafsson *et al.* 1994, Tilburg *et al.* 2006) y depende del comportamiento de las larvas, de los patrones de corrientes a los que están expuestas, y de qué tan lejos se encuentran las larvas de su área parental (Sponaugle *et al.* 2002). Por lo tanto, para comprender el acoplamiento entre la disponibilidad de larvas y el reclutamiento a poblaciones adultas es necesario entender las interacciones físico- biológicas que determinan las escalas de tiempo de variabilidad larval.

Con frecuencia, en ambientes estuarinos los crustáceos decápodos bentónicos producen larvas planctónicas que eclosionan en marea vaciante y son transportadas por la corriente de marea a zonas costeras marinas donde las salinidades son más altas y más constantes (ej. *Chasmagnathus granulata*, Anger *et al.* 1994, y *Callinectes sapidus* Epifanio 1995, *Carcinus maenas* Queiroga & Blanton 2005). Luego de completar su desarrollo planctónico, el estadio competente retorna al hábitat estuarino donde eventualmente se asienta y recluta a la

población bentónica adulta (Luppi *et al.* 2002). La migración costa afuera de estadios tempranos podría reducir la depredación, exponer las larvas a variabilidad ambiental más tolerable y, ocasionalmente, disminuir la competencia por alimento con suspensívoros bentónicos en áreas costeras o estuarinas (Sponaugle *et al.* 2002).

Existen especies estuarinas obligadas, especies estuarinas que exportan larvas a la plataforma, especies de la plataforma que pueden penetrar los estuarios como adultos, y especies de plataforma que usan los estuarios como hábitats de crianza. Estadios larvales de especies de decápodos que ocurren en estuarios durante al menos parte de su ciclo de vida hacen algún tipo de migración mareal (Queiroga & Blanton 2005). En especies estuarinas obligadas, todos los estadios realizan migración vertical en marea llenante. En especies estuarinas que exportan larvas a la costa ocurre un cambio ontogenético de migración en vaciante en el primer estadio, a migración en llenante en el último. Lo mismo ocurre en especies costeras que ingresan a los estuarios en su fase adulta (Queiroga & Blanton 2005).

El desarrollo larval de los cirripedios consta de seis fases nauplius y una cypis. El paso de una a otra fase siempre va acompañado de muda. Las larvas al final del estado cypis eligen el sustrato donde fijarse y realizar su metamorfosis (Barnes 1969).

Los bivalvos marinos han desarrollado estrategias reproductivas que varían desde viviparidad completa donde los adultos incuban a sus crías por todo el periodo de desarrollo, a liberación de gametos y posterior fertilización externa (Zardus & Martel 2002). Las larvas de bivalvos pasan por cuatro estadios de desarrollo. El primer estadio, trocófora, es efímero, dura hasta un día. El segundo estadio (veliger) ocurre luego que la larva desarrolla una concha. Con la aparición de un apéndice ciliado llamado velum, la larva veliger es capaz de nadar verticalmente y alimentarse de fitoplancton en la superficie. A medida que la larva crece, la conchilla se engrosa y se hace más redondeada, generando una veliger umbonada. Durante estos estadios, las larvas son susceptibles a ser transportadas por las corrientes porque sus capacidades de nado ($<10^{-4} \text{ m s}^{-1}$) son mucho menores a las velocidades típicas de las corrientes horizontales (Chia *et al.* 1984). Cuando la larva es competente para asentarse, se convierte en pedi-veliger y desarrolla un apéndice llamado pie que le permite asentarse en el sustrato bentónico. Cuando encuentra un lugar adecuado para asentarse, la pedi-veliger se asienta y metamorfosea a juvenil.

1.3 Procesos físicos importantes para el transporte de larvas

La dispersión del meroplancton depende principalmente de la interacción entre el comportamiento natatorio larval y el régimen hidrodinámico y, secundariamente, de la duración del desarrollo planctónico. La variabilidad en el reclutamiento de larvas en el océano costero depende de la interacción entre una serie de forzantes físicos, entre los que se cuentan el viento (ej. Roughgarden *et al.* 1988, Wing *et al.* 1995, 1998, Roegner *et al.* 2007, Morgan *et al.* 2009, 2011), y las corrientes (Queiroga *et al.* 2006)

La dispersión larval se debe a una combinación de advección y difusión turbulenta (Pineda 2000). Aunque se conoce en detalle cómo el comportamiento larval afecta su advección, la influencia sobre su transporte debido a difusión no se conoce en profundidad. Por ejemplo, Cowen *et al.* (2000) usando un modelo de advección-difusión-mortalidad, estimaron que el transporte larval exitoso en hábitats de arrecifes de coral disminuye a cero cuando se incluye difusión realística ($100 \text{ m}^2 \text{ s}^{-1}$) y/o mortalidad larval (mortalidad=0.2). Siendo ésta una típica tasa de difusión turbulenta usada en estudios de transporte larval (Okubo 1994).

Sin embargo, la suposición de que las larvas actúan pasivamente en la difusión en el ambiente marino no es siempre aplicable, en particular para estadios más avanzados. Las larvas pueden permanecer en capas finas de alimento (Lasker 1975) y reducir su difusión debido a diferencias verticales en el flujo (difusión cizalle). Las larvas también pueden acumularse en frentes de surgencia o hundimiento nadando en la corriente (Metaxas 2001), disminuyendo la difusión. Por lo tanto, respuestas de comportamiento de pequeña escala vertical y horizontal podrían limitar la difusión y afectar el transporte larval. Por ejemplo la duración de la estación de desove y el número de años que los adultos desovan puede aumentar la difusión efectiva al aumentar la probabilidad de que algunas larvas “atrapen” flujos opuestos a los flujos medios (Largier 2003). Además, el comportamiento migratorio podría controlar su advección y difusión por migraciones verticales correlacionadas con fluctuaciones temporales en el flujo, en particular donde el flujo es determinista como en mareas estuarinas (Largier 2003).

En estuarios la circulación gravitacional es un mecanismo importante en el transporte de larvas de decápodos (Dong *et al.* 2007). La circulación gravitacional puede dominar el transporte en algunas ocasiones (por ejemplo durante marea viva y muerta en la cabecera del

estuario Sumjin en Corea, Shaha *et al.* 2010). Sin embargo, el modelo más comúnmente aceptado para el transporte de larvas de decápodos en estuarios, es el transporte mareal selectivo, conocido como “STST” por su sigla en inglés, el cual ha sido estudiado principalmente en la costa oriental de Norteamérica y en Europa occidental (Forward *et al.* 2001, Queiroga & Blanton 2005, Fig. 1 en anexo I). La mejor descripción del control biofísico de STST surgió de una serie de estudios de campo y laboratorio en megalopas de cangrejos, las cuales son consistentemente más abundantes en estuarios durante las mareas llenantes nocturnas (Little & Epifanio 1991, Queiroga *et al.* 1994). Este patrón surge de la combinación de una inhibición de la actividad natatoria y consecuente hundimiento de las larvas por altas intensidades de luz, y de su ascenso gatillado por aumentos en presión hidrostática y salinidad durante marea llenante, así como por altos niveles de turbulencia. Durante la fase de ingreso al estuario las larvas se ubican cerca del fondo durante marea vaciante y ascienden en la columna de agua durante marea llenante, resultando en un movimiento neto hacia la cabeza del estuario (Fig. 1 Anexo I). Este modelo ha sido desarrollado para estuarios someros.

El volumen de agua oceánica entrando en un estuario durante un ciclo de marea se denomina prisma de marea (Valle-Levinson 2010). Como mecanismo puramente pasivo, el mayor volumen de agua oceánica entrando en un estuario en mareas vivas, podría llevar a mayores tasas de transporte larval y asentamiento durante éstas que en mareas muertas (Roegner *et al.* 2007).

Además, la circulación en frentes costeros, regiones de fuertes gradientes entre dos masas de agua, puede actuar como una barrera a la dispersión de larvas, controlando el reclutamiento a poblaciones bentónicas (Roughgarden *et al.* 1988, Farrell *et al.* 1991). La barrera frontal puede ser puramente física, mediante la retención pasiva de organismos (Franks & Anderson 1992), o puede reflejar la demarcación de hábitat, con especies particulares prefiriendo un determinado lado del frente (Graham 1993). Los frentes costeros limitan el flujo perpendicular a través de los mismos, y desvían el flujo incidente, resultando en flujo intenso a lo largo del frente y flujos de hundimiento que transportan larvas colectadas en el frente (Largier 1993). Así, para larvas fuertemente nadadoras que se mantienen en aguas superficiales, los frentes pueden servir como conductos larvales dado que estas larvas probablemente se asientan donde el frente intercepta hábitat de asentamiento adecuados.

Organismos que flotan o tienden a nadar hacia arriba en la columna de agua pueden formar densas acumulaciones en la superficie dentro de la zona frontal. Numerosos estudios han documentado cómo la circulación frontal influencia la distribución y movimiento de estadios pre-competentes de crustáceos y peces en ambientes estuarinos y cercanos a la costa (Zeldis & Jillett 1982, Shanks 1983, 1986, Roughgarden *et al.* 1988, Farrell *et al.* 1991, Pineda 1994). Los comportamientos de nado hacia arriba en respuesta a flujos de hundimiento transitorios en flujos en propagación determinan transporte larval eficiente (Pineda 1999, Scotti y Pineda 2007).

Los flujos secundarios en estuarios son asociados con frentes. Tales frentes son comunes y persistentes en muchos estuarios. Poco se conoce sobre la respuesta de las larvas a frentes axiales convergentes en estuarios (Largier 1993, Queiroga & Blanton 2005, Fig. 2 en Anexo I). Éstos son importantes porque, en general, están asociados con flujos secundarios que pueden afectar la circulación local y, por lo tanto, la distribución de organismos planctónicos y su exposición a lugares de asentamiento más favorables (Largier 1993).

1.4 Principales factores que determinan la circulación en fiordos

Los fiordos son un tipo particular de estuarios asociados con altas latitudes e intensa actividad glacial, caracterizados por un canal elongado y profundo con una morrena o “sill” (Valle-Levinson 2010). En los fiordos la circulación gravitacional está bien descrita, existe un fuerte flujo superficial hacia el océano y flujos promedio débiles en profundidad, típico de cuencas profundas. Las características de estuarios tipo fiordo han sido revisadas por Pickard (1961) y Rattray (1964). Cerca de la fuente de agua dulce, en la cabecera del fiordo, éstos son altamente estratificados y la circulación no mareal está confinada a la región cercana a la superficie. A medida que la capa superficial fluye hacia el océano, se produce mezcla con una capa de mayor salinidad que progresivamente reduce la estratificación. Donde hay morrenas someras o constricciones laterales en el fiordo, los procesos de mezcla pueden aumentar localmente a un punto que la estratificación local es prácticamente eliminada.

En fiordos y estuarios profundos (más de 20 m) la estratificación permanece fuerte durante todo el ciclo mareal (Valle-Levinson 2010), mantenida por el aporte de agua dulce. La fuerte estratificación cerca a la superficie inhibe la turbulencia generada convectivamente en la capa superficial, excepto en periodos de muy poca escorrentía (Farmer & Freeland 1983). La

mayor turbulencia generada en fiordos es de aporte mecánico: viento, acción mareal, corrientes turbulentas de gravedad en profundidad y por flujos tipo cizalle que surgen de la descarga de ríos. Sólo en invierno, con bajas temperaturas superficiales, la convección térmica puede ser importante. Los procesos de mezcla son centrales al tema de circulación gravitacional en estuarios porque son responsables de alterar los gradientes de densidad que establece el flujo. Los flujos horizontales a lo largo de un fiordo son principalmente advectivos mientras que en el sentido perpendicular al fiordo la mezcla horizontal y la difusión son importantes (Farmer & Freeland 1983). La mezcla por viento está limitada a la superficie y el efecto mareal se puede observar en toda la columna de agua. Además, el enfriamiento invernal superficial produce un gradiente vertical de temperatura con el mismo signo que el gradiente de salinidad, lo que genera un proceso de doble difusión. El forzamiento periódico de un fiordo con flujo mareal proporciona energía cinética para la mezcla. Las corrientes mareales son débiles excepto cerca de constricciones y en “sills”, que son efectivos en distribuir la energía mareal generando ondas internas (Farmer & Freeland 1983).

1.5 Particularidades del meroplancton y del área de estudio

Pocos estudios se han enfocado en la comunidad meroplanctónica en fiordos (ej. Norden 1984, Hansen *et al.* 2002, Nielsen & Andersen 2002), en particular en Chile (ej. Antezana 1999, Defren-Janson *et al.* 1999, Thatje *et al.* 2003). En fiordos del Sur de Patagonia (53-55°S), se ha observado alta abundancia del meroplancton durante periodos de “bloom” primaveral (Antezana 1999, Defren-Janson *et al.* 1999), con dominancia numérica de larvas de equinodermos (20-65%) y cirripedios (6-20%), además de poliquetos y briozoos (Defren-Janson *et al.* 1999). En general, el meroplancton Subantártico presenta baja riqueza de especies que está dominada por crustáceos decápodos con reproducción estacional, mayoritariamente en primavera (Lovrich 1999).

En altas latitudes, los invertebrados están sujetos a fuertes fluctuaciones estacionales en las condiciones ambientales. En el fiordo del río Baker, se registran fuertes variaciones en la descarga del río, temperatura del agua y salinidad superficial (Meerhoff *et al.* 2013). Los aportes de agua dulce a esta área estuarina se asocian principalmente a las descargas de los ríos Baker y Pascua (González *et al.* 2013), que muestran fluctuaciones coherentes en el

caudal, con máximo en verano (Meerhoff *et al.* 2013). Esta es la época más cálida del año y consecuentemente, con las tasas más altas de derretimiento de hielo y nieve en la región.

El Canal Martínez, en el complejo de fiordos del río Baker, se ubica entre la desembocadura del río Baker y el Golfo de Penas en el océano Pacífico, es un ambiente inestable, desde el punto de vista de estabilidad ecológica, debido a eventos de alta descarga de agua dulce (Dussaillant *et al.* 2010), que probablemente tengan un fuerte efecto sobre las comunidades planctónicas. La producción primaria es fuertemente estacional, con mayores valores observados en primavera-verano, como se observa en general en fiordos de la Patagonia chilena (Iriarte *et al.* 2007, Aracena *et al.* 2011, González *et al.* 2013). Al mismo tiempo, las menores tasas de producción primaria para los fiordos de Patagonia han sido observadas en Canal Martínez cerca a la desembocadura del río Baker ($91 \text{ mg C m}^{-2}\text{d}^{-1}$), donde hay fuerte influencia del derretimiento glacial con una alta carga de sedimentos glaciales (Aracena *et al.* 2011, González *et al.* 2013). Este fiordo, difiere de fiordos de la Patagonia Norte en que los aportes de agua dulce son mayormente compuestos de agua de derretimiento glacial, con altos aportes de sedimento fino, que limitan fuertemente la disponibilidad de luz para la producción primaria (Jacob *et al.* en prensa).

El aporte de agua dulce desde los ríos y derretimiento glacial a los fiordos y canales de la Patagonia, contribuye a la formación de una capa superficial delgada caracterizada por baja temperatura y baja salinidad (Silva & Calvete 2002). Debajo de esta capa las aguas oceánicas ocupan el resto de la columna de agua. Los dos cuerpos de agua forman un sistema de dos capas, caracterizado por una fuerte pycnoclina en la cual la salinidad cambia desde 0 a 30 en una profundidad de 7 a 12 m (Silva & Calvete 2002). Así, la circulación en los canales Baker y Martínez, en el complejo de fiordos del río Baker, es en un sistema de dos capas típicamente estuarino, donde la corriente de marea tiene baja influencia en las corrientes totales (Cáceres 2007). En el Canal Martínez, próximo a la desembocadura del río Baker, las magnitudes de corrientes superficiales típicas en invierno alcanzan valores máximos de $5 \text{ a } 10 \text{ cm s}^{-1}$, y en verano entre $15 \text{ y } 20 \text{ cm s}^{-1}$. Las variaciones de la corriente en invierno han sido atribuidas al viento, mientras que en verano se debería al efecto combinado del viento y el caudal del río (Cáceres 2007). Aunque, la descarga en la cabeza del fiordo es dominada por régimen estacional, también se ha mostrado que fluctuaciones sinópticas en el campo de densidad en el

Golfo de Penas dirigen significativo intercambio horizontal limitado espacialmente a la boca del Canal Martínez (Aiken 2012).

Además, en esta área, Ross *et al.* (2014) describieron la existencia de ondas internas de marea semidiurnas. Estas ondas internas fueron detectadas como fluctuaciones cerca de la picnoclina, en paquetes esporádicos correlacionados a pulsos de alta descarga del río Baker. Desde el punto de vista ecológico, una implicancia de las ondas internas es aumentar la mezcla vertical de nutrientes hacia la superficie (Munk y Wunsch, 1998), pudiendo traer agua más densa y material sub-superficial hasta la superficie (Pineda, 1994). Finalmente, en un ambiente limitado por la luz como este, el paso de ondas internas podría llevar a cambios en la comunidad fitoplanctónica y aumento en la biomasa de algas (Evans *et al.* 2008, Pannard *et al.* 2011) por un impacto directo en la disponibilidad de luz (Cuypers *et al.* 2011), y consecuentemente podría tener efectos sobre el meroplancton. Por último, un importante transporte de partículas puede ocurrir por efecto de ondas internas no lineales (Lamb 1997, Vlasenko *et al.* 2005). El transporte horizontal generado por estas ondas depende de la posición vertical inicial de las partículas (Lamb 1997), por lo cual podrían afectar el transporte de larvas en un fiordo.

1.6 *Munida gregaria*: generalidades y antecedentes

El langostino de los canales, “squat lobster” o “lobster krill” en inglés, *Munida gregaria* (Fabricius 1793) (Decapoda, Anomura, Munididae) tiene amplia distribución en el hemisferio sur, desde Cabo de Hornos hasta Isla Chiloé (41°S) en el Pacífico sudeste (Boschi *et al.* 1992), Tasmania y este de Nueva Zelanda en el Pacífico sudoeste (Zeldis 1985), en la plataforma continental del Atlántico sudoeste desde Uruguay (35° S) hasta Cabo de Hornos (55° S), incluyendo las islas Falkland (51° S). En los límites sur del rango de distribución sudamericana, las agregaciones bentónicas pueden alcanzar densidades hasta de 27 indiv m⁻² (Tapella 2002), y puede constituir cerca del 50% de la biomasa macrobentónica (Arntz *et al.* 1999). Dadas sus altas abundancias, varias especies de galateidos han sido consideradas como un potencial recurso pesquero (Longhurst 1968, Vinuesa 1990, Auriolles-Gamboa 1995, Lovrich *et al.* 1998). Además, en esta región, *M. gregaria* tendría un rol ecológico equivalente al del krill antártico *Euphausia superba*, especialmente en aguas costeras (Antezana 1976, Diez *et al.* 2012). A diferencia del krill, sin embargo, *M. gregaria* cumple el rol de acortar las

tramas tróficas dada su alimentación depositívora, y de hacer transferencia energética a niveles tróficos superiores más eficientemente (Romero *et al.* 2004). *Munida gregaria* forma parte de la dieta de numerosos depredadores tope tales como calamares, cangrejos, peces, aves marinas y ballenas (Romero 2003, Varisco & Vinuesa 2007).

En el Canal Beagle el ciclo reproductivo de *M. gregaria* comienza en abril, las hembras portan los huevos por 8-9 meses, y la eclosión de larvas ocurre entre octubre y enero (Rodríguez & Bahamonde 1986). Las larvas de *M. gregaria* pasan por 5 estadios larvales hasta la metamorfosis postlarval (Vinuesa 2013). El primer estadio zoea aparece en septiembre, con máximos de densidad a comienzos de noviembre, y algunos individuos persisten hasta enero (Lovrich 1999).

Mujica *et al.* (2013) reportan una amplia distribución de las larvas de *M. gregaria* entre Puerto Montt (41°30'S) y Laguna San Rafael (46°30'S), coincidente con la distribución de los adultos de la especie, que con sus dos morfotipos (Pérez-Barros *et al.* 2008), de hábitos pelágicos y bentónicos (Varisco & Vinuesa 2007), liberan sus larvas en un amplia área de distribución. En fiordos de la región de Aysén, las hipótesis sobre el ciclo de vida de *M. gregaria* plantean que la liberación de larvas ocurriría al interior de los canales, desde donde los primeros estadios larvales serían dispersados hacia aguas con mayor influencia oceánica. Se ha propuesto que el mecanismo por el cual los juveniles regresarían a los canales está asociado con el flujo sub-superficial hacia la costa (León *et al.* 2008).

El estadio postlarval de *M. gregaria* es pelágico y con frecuencia forma grandes agregaciones previo al asentamiento en el fondo e inicio de la fase adulta bentónica, que puede durar 2 a 3 años e incluir hasta 3 desoves. En la plataforma continental de Nueva Zelanda, estos cardúmenes aparecen en verano y se caracterizan por una distribución espacial muy heterogénea (Zeldis 1985). En el sur de Sudamérica, los registros de agrupaciones de juveniles son escasos y están restringidos a la plataforma continental del sur de Argentina (Matthews 1932, Rayner 1935, Kawamura 1976, Varisco & Vinuesa 2010), con sólo dos registros publicados para la Patagonia chilena (Tabeta & Kanamaru 1970, Antezana 1976).

La aparición de agregaciones pelágicas de *M. gregaria* en la costa de la Patagonia Argentina y Nueva Zelanda se asocia con plumas de ríos y frentes costeros (Rayner 1935, Zeldis & Jillett 1982) así como con áreas influenciadas por la actividad de ondas internas (Zeldis & Jillett 1982). En la costa del sur de Argentina, en tanto, las agregaciones de *M.*

gregaria se asocian con sitios altamente productivos (Rayner 1935, Carranza *et al.* 2008, Varisco & Vinuesa 2010). En el complejo de fiordos del río Baker (47°48' S, 73°42' W), observaciones derivadas de un programa de monitoreo mensual iniciado en marzo de 2009, indican la presencia consistente de abundantes juveniles pelágicos de *M. gregaria* hasta 1.87 indiv/m³ en meses de verano (Meerhoff *et al.* 2013). Sin embargo, un estudio reciente de patrones latitudinales de productividad en fiordos de la Patagonia (41–55° S) ha demostrado que esta área tiene la menor productividad (91 mg Cm⁻² d⁻¹) de toda la región (Aracena *et al.* 2011), y se ha propuesto que esto se debe a la alta carga de sedimentos de origen glacial en la descarga del río que afecta negativamente la disponibilidad de luz en la columna de agua. Se desconoce la periodicidad y escala espacial de las agregaciones de *M. gregaria* en el fiordo del río Baker. Los planes de construcción de embalses para generación hidroeléctrica en su cuenca, hacen que sea más relevante evaluar el rol de la variabilidad hidrológica sobre el ciclo de vida de *M. gregaria* y, a través suyo, en la dinámica poblacional de muchas especies de peces e invertebrados en aguas Patagónicas.

En este contexto, el objetivo general de este trabajo fue caracterizar la composición y estructura espacial del meroplancton a lo largo del fiordo del río Baker, y evaluar su asociación con cambios espaciales y estacionales en la estructura hidrográfica. Además se evalúa el rol del río Baker como regulador de la hidrodinámica y transporte larval de invertebrados bentónicos en el fiordo del río del mismo nombre, en particular en larvas de cirripedios y larvas y juveniles del decápodo *M. gregaria*. Se discute la implicancia de estos resultados en términos de la tendencia actual de aportes de agua dulce a la región, y su potencial impacto sobre la composición y distribución del meroplancton en este sistema.

2. HIPÓTESIS Y OBJETIVOS ESPECÍFICOS

La variabilidad en el caudal del río Baker podría tener efectos sobre el transporte y retención de larvas de invertebrados bentónicos, en particular de larvas y postlarvas de *M. gregaria* en el fiordo. Se plantean las siguientes hipótesis:

- I) Aumentos estacionales en la abundancia de larvas de invertebrados bentónicos, en particular larvas y juveniles de *M. gregaria* en el fiordo del río Baker, se asocian a aumentos en el caudal del río.
- II) La estructura espacial de la comunidad meroplanctónica en el fiordo del río Baker está determinada por cambios estacionales en las condiciones hidrográficas.
- III) Como consecuencia de un patrón ontogenético de migración vertical, existen diferencias entre la distribución vertical de larvas y juveniles de *M. gregaria* en el área de estudio, con estadios larvales tempranos ubicados a una profundidad promedio menor que los juveniles.
- IV) Existen flujos netos de exportación de larvas de invertebrados desde el fiordo hacia el océano.

Objetivos específicos

- I) Caracterizar la variabilidad de las condiciones hidrográficas e hidrodinámicas del fiordo en función de cambios en la descarga del río Baker.
- II) Caracterizar la estructura de la comunidad meroplanctónica y determinar su variabilidad espacial y temporal.
- III) Establecer si aumentos estacionales en la abundancia de larvas y juveniles de *M. gregaria* en el fiordo del río Baker se asocian a aumentos en el caudal del río.
- IV) Determinar si existen diferencias entre la distribución vertical de larvas y juveniles de *M. gregaria*.
- V) Determinar el flujo larval instantáneo en el fiordo durante la estación de máxima descarga de los ríos.

3. MATERIAL Y MÉTODOS

3.1. Área de estudio

La cuenca del río Baker (27.000 km^2) está ubicada en una de las áreas más prístinas y remotas del planeta. Su régimen hidrológico podría sufrir cambios drásticos en el futuro cercano debido al desarrollo de proyectos hidroeléctricos y al cambio climático (Dussaillant *et al.* 2012). Este río es el más grande del bosque templado de Sudamérica (Rozzi *et al.* 2012) y el más grande de Chile en términos de descarga ($1133 \text{ m}^3 \text{ s}^{-1}$ media anual). El mismo se origina en el lago Bertrand, el cual recibe el aporte de agua del lago General Carrera corre a lo largo del lado este del campo de hielo Norte y se vacía hacia el Canal Martínez en el fiordo del río Baker, ($47^\circ 48'S$, $73^\circ 34'W$), cerca de Caleta Tortel (Fig. 3).

El río Pascua presenta una cuenca de 14.760 km^2 y un caudal medio anual de $753 \text{ m}^3 \text{ s}^{-1}$, se origina en el Lago O'Higgins y recorre 67 km hasta alcanzar su desembocadura cerca del glaciar Jorge Montt, en el extremo SE de la cuenca del fiordo. Este glaciar sufre una de las mayores tasas de derretimiento registradas en Patagonia ($2,4 \text{ km}^3 \text{ año}^{-1}$, Rivera *et al.* 2012). Cálculos recientes muestran que la contribución de los campos de hielo de Patagonia al aumento del nivel del mar ha aumentado marcadamente en el siglo XX (Glasser *et al.* 2011).

3.2. Caracterización de las condiciones hidrográficas e hidrodinámicas del fiordo en función de cambios en la descarga del río Baker

Para evaluar cambios estacionales en las condiciones hidrográficas se compararon datos colectados a lo largo del Canal Martínez durante periodos contrastantes de descarga del río: octubre 2012 y febrero 2013, con mínima y máxima descarga del río respectivamente. Se realizaron mediciones hidrográficas en seis estaciones de muestreo a lo largo del Canal Martínez, entre la desembocadura del río Baker y el Golfo de Penas en el Océano Pacífico (Fig. 3 en Anexo I) en ambas épocas del año. Simultáneamente, cuatro estaciones fueron muestreadas a lo largo del Canal Baker en octubre de 2012. Las mediciones hidrográficas se realizaron utilizando CTD SBE-25 (Seabird Electronics, EE.UU.) equipado con sensores de oxígeno disuelto, turbidez y fluorescencia. La estructura espacial de las condiciones hidrográficas a lo largo del fiordo se visualizó y comparó entre canales usando Ocean Data View (Schlitzer 2012).

3.3 Estructura de la comunidad meroplanctónica y su variabilidad espacio temporal

3.3.1 Diseño de muestreo

Se compararon datos colectados a lo largo del Canal Martínez durante periodos contrastantes de descarga del río: octubre 2012 y febrero 2013, meses correspondientes a la mínima y máxima descarga anual del río, respectivamente. La variabilidad espacial de la estructura comunitaria se estudió comparando entre canales (Martínez y Baker) durante octubre 2012. Muestras de zooplancton y mediciones hidrográficas se obtuvieron de seis estaciones de muestreo a lo largo del área estuarina del Canal Martínez, entre la desembocadura del río Baker y el Golfo de Penas en el Océano Pacífico (Fig. 3 en anexo I) en ambas épocas del año. Además, cuatro estaciones fueron muestreadas a lo largo del Canal Baker en octubre de 2012. Las muestras de zooplancton fueron colectadas mediante arrastre vertical desde 50 m de profundidad hasta la picnoclina (5-10 m de profundidad), y desde la picnoclina a la superficie, usando una red WP2 con 150 μm de trama y 50 cm de diámetro. El volumen del agua filtrada fue estimado multiplicando el área de la boca de la red por la extensión vertical de cada arrastre, no se utilizó flujómetro debido a que no siempre demostró mediciones correctas. Las muestras fueron preservadas en solución tamponada de formaldehído 5% hasta la identificación y conteo de los grupos de meroplancton en laboratorio.

3.3.2 Análisis de datos

Para evaluar la relación entre la estructura de la comunidad meroplanctónica y las variables ambientales medidas a lo largo de los Canales Martínez y Baker en febrero de 2013, se utilizaron modelos lineales basados en distancia (DISTLM) y análisis de redundancia basado en distancia (dbRDA), usando PRIMER v6 (Clarke y Gorley 2006) el cual incluye PERMANOVA+ (Anderson *et al.* 2008). Se realizó una partición de la varianza de acuerdo a grupos de variables predictivas: un grupo de variables ambientales (salinidad, temperatura, turbidez, clorofila a) un grupo de variables espaciales (latitud y longitud, de acuerdo a Borcard 1992), y variables temporales (Anderson y Gribble 1998).

3.4 Asociación entre aumentos estacionales en la abundancia de larvas y juveniles de *M. gregaria* en el fiordo del río Baker y aumentos en el caudal del río.

Se estudiaron series de tiempo de los caudales de los ríos Baker y Pascua y una serie de tiempo de temperatura y nivel del mar en la columna de agua en una estación cercana a la desembocadura del río, en Caleta Tortel ($47^{\circ}49'13''$ S, $73^{\circ}32'22''$ W, Fig. 3). Se analizaron datos de caudal del río Baker proporcionados por la Dirección General de Aguas para las estaciones Angostura Chacabuco ($47^{\circ}08'32''$ S, $72^{\circ}43'35''$ W) y Colonia ($47^{\circ}20'47''$ S, $72^{\circ}51'36''$ W). Para el río Pascua se utilizaron las estaciones lago O'Higgins ($48^{\circ}22'06''$ S, $72^{\circ}57'40''$ W) y Quetru ($48^{\circ}10'17''$ S, $73^{\circ}04'24''$ W). En ambos casos, las series de tiempo cubrieron el periodo de enero 2008 a 2012. Las brechas en las series de tiempo fueron resueltas mediante interpolación lineal o a través de análisis armónico (Emery y Thomson 2001) dependiendo de la longitud de cada brecha.

Los datos de la temperatura del agua y nivel del mar fueron obtenidos cada diez minutos mediante sensores (HOBO) anclados en la zona desde septiembre de 2008 a diciembre de 2012. Los sensores de temperatura tienen una precisión de $\pm 0,2^{\circ}\text{C}$ entre 0°C y 50°C , con una resolución de $0,02^{\circ}\text{C}$ a 25°C . Se aplicó análisis armónico a los datos de nivel del mar para determinar los principales constituyentes de la marea para esto se utilizó la herramienta t-tide implementada en MATLAB por Pawlowicz *et al.* (2002).

Para caracterizar la variabilidad estacional en la presencia y abundancia de larvas y juveniles de *M. gregaria* se estudió una serie de tiempo generada a partir de muestreos mensuales de zooplancton desarrollados entre 2009 y 2012 en 3 estaciones a lo largo de una transecta de 6,5 km a lo largo del Canal Martínez, desde la desembocadura del río Baker (Fig.3). Las muestras de zooplancton fueron obtenidas mediante arrastres oblicuos de una red Bongo de 300 μm y 60 cm de diámetro de boca, entre 25 m de profundidad y superficie. Las larvas de *M. gregaria* fueron identificadas y clasificadas por estadio de desarrollo según Roberts (1973). Para establecer si cambios estacionales en la abundancia de larvas y juveniles de *M. gregaria* en el fiordo se asociaban a aumentos en el caudal del río, se realizaron análisis de correlación entre las abundancias de larvas y parámetros ambientales como salinidad superficial, caudal del río y estratificación térmica de la columna de agua.

3.5 Distribución vertical de larvas y juveniles de *M. gregaria*.

Para determinar si existía un patrón definido de variabilidad temporal en la distribución vertical de larvas y juveniles de *M. gregaria*, y evaluar la asociación entre estos

cambios y fluctuaciones de origen mareal se analizaron muestras estratificadas de zooplancton obtenidas cada 3 h durante muestreos de 24 h. Se analizaron muestras ya obtenidas durante el crucero CIMAR 14, realizado a bordo del AGOR “Vidal Gormaz”, en noviembre de 2008, así como muestras obtenidas durante campañas en primavera (2012) y verano (2013). Para evaluar la asociación entre la distribución de larvas y la hidrografía en el área de estudio, se utilizaron los perfiles de temperatura, salinidad y oxígeno disuelto obtenidos con CTDO. Se realizaron diagramas T/S para identificar las masas de agua detectadas en el área de estudio.

Para establecer si los cambios en abundancia de megalopas y zoeas de *M. gregaria* durante estos muestreos intensivos estaban asociados con fluctuaciones mareales, se usó una regresión no lineal por mínimos cuadrados para ajustar una función sinusoidal, que describe el cambio en abundancia en función del tiempo

$$Y_i(t) = M + A \cos\left(\frac{2\pi t}{\lambda - \theta}\right) + v \sin\left(\frac{2\pi t}{\lambda - \theta}\right) + \varepsilon$$

Donde Y_i es el logaritmo de la abundancia del estadio i en el tiempo t , M es la abundancia media durante el muestreo, A es la amplitud y λ es el periodo de las oscilaciones de Y , t es la hora de muestreo, θ es el ángulo de acrofase, v es un parámetro que indica el grado de apuntamiento de la curva y ε es el término de error aleatorio. Este análisis ha sido usado previamente para describir variaciones cíclicas en la abundancia del plancton costero (Yannicelli *et al.* 2006, Castro *et al.* 2011) así como para explorar la periodicidad en asentamiento de crustáceos (Amaral *et al.* 2007).

3.6 Flujo larval instantáneo en el fiordo durante la estación de máxima descarga de los ríos.

Con el objetivo de caracterizar la estructura vertical de las corrientes horizontales, y determinar el efecto de los flujos instantáneos en la abundancia larval de los principales taxa del meroplancton en el fiordo del río Baker, se realizó un muestreo con ADCP remolcado (307 KHz RDI Workhorse) junto con muestreos de zooplancton y perfiles hidrográficos en febrero de 2013. En tres puntos a lo largo del canal Martínez, uno cercano a la desembocadura del río Baker, uno más cercano al Golfo de Penas, y uno intermedio (Fig.3) se realizaron mediciones continuas con un ADCP ubicado a 1 m bajo la superficie, mirando hacia abajo. Se realizó a la vez un muestreo estratificado de zooplancton cada 3 horas aproximadamente. Los transectos

interno y externo se muestrearon durante 24 h, mientras que en el transecto intermedio se realizaron observaciones durante 12 h. Las muestras de zooplancton fueron colectadas por arrastres oblicuos desde 25 m hasta la picnoclina (5-10 m de profundidad), y desde la picnoclina hasta la superficie, usando una red Bongo con 300 μm de malla y 60 cm de diámetro. El volumen de agua muestreado con la red se estimó mediante flujómetro mecánico (General Oceanics) adosado a la boca de la red. Las muestras fueron preservadas en una solución tamponada de formaldehído 5% hasta la identificación y conteo de grupos de meroplancton en el laboratorio.

3.6.1 Análisis de datos

Los datos de velocidad de las corrientes horizontales fueron colectados cada intervalos de 3 s (pings) y registradas como el promedio cada 1 minuto. Los vectores de velocidad fueron descompuestos y rotados en componentes a lo largo del canal (u) y a través del canal (v). El control de calidad de los perfiles de corriente consideró la eliminación de datos erróneos, y criterios estándar de bondad sobre 50%, flujo $< 100 \text{ m}^3 \text{ s}^{-1}$ y error menor que $0.08 \text{ m} \cdot \text{s}^{-1}$.

Finalmente, sólo se consideraron para el análisis los perfiles cuyas diferencias entre velocidades registradas por el bottom track y las registradas por el GPS fueron menores que 3 m s^{-1} (ej. Valle-Levinson *et al.* 2007, Castillo *et al.* 2012). Un segundo criterio consideró la corrección de la dirección, debido al hecho que el compás magnético del ADCP es afectado por los campos magnéticos generados por el barco y desviación magnética local (Joyce 1989, Trump y Marmorino 1997). Se extrapoló verticalmente hasta la superficie asumiendo velocidad constante de acuerdo a Kirincich *et al.* (2005). Se necesitaron 5 m de extrapolación hasta la superficie.

Las abundancias de larvas de cada taxon fueron comparadas entre estratos y fase de la marea (vaciente o llenante) a través de análisis de varianza no paramétrico Kruskal-Wallis (Zar 1999). El desplazamiento horizontal neto de una larva que migra depende de los flujos instantáneos a que es expuesta durante los desplazamientos verticales (Queiroga y Blanton, 2005). Por lo tanto se calculó primero el flujo instantáneo de organismos (org/s), mediante la ecuación: $Ti = Do * Vcm * A$,

donde Do es la densidad de organismos en la muestra (org. m^{-3}), Vcm es la velocidad de corriente media (m/s) en el momento de muestreo multiplicada por el área A (m^2).

4. RESULTADOS

4.1. Capítulo 1. Estructura espacial de la comunidad meroplanctónica a lo largo de un fiordo Patagónico, el rol del cambio en los aportes de agua dulce.

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Resumen

En muchos estuarios, los aportes de agua dulce son los principales forzantes de la circulación, estructura hidrográfica y patrones de productividad a lo largo del sistema estuarino. Se investigó el grado en que la estructura de la comunidad meroplanctónica en el fiordo del río Baker (Patagonia chilena, 47.5°S) responde a cambios espaciales y temporales en las condiciones hidrográficas inducidas por cambios estacionales en la descarga del río. Se realizaron mediciones hidrográficas y de zooplancton a lo largo del fiordo a comienzos de primavera (octubre 2012) y fines de verano (febrero 2013), cuando la descarga del río era mínima y máxima, respectivamente. Los principales grupos de meroplancton encontrados fueron larvas de cirripedios, decápodos, bivalvos y gastrópodos. Hubo un cambio en la estructura comunitaria entre octubre y febrero, explicado por un cambio en el grupo dominante desde larvas de cirripedios a larvas de bivalvos. El cambio en la estructura comunitaria fue consistente con cambios en la estructura hidrográfica a lo largo del fiordo, los cuales están principalmente asociados con cambios estacionales en la descarga del río Baker. Un análisis de partición de la varianza mostró que no hubo un patrón espacial significativo que pudiera dar cuenta de la variación en el meroplancton a lo largo del Canal Martínez, mientras que la variabilidad temporal y las variables ambientales explicaron 36,6% y 27,6% de la varianza, respectivamente. Cuando se comparó el meroplancton entre los canales Baker y Martínez en octubre de 2012, cambios en las variables ambientales dieron cuenta de 23,5% de la varianza. Los nauplios y ciris de cirripedios fueron más abundantes en agua con menor temperatura y mayor oxígeno disuelto y concentración de clorofila-a, mientras que las larvas de bivalvos estuvieron asociadas con aguas más cálidas. El cambio estacional en la dominancia numérica, de larvas de cirripedios en primavera a larvas de bivalvos en verano, sugiere que la reproducción de estos grupos es gatillada por diferentes condiciones, en términos de hidrografía y disponibilidad de alimento.



Spatial structure of the meroplankton community along a Patagonian fjord – The role of changing freshwater inputs

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ABSTRACT

Freshwater inputs are major drivers of circulation, hydrographic structure, and productivity patterns along estuarine systems. We assessed the degree to which meroplankton community structure in the Baker/Martinez fjord complex (Chilean Patagonia, 47.5°S) responds to spatial and temporal changes in hydrographic conditions driven by seasonal changes in Baker river outflow. Zooplankton and hydrographic measurements were conducted along the fjord in early spring (October) and late summer (February), when river outflow was minimal and maximal, respectively. Major meroplankton groups found on these surveys were larval barnacles, crabs, bivalves and gastropods. There was a clear change in community structure between October and February, explained by a switch in the numerically dominant group from barnacle to bivalve larvae. This change in community structure was related to changes in hydrographic structure along the fjord, which are mainly associated with seasonal changes in the Baker river outflow. A variance partition analysis showed no significant spatial trend that could account for the variation in meroplankton along the Martinez channel, whereas temporal variability and environmental variables accounted for 36.6% and 27.6% of the variance, respectively. When comparing meroplankton among the Baker and Martinez channels in October, changes in environmental variables explained 44.9% of total variance, whereas spatial variability accounted for 23.5%. Early and late-stage barnacle larvae (i.e. nauplii and cyprids) were more abundant in water with lower temperature, and higher dissolved oxygen and chlorophyll-*a* concentration, whereas bivalve larvae were more strongly associated to warmer waters. The seasonal shift in numerical dominance, from barnacle larvae in early spring to bivalve larvae in late summer, suggests that reproduction of these groups is triggered by substantially different sets of conditions, both in terms of hydrography and food availability. The analysis of a monthly zooplankton time series showed that barnacle nauplii were most abundant in spring, and one order of magnitude more abundant than cyprids. Larvae of decapods were most abundant in summer.

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Introduction

Estuarine systems are physico-chemically more variable than other aquatic ecosystems (Elliott and Whitfield, 2011), encompassing several ecotones (sensu Attrill and Rundle, 2002), into the estuary from adjacent freshwater catchments, and out of the estuary into the marine/coastal area (Elliott and Whitfield, 2011). Such strong variability in physical–chemical conditions is reflected in community dynamics, particularly in the plankton, since spatial–temporal variation and habitat types are among the most important factors affecting patterns of species abundance, composition and size structure of estuarine plankton (Kennish, 1990). Estuarine

zooplankton frequently exhibits distinct patterns of horizontal zonation that vary with the prevailing tide and freshwater discharge (Benfield, 2013). In fjords, the strong vertical and horizontal gradients in hydrographic structure shape productivity patterns, zooplankton biomass, and community structure (Nielsen and Andersen, 2002; Goebel et al., 2005; González et al., 2013). Freshwater inflow into estuaries has been linked to an increased diversity of niches and food sources available to animals in these systems (Whitfield and Bruton, 1989; Ter et al., 1994).

Salinity is a key physical factor that constrains the spatial distribution of estuarine zooplankton (Benfield, 2013), since most species are able to tolerate a certain range of salinities. Temperature may also influence estuarine zooplankton over a range of temporal scales, given its effect on metabolic rates and swimming behavior (O'Connor et al., 2007; Benfield, 2013). Additionally, food availability (Toumi et al., 2005) and predation pressure (Williams, 1998),

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both of which are affected by salinity and temperature gradients, may significantly alter the structure of zooplankton communities in estuarine environments.

Salinity gradients driven by freshwater inputs interact with tidal currents to produce estuarine circulation patterns that often result in net landward transport of sub-surface saline water and seaward transport of fresher surface water (Pritchard, 1953). This type of circulation may promote the retention of certain zooplankton within an estuary (Dyer, 1997), and is known to influence productivity, community composition, age structure, biomass and distribution of zooplankton in fjordic systems (Basedow et al., 2004).

Few studies have focused on the whole meroplanktonic community in fjords (e.g. Norden Andersen, 1984; Hansen et al., 2002; Nielsen and Andersen, 2002), in particular in Chile (e.g. Antezana, 1999; Defren-Janson et al., 1999; Thatje et al., 2003). In fjords of southern Patagonia (53–55°S), high abundance of meroplankton has been observed during spring-bloom periods (Antezana, 1999; Defren-Janson et al., 1999), with numerical dominance of echinoderm larvae (20–65%) and barnacle larvae (6–20%), as well as polychaetes and bryozoans (Defren-Janson et al., 1999). In general, species richness in Subantarctic meroplankton is low and dominated by decapod crustaceans with seasonal reproduction that mainly takes place in spring (Lovrich, 1999).

In high latitude regions, invertebrates are subject to dramatic seasonal changes in physical–chemical conditions and productivity. In the Baker river fjord complex, central Patagonia, variations in river outflow, water temperature and salinity are conspicuous (Meerhoff et al., 2013). It differs from northern Patagonian fjords in that freshwater inputs are mostly composed of glacial meltwater, with high loads of fine sediments, which strongly limit light availability and primary production (Jacob et al., this volume). In fact, primary production estimates for this fjord are the lowest reported for Chilean Patagonia (Aracena et al., 2011; González et al., 2013; Jacob et al., this volume). In addition to seasonal changes in precipitation and glacier melting, the Baker river fjord

is influenced by semi-periodic events of abnormally high freshwater discharge due to the sudden draining of a glacial lake ca. 100 km upstream (Dussailant et al., 2010), which probably affect benthic communities along the fjord. Such instability of the freshwater regime may affect the biomass and composition of benthic communities in this fjord (Quiroga et al., 2012), and further shape patterns of meroplankton abundance and composition.

In this framework, the aim of this study was to characterize the composition and spatial structure of meroplankton along the Baker river fjord complex, and to assess its association with spatial (among channels of the same fjord) and seasonal changes (among periods with contrasting river outflow) in hydrographic structure. Additionally, we focus on numerically dominant groups to compare spatial and temporal changes in their relative abundance with those observed for key physical–chemical variables along the fjord. We discuss the implications of our findings in terms of current trends in freshwater inputs to this region, and their potential impact on the composition and distribution of zooplankton assemblages in this and comparable systems.

Material and methods

Study area

Fjords and channels from Chilean Patagonia receive freshwater discharges from rivers, surface runoff and groundwater flows fed by high rainfall (100–700 cm y⁻¹, MOP-DGA 1987), as well as glacier melting. Two major rivers in this region (Baker and Pascua) discharge water from glacial lakes and glacier melting into the large estuarine basin known as Baker river fjord complex, which is situated in between the extensive Northern and Southern Patagonian ice fields (47°–51°30'S), and comprises two main channels: Martinez and Baker (Fig. 1). The Baker river, with a mean annual outflow of 1133 m³ s⁻¹ (DGA), flows from Lake Bertrand and runs over 370 km along the eastern side of the Northern Patagonian

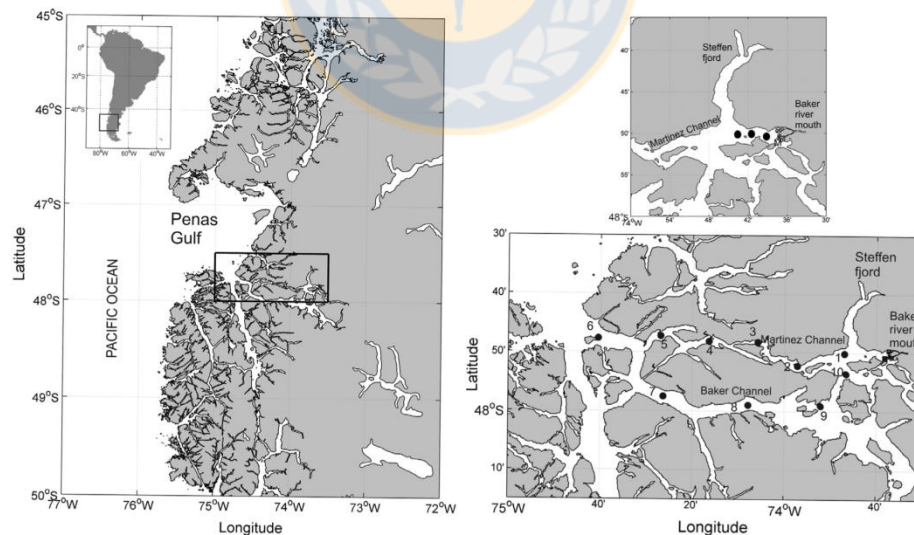


Fig. 1. Study area and sampling stations along the Baker river estuary. Upper-right panel shows zooplankton sampling stations (circles) for the monthly sampling, and location of the mooring (M) from which continuous records of temperature and sea level were gathered.

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ice field, to finally meet the estuary at the NE corner of the Baker fjord, near the town of Caleta Tortel. The Pascua River, with a mean annual flow of $753 \text{ m}^3 \text{ s}^{-1}$ (DGA), originates from Lake O'Higgins and runs over 67 km flows to reach its mouth near the Jorge Montt glacier, at the SE corner of the Baker Channel basin.

Zooplankton and hydrographic sampling

Variability in meroplankton community structure relative to seasonal changes in hydrographic conditions was assessed by comparing data collected along the Martinez channel during contrasting periods of river outflow: October 2012 and February 2013, with minimal and maximal river discharges, respectively. Spatial variability in community structure was assessed by comparing among channels (Martinez and Baker) during October 2012.

Zooplankton samples and hydrographic measurements were obtained from six sampling stations along the estuarine area of Martinez channel, between Baker river mouth and Penas Gulf in the Pacific Ocean (Fig. 1) in both seasons. Concurrently, four stations were sampled along the Baker channel in October 2012 (Fig. 1). The hydrographic conditions were determined from a set of CTD profiles (SBE-25, Seabird Electronics, USA) collected along the transects and included dissolved oxygen, turbidity and fluorescence. Sections along the fjord were then produced using Ocean Data View (Schlitzer, 2012) to visualize hydrographic spatial structure, and to compare among seasons and channels.

Zooplankton samples were collected by means of vertical tows from a 50 m depth up to the pycnocline (5–10 m depth), and from the pycnocline up to the surface, using a WP2 net with $150 \mu\text{m}$ mesh and 50 cm mouth diameter. Volume of water filtered was estimated by multiplying net mouth area by the vertical span of each tow. Samples were preserved in buffered 5% formaldehyde until laboratory sorting, identification, and enumeration of meroplanktonic groups.

Seasonal variation in the distribution of decapod and barnacle larvae and its association with environmental variability

To determine seasonal variability in the distribution and abundance of larvae, we analyzed a two-year monthly time series of zooplankton samples (January 2010 to February 2012) collected from three stations near the Baker river mouth (Fig. 1). Samples were collected with oblique tows (0–25 m) of a bongo net with $300 \mu\text{m}$ mesh and 60 cm mouth diameter, equipped with a mechanical flow meter (General Oceanics, USA). Samples were preserved in buffered 5% formaldehyde. In the laboratory, larvae of barnacles (nauplii and cyprids) and decapods (zoea) were sorted and enumerated.

River outflow data spanning the sampling period were obtained from a monitoring station in the Baker river (Colonia, $47^\circ 20.78' \text{S}$ $72^\circ 51.60' \text{W}$) maintained by the Direccion General de Aguas (<http://www.dga.cl>). A continuous record of water-column temperatures was collected from a mooring deployed at Caleta Tortel, near the river mouth ($47^\circ 49.13' \text{S}$, $73^\circ 32.22' \text{W}$) since September 2008. The mooring was equipped with temperature loggers (HOBO Pro, Onset Computer, USA) placed at 4, 10, 14 and 18 meters above bottom (mab). Finally, surface salinity was recorded monthly during plankton sampling at the three stations.

Data analysis

To evaluate the relationship between meroplankton community structure and the ensemble of environmental variables measured along the Martinez and Baker channels in October 2012, we applied distance based linear models (DISTLM) and distance based redundancy analysis (dbRDA) to both multivariate data sets using

PRIMER v6 (Clarke and Gorley, 2006), which includes PERMANOVA+ in the package (Anderson and Gorley, 2008). Distance-based linear models (DISTLM) is a routine for analyzing and modeling the relationship between a multivariate data cloud, as described by a resemblance matrix, and one or more predictor variables. DISTLM provides quantitative measures and tests of the variation explained by one or more predictor variables, allowing the partitioning of variance according to a regression (or multiple regression) model (Anderson and Gorley, 2008). Separate analyses were conducted to test for associations between meroplankton and environmental variables along the Martinez channel in October 2012 and February 2013, and between Martinez and Baker channels in October 2012. Environmental data were log transformed, community data were previously transformed to square root, Bray–Curtis distance was used for creating the resemblance matrix. The partition of the variability in the data cloud was performed according to sets of predictor variables, a set of environmental variables, a set of spatial variables (latitude and longitude, following Borcard et al., 1992), and temporal variables (Anderson and Gribble, 1998). We ran marginal tests, the test of the relationship between a response variable (or multivariate data cloud) and an individual variable alone, and the partial tests, the test for a relationship after fitting one or more variables (Anderson and Gorley, 2008). Canonical partitioning is the proper statistical procedure for partitioning the spatial variation of community composition data among environmental and spatial components, and for testing hypotheses about the origin and maintenance of variation in community composition among sites (Legendre et al., 2005).

Larval abundances were compared among seasons through analysis of variance (ANOVA) when homocedasticity and normality assumptions were met (Bartlett and Cochran test). Pairwise differences were tested using the a posteriori Tukey test (Zar, 1999). When data did not meet the respective distributional assumptions, comparisons were conducted using a Mann–Whitney test.

Results

Freshwater input and hydrographic gradients along the fjord

Baker river mean discharges in October 2012 and February 2013 were $600.4 \text{ m}^3 \text{ s}^{-1}$ and $1480.4 \text{ m}^3 \text{ s}^{-1}$, respectively, thus matching the climatological minimum and maximum values.

In October 2012, there was a longitudinal gradient in water temperature along the Martinez channel, and strong thermal stratification from the Baker river mouth up to 40 km seaward, with near-surface temperatures $<8.5^\circ \text{C}$ overlying a warmer layer ($>9.5^\circ \text{C}$) between 20 and 80 m depth (Fig. 2). Surface salinity also exhibited a longitudinal gradient, and varied from 0 near river mouth to ca. 20 beyond 60 km seaward (Fig. 2). Salinities >30 were found below 10 m throughout this transect. Dissolved oxygen was uniformly high at the surface ($>7.5 \text{ mL L}^{-1}$), though below the pycnocline it was clearly lower near the river mouth than at the seaward end of the transect. A strong signal of surface turbidity was observed up to 10 km away from the river mouth. Chlorophyll-fluorescence was higher and closer to the surface almost halfway up the Martinez channel (50 km), with maximum values of 4.5 mg m^{-3} (Fig. 2).

Contrasting conditions were found along the Baker channel in October 2012 (Fig. 3), with a thermal inversion that, unlike the Martinez channel, spanned the whole transect but deepened from 20 m near the river mouth to $>50 \text{ m}$ at the seaward end. Salinity distribution was similar to that observed along the Martinez channel with values <5 near the surface at the river mouth end of the transect. Dissolved oxygen concentrations were highest at the

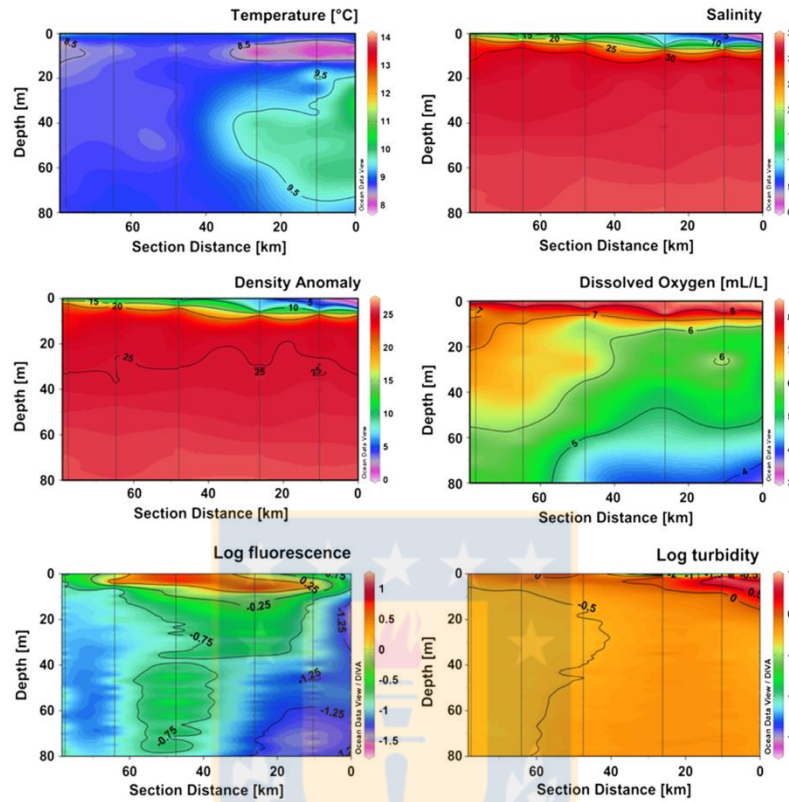


Fig. 2. Hydrographic sections along the estuarine gradient in Martinez channel, October 2012. Along-section distances are relative to the station closest to the Baker river mouth.

surface ($>7.5 \text{ mL L}^{-1}$) and decreased with depth in a way that closely resembled the pattern observed along the Martinez channel. Fluorescence values along this channel were much lower, with peaks that were close to 1 mg m^{-3} at all stations, but that were closer to the surface at the seaward end. A strong surface turbidity signal ($>5 \text{ NTU}$) was not detected beyond 5 km from the Baker river mouth.

A comparison of depth-integrated fluorescence at the Martinez channel stations (Table 1) showed higher values in October (mean $18.7 \pm 5 \text{ mg m}^{-2}$) than in February (mean $13 \pm 3 \text{ mg m}^{-2}$), as well as a change in the spatial location of the maximum value. While in October it was found near the center of the channel, in February it was located at the oceanic station.

In February 2013, hydrographic conditions along the Martinez channel exhibited a number of differences with respect to October 2012. First, the temperature section showed a warm surface layer ($>12^\circ\text{C}$) that reached ca. 30 m depth at the seaward end, near the Gulf of Penas, and became thinner ($<10 \text{ m}$) near the Baker River mouth (Fig. 4). Salinity was low at the surface all along the fjord (Fig. 4), whereas surface dissolved oxygen was high ($>7 \text{ mL L}^{-1}$) and decreased with depth. At any point along the channel, oxygen concentration below 50 m was lower than in October 2012 (see Fig. 2). High surface turbidity ($>5 \text{ NTU}$) was detected up to 40 km from the river mouth (i.e. 4 times as far as in October), whereas

fluorescence was close to zero over much of the transect and reached maximum values at the seaward end (1.25 mg m^{-3}) that were only a third of those found in October (Fig. 4).

Meroplankton community along the fjord

In October 2012, the meroplankton assemblage found along both channels was composed by decapod zoeae, barnacle nauplii and cyprids, as well as bivalve and gastropod larvae (Fig. 5). Decapod larvae consisted of zoeae of the anomuran “squat lobster” *Munida gregaria*, porcellanids and brachyurans. Barnacle cyprids and nauplii were numerically dominant above the pycnocline, representing more than 80% of total abundance. In the Martinez channel, above-pycnocline abundance of nauplii decreased from the oceanic stations ($78.8 \pm 8 \text{ indiv. m}^{-3}$, mean $\pm$ standard error) towards the river mouth ($18.6 \pm 10 \text{ indiv. m}^{-3}$) ($p = 0.049$, $U = 0$) over the pycnocline, whereas cyprid abundance remained rather constant through much of both transects (Fig. 5). Nauplii (mean $37.2 \pm 9 \text{ indiv. m}^{-3}$) were more abundant than cyprids (mean $5 \pm 1 \text{ indiv. m}^{-3}$) along the Martinez channel than in the Baker channel ($p = 0.037$, $U = 36$).

Along both channels, and in both strata, decapod larvae were most abundant at the outer stations, although a few specimens were found at the station that is closest to the Baker river mouth

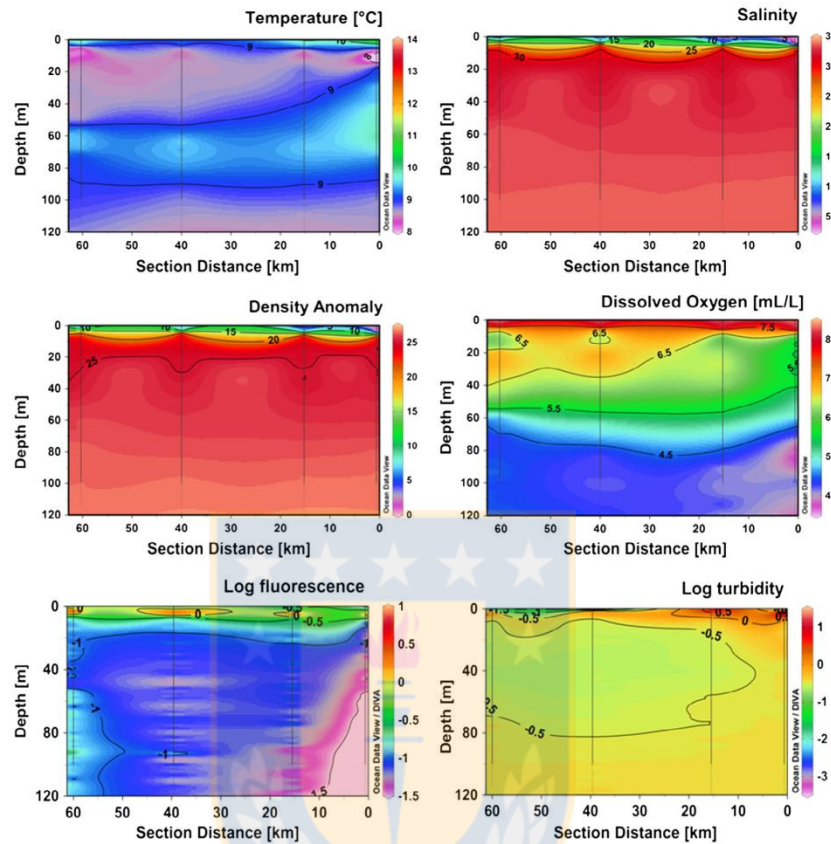


Fig. 3. Hydrographic sections along the estuarine gradient in Baker channel, October 2012. Along-section distances are relative to the station closest to the Baker river mouth.

Table 1
Integrated chlorophyll values between 0 and 50 m for each station.

Station	October 2012 Chl 0–50 m (mg m^{-2})	February 2013 Chl 0–50 m (mg m^{-2})
1	6.99	7.89
2	14.24	7.65
3	36.28	8.25
4	34.42	12.94
5	14.76	21.58
6	5.95	20.24
7	14.21	
8	13.13	
9	12.40	
10	7.50	

(Fig. 5). Abundance of bivalve larvae did not change across the pycnocline ($p = 0.65$, $U = 44$), whereas gastropod larvae were only found, and in very low numbers, below the pycnocline and in the outer stations of both channels.

In February 2013, meroplankton along the Martinez channel exhibited the same composition as in October 2012, but there was an important change in relative abundance. Bivalve larvae were clearly dominant (60–80% total abundance) above the

pycnocline throughout the channel (Fig. 5), whereas barnacle larvae dropped from 80% in October to <20% in February. Decapod larvae were also found along the fjord, with brachyuran and porcellanid larvae only present at the outer station (E6). Gastropod larvae were found only at the outer stations E6 and E5 (Fig. 5). A similar pattern was observed below the pycnocline, with bivalve larvae as the most abundant group along the channel. Barnacle larvae, though present throughout the transect, were less abundant below the pycnocline than above the pycnocline ($p = 0.024$, $U = 4$) (Fig. 5).

When comparing Martinez and Baker channels, for the DISLM we fitted geographical (spatial) set of variables first, followed by the environmental set because we were interested in testing the hypothesis of there being no relationship between meroplankton abundance and environmental variables, given the spatial variables. Two spatial variables (x and y) alone accounted for 23.5% of the variation in the meroplankton ($p = 0.016$), while the environmental variables accounted for 62.6% ($p < 0.01$). However, after fitting the spatial variables (sequential tests) the environmental variables explained 44% ($p = 0.001$) resulting in a total explained variation of 68.4% (Fig. 6c). Of the variation in meroplankton between channels 23.5% was spatially structured and a large part

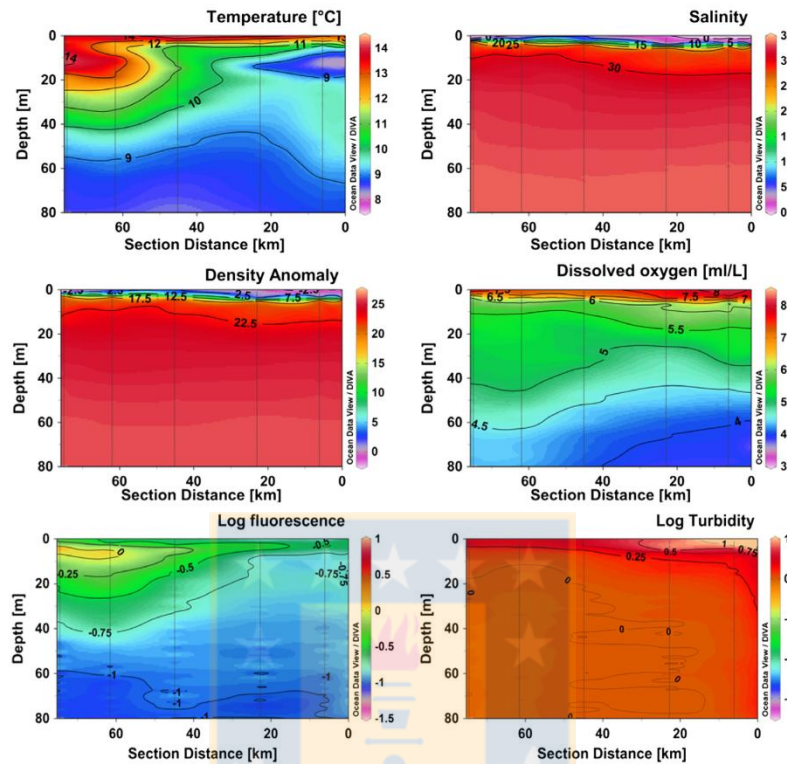


Fig. 4. Hydrographic sections along the estuarine gradient in Martinez channel, February 2013. Along-section distances are relative to the station closest to the Baker river mouth.

of this was explained by environmental variables mainly turbidity, salinity and oxygen (overlap, Fig. 6c).

The full model is visualized in the dbRDA ordination, where the first two dbRDA axes captured 84.6% of the variability in the fitted model and 57.8% of the total variation in cloud data (Fig. 6a). The vector overlay shows how the first dbRDA axis was strongly related to fluorescence and oxygen. The second dbRDA axis was related to salinity, oxygen and turbidity. The multivariate ordination of community-structure data did not separate stations from the Martinez and Baker channels (Fig. 6a). Instead, stations closer to the ocean along both channels (E7, E8, E6 and E5) were grouped together, and were more strongly correlated with along-fjord changes in fluorescence and dissolved oxygen. A cluster of samples from below the pycnocline at stations closer to the Baker river mouth (E12, E32, E92, E42) was more strongly influenced by spatial changes in turbidity (Figs. 2 and 3). Community structure above the pycnocline was clearly influenced by fluorescence. Barnacle nauplii and cyprids were more abundant at the outer stations of both channels and above the pycnocline, where the fluorescence was higher (Fig. 6b). Gastropod, brachyuran and *M. gregaria* larvae were more abundant at Martinez channel outer stations and below the pycnocline; these stations were explained by higher salinity and oxygen.

In Martinez channel, between October and February, spatial variables did not account for the variation in meroplankton ($p = 0.4$), whereas the environmental variables accounted for

49.5% ($p < 0.001$). Since spatial variability was not significant, we ran the analysis without this predictor variable, and the results showed that temporal variability accounted for 36.6% of the variance ($p < 0.001$), while environmental variables accounted for 49.5% ($p < 0.001$). However, after fitting the temporal variables, the environmental variables explained 27.6% ($p = 0.002$), with a high percentage of overlap with temporal variability, resulting in total variance explained of 64% (Fig. 7c).

The full model is visualized in the dbRDA ordination. The first two dbRDA axes captured 84.7% of the variability in the fitted model, 57% of the total variation in cloud data (Fig. 7a). The vector overlay shows how the first dbRDA axis is strongly related to water temperature, fluorescence and month (temporal variability). The second dbRDA axis is related to oxygen and fluorescence. The multivariate ordination of community-structure data clearly separated samples from October and February (Fig. 7). This separation was mostly determined by changes in temperature, oxygen and fluorescence produced by the seasonal change in river outflow. There was no separation among February 2013 zooplankton samples. Within the October samples, however, those from above the pycnocline were separated from the ones below the pycnocline, due mainly to spatial changes in chlorophyll fluorescence (Fig. 7a). The Martinez channel in October was characterized by higher abundances of cyprids, nauplii, *M. gregaria*, and brachyuran larvae, while in February it was characterized by bivalve and gastropod larvae higher water temperature and turbidity (Fig. 7a and b).

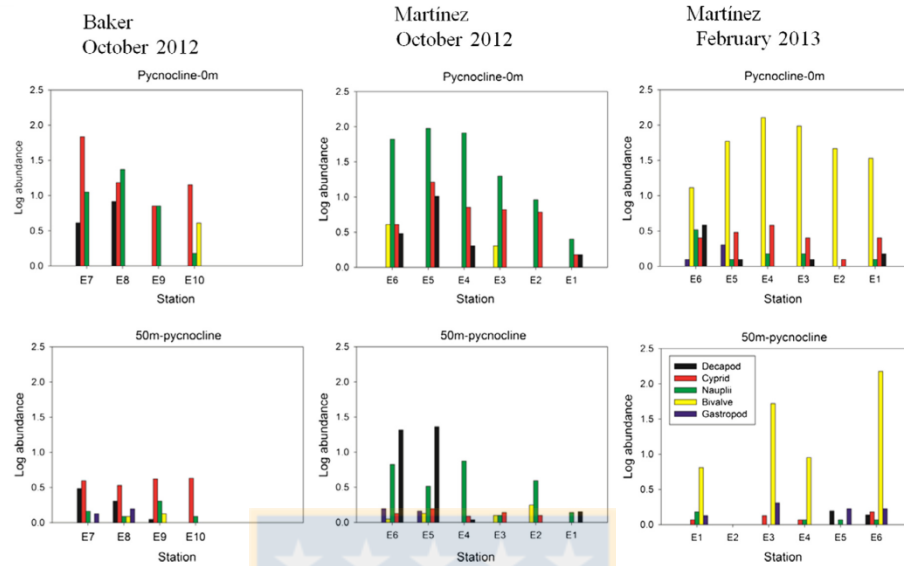


Fig. 5. Abundance of planktonic larvae (log-transformed ind/m³) above and below the pycnocline along the Baker channel in October 2012 (left), Martinez channel in October 2012 (middle), and Martinez channel in February 2013 (right). In all panels, stations on the right hand side are closest to the Baker river mouth. See Fig. 1 for station numbers.

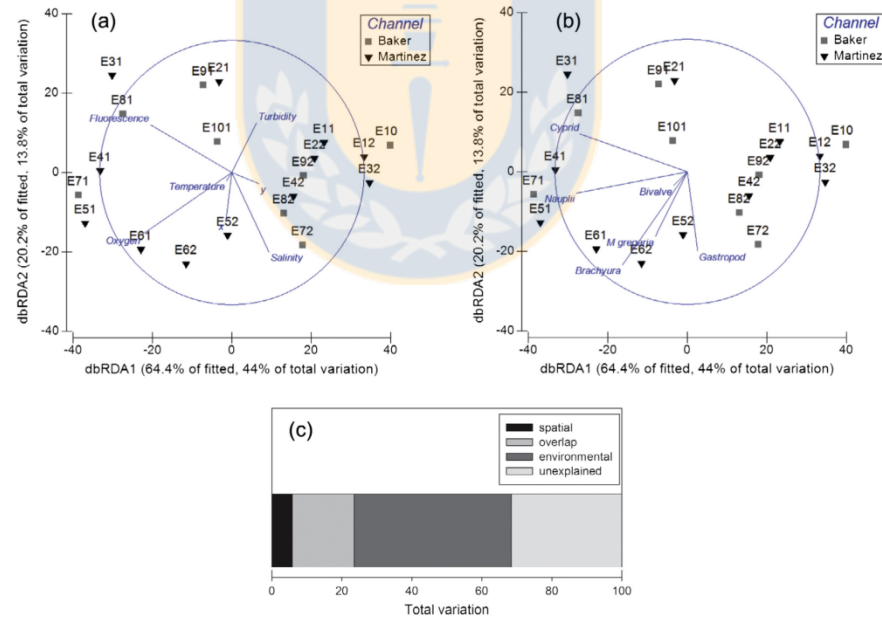


Fig. 6. Distance-based redundancy analysis (dbRDA) ordination for zooplankton composition constrained by environmental variables (based on Bray-Curtis after square root transformation of abundances) along Martinez and Baker channels in October 2012. (a) Vectors represent environmental variables, (b) vectors correspond to zooplankton groups, and (c) schematic diagram of variance partitioning according to two sets of predictor variables (space and environment).

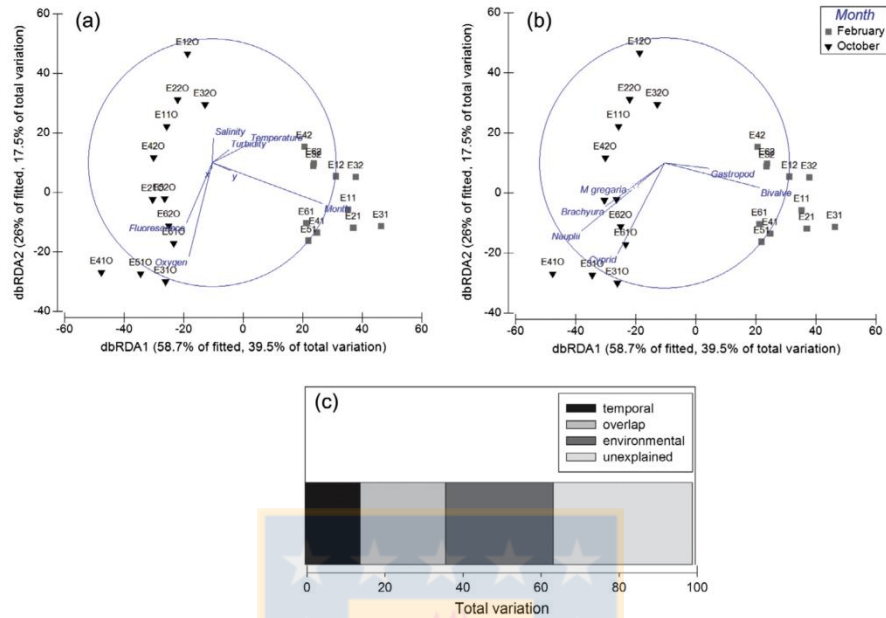


Fig. 7. dbRDA ordination for the fitted model of meroplankton data (based on Bray–Curtis after square root transformation of abundances) versus environmental variables along Martinez channel in October 2012 and February 2013. (a) Vectors represent environmental variables, (b) vectors correspond to meroplankton groups, and (c) schematic diagram of variance partitioning according to two sets of predictor variables (time and environment).

Spatial–temporal patterns of larval abundance

Seasonal changes in abundance were observed for barnacle nauplii, which were most abundant in spring (Fig. 8, mean spring–summer 11.1 ± 5.4 indiv. m^{-3} , mean fall–winter 8.1 ± 3.4 , $F_1 = 5.4$, $p = 0.024$). Nauplii were one order of magnitude more abundant than cyprids. Except for the high abundance of nauplii at station Baker in August, nauplii tended to decrease in abundance from the outermost stations towards the Baker river mouth during spring. Decapod larvae were significantly more abundant in summer ($F_{2,39} = 3.66$, $p = 0.016$).

Discussion

Along fjord hydrographic gradients

The strong hydrographic gradients and clear differences in water-column conditions detected between October 2012 and

February 2013 can, to a large extent, be ascribed to seasonal changes in solar radiation and freshwater discharges. The salinity gradient was consistent with general patterns observed for estuarine systems, with surface salinity gradually increasing seawards, and a salinity increase with depth (Day et al., 2013). As for temperature, on both surveys we detected warmer sub-surface waters (20–80 m) near the Baker river mouth. Warming of sub-surface waters along this fjord has been previously reported for summer and autumn, and hypothesized to result from the intrusion of warmer water from the Penas Gulf (Aiken, 2012). If such intrusions occur in a consistent fashion, patterns of larval transport and retention along the fjord may be largely influenced by oceanic, larger-scale processes.

On both surveys, dissolved oxygen concentrations reached their minimum values at depth near the Baker river mouth, although the volume of low-oxygen water appeared to increase in February, which is consistent with the annual peak in freshwater discharges (Aiken, 2012; Meerhoff et al., 2013) and, presumably, a concurrent

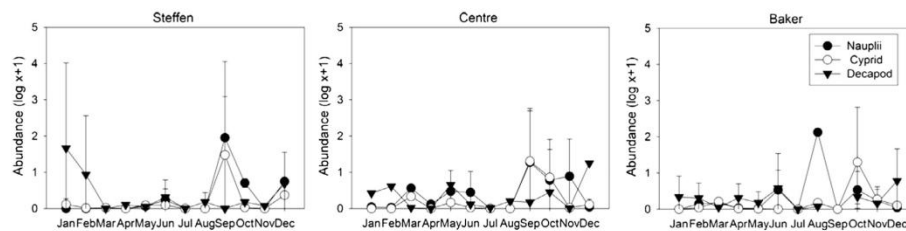


Fig. 8. Two-year composite of monthly data that outlines the annual cycle in abundance (larval abundances before log-transformation ind/m^3) of decapod larvae and barnacle larvae (nauplii and cyprids) at the three time-series stations: (a) Steffen, (b) Center, and (c) Baker (see Fig. 1).

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increase in particulate organic matter of terrestrial origin that enters this estuarine area. Lower sub-surface oxygen concentrations in summer months may be due to remineralization of this river-borne particulate organic matter, which may be as high as $190 \mu\text{g C L}^{-1}$ at 10 km from the Baker river mouth (Vargas et al., 2011). The near-zero fluorescence values observed in this section of the fjord during our February 2013 survey suggest low *in situ* production of organic matter, and support the idea that the river may indeed be carrying most of the particulate organic matter that reaches deeper waters.

The turbidity gradient we observed is consistent with the model results from Marín et al. (2013), which prescribed maximum concentration of suspended solids near the Baker river mouth. Although this turbidity maximum is a feature common to many estuarine systems, its nature differs from many due to the glacial origin of suspended sediments (Dowdeswell and Vásquez, 2013) and their strong and persistent effect on light attenuation at the surface, which is known to limit primary productivity (Pizarro et al., 2005; Aracena et al., 2011; Jacob et al., this volume).

Chlorophyll-*a* concentrations were relatively low when compared to values observed at other Patagonian fjords, with values that were higher in spring midway along the estuary (ca. 4 mg/m^3), and four times as high as maximum values observed in late summer (ca. 1 mg/m^3), when fluorescence peaks were constrained to outer stations and located deeper in the water column.

Along fjord gradient in the meroplanktonic community

The meroplankton community composition observed along the Baker river fjord complex was dominated by larval barnacles, decapods, bivalves and gastropods, and differed from that described by Defren-Janson et al. (1999) for Patagonian fjords located further south.

In October, the phytoplankton-feeding barnacle nauplii were more abundant than the non-feeding cyprid stage, and more abundant along the Martínez channel than the Baker channel. This is consistent with the higher near-surface fluorescence measured along the Martínez channel.

Barnacle larvae are an important component of the meroplankton in estuarine Patagonian waters, with the barnacle *Elminius kingii* being the most abundant and typical benthic species (Viviani, 1963). The abundance of barnacle nauplii tended to decrease towards the Baker river mouth, whereas cyprid abundance remained relatively constant. The estuarine retention of barnacle larvae has been described for species such as *E. modestus* in several northern-hemisphere estuaries, suggesting a vertical migration behavior (Martin and Foster, 1986; Lawson et al., 2004; Macho et al., 2010).

Nauplii were more abundant at outer stations and above the pycnocline on both channels during the October 2012 survey, in close association with higher chlorophyll-*a* concentrations and, presumably, greater food availability for this larvae. González et al. (2013) found that in November the oceanic station near Penas Gulf, exhibits a more conspicuous diatom community with *Skeletonema* spp., *Leptocylindrus minimus*, *Thalassiosira* spp., *Chaetoceros* spp., and *Pseudonitzschia* spp., which would constitute a more suitable food for barnacle larvae than the thecate dinoflagellates found at the Baker fjord. Adequate food availability appears to be a key condition for larval hatching in *E. kingii* (Jana, 1978), and may have triggered the release of nauplii found along the estuary during our October 2012 survey.

Bivalves produce large numbers of pelagic planktotrophic larvae which spend several weeks in the water column before settling (Raby et al., 1994). In temperate estuaries, spawning of benthic bivalves is often triggered by rising water temperatures (Ingle, 1951). The numerical dominance of bivalve larvae in February,

when the near-surface temperature was higher than in October, suggests that this may also be the case for adult bivalves in the Baker/Martínez fjord complex. Together with water temperature, food availability is one of the main factors affecting larval development times (Raby et al., 1994). The fact that chlorophyll concentrations in summer were much lower and constrained to outer stations than in early spring raises the question of what these bivalve larvae might be feeding upon. Recent observations at a station close to the Baker river mouth have shown that picoplankton ($<2 \mu\text{m}$) and nanoplankton ($2\text{--}20 \mu\text{m}$) may account for 45% of depth-integrated net primary production in this section of the estuary, and that bacterial secondary production may be as high as 70% of primary production (González et al., 2013). It has been shown that larvae of some bivalves such as the oyster *Crassostrea gigas* (Dauvin, 1993) and *Pinctada fucata martensii* (Tomaru et al., 2000) may feed upon bacteria, which in the first case may account for up to 50% of their metabolic carbon requirements (Dauvin, 1993). Whether bivalve larvae in the Baker river estuary depend on small-size phytoplankton and/or planktonic bacteria to feed and complete their development is a question that warrants further investigation.

Gastropod larvae were found near the surface only at the outermost station, and below the pycnocline along the entire fjord, indicating that salinity may be a limiting factor in their spatial distribution, either by providing a density barrier against passive larval dispersal (e.g. Ayata et al., 2011; Shanks et al., 2002) or by setting physiological constraints to the vertical migration of larvae (Sameoto and Metaxas, 2008). In the outer stations the dissolved oxygen was also higher and determined the gastropod larvae distribution. Effects of low dissolved oxygen on early development and swimming behavior of veliger larvae have been found for the gastropod larvae of *Nassarius festivus*. Dissolved oxygen levels well above hypoxia levels ($2.8 \text{ mg O}_2 \text{ l}^{-1}$) have significant impact on the hatching success and larval development in gastropods (Chan et al., 2008).

Although meroplankton community structure in October was similar among the Martínez and Baker channels, we observed differences along the river-ocean gradient, with stations closer to the ocean grouped together, and correlated with chlorophyll concentration (i.e. food availability). The grouping of stations closer to the Baker river mouth and below the pycnocline was explained by estuarine hydrographic structure (temperature and salinity), whereas community structure above the pycnocline was mainly explained by turbidity. High turbidity may affect meroplankton determining the distribution of adult benthos. Farrow et al. (1983) reported that in a highly turbid fjord, filter feeders (e.g. barnacles) abundance increased far from the turbidity maximum, especially where currents were stronger (Farrow et al., 1983). High sediment concentrations can also influence plankton species composition of glacially influenced fjords, by affecting the capability of carbon turnover in some species (Arendt et al., 2011).

In February, when river outflow reaches maximum values, the community structure was not spatially differentiated. Our results also showed a clear change in community structure along the Martínez channel between October and February, which was mainly due to a switch in numerical dominance from barnacle to bivalve larvae. A change in meroplankton composition and its relation to local hydrographic patterns was reported also for the southern Kara sea by Fetzner (2012).

The interaction of hydrographic structure with space is responsible for meroplankton community variations in estuaries and coastal areas (Belgrano et al., 1999; Ayata et al., 2011). Belgrano et al. (1995) suggested that the spatial structure of the environment should be taken into consideration when describing zooplankton spatial patterns. However, our results show that hydrographic variability explained a considerable fraction of

meroplankton variability that was neither spatially nor temporally structured. In all likelihood, this is mainly due to changes in river outflow that force the horizontal (i.e. along-fjord) displacement of salinity and turbidity fronts between minimum and maximum outflow in spring and summer months (i.e. October and February surveys). Using a fixed reference frame to assess spatial variation in a dataset like the one presented here will fail to capture all spatially structured variation because gradients along estuaries vary in time (McLusky, 1993).

Advective processes in estuaries partly explain why measured environmental variables fail to capture all spatially and temporally structured variation in the species data (Muylaert et al., 2000), because time-lag effects linked to growth and loss processes are projected on a spatial gradient due to advective transport. It is the interaction of growth and decay rates with transport processes that ultimately determines spatial patterns in the species composition of meroplankton. Furthermore, considering the documented effects of temporally varying salinity on the adults of estuarine benthic species (Ysebaert et al., 2002), and the good correspondence between occurrence of most estuarine species and spatial and seasonal changes in salinity (Atrill, 2002), gradients and seasonal changes in this variable along the Baker/Martinez fjord may represent a strong density-independent factor explaining the patterns of abundance and composition of meroplankton in this estuarine system.

Conclusions

Strong horizontal and vertical gradients in hydrographic conditions and fluorescence were observed along the Baker river estuary both in early spring (October) and late summer (February). The meroplankton community consisted mostly of larval barnacles, decapods, bivalves and gastropods. Barnacles dominated in spring, when river outflow was at a minimum, whereas bivalves were most abundant in summer, when river outflow was close the annual maximum. Community structure in spring did not differ among channels (Martinez and Baker), but showed a clear separation between outer stations and those closer to the Baker river mouth. Community structure at outer stations was correlated with chlorophyll concentration and dissolved oxygen, whereas at inner stations it was explained by turbidity above the pycnocline, and by water temperature and salinity below the pycnocline.

Nauplii and cyprids were numerically dominant when surface turbidity and salinity effects from river discharges were at a minimum, and phytoplankton biomass (inferred from chlorophyll fluorescence) was higher relative to summer observations. Bivalve larvae dominated when surface water temperatures were higher, but chlorophyll values were 4 times lower than in October.

Meroplankton community structure in February, when compared with October along the same transect, was explained by water temperature and turbidity.

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4.2. Capítulo 2. Influencia de la descarga de agua dulce y mareas en la abundancia y distribución de larvas y juveniles de *Munida gregaria* en el estuario del río Baker, Patagonia Chilena.

Erika Meerhoff, Leonardo Castro, Fabián Tapia

Resumen

Series de tiempo de zooplancton con diferente resolución temporal y cobertura fueron examinadas para caracterizar patrones estacionales y diurnos en la abundancia de larvas y juveniles de *Munida gregaria* en el estuario del río Baker. Las zoeas fueron más abundantes a fines de invierno y en primavera, coincidente con la estación de menor transporte de sedimentos y mayor producción primaria en la región. Los juveniles fueron encontrados exclusivamente en verano. Hubo una correlación significativa entre la abundancia de zoeas y la variabilidad de alta frecuencia en la temperatura cerca a la picnoclina en periodos de 7-20 y 26-30 días antes de cada muestreo de plancton. Estas escalas temporales de correlación sugieren que movimientos internos podrían ser una indicación ambiental proximal para los ritmos lunares en la eclosión larval, más que directamente causar la agregación de larvas en el área muestreada. Para caracterizar patrones temporales de menor periodo en la abundancia larval y la distribución vertical, muestras estratificadas fueron colectadas cada 3 h durante 24 h en primavera (Noviembre 2008) cerca de una de las estaciones de monitoreo. Las zoeas fueron significativamente más abundantes en la capa sub-superficial de 10-25 m ($p=0,039$), y los cambios en la abundancia integrada de zoeas y megalopas se asociaron con el ciclo mareal. En conjunto, estos resultados sugieren que la estructura espacial y dinámica poblacional de *M. gregaria* en esta región pueden responder a forzamiento combinado de cambios estacionales en aportes de agua dulce, procesos dirigidos por la marea como transporte larteral de larvas y juveniles, y cambios en condiciones locales mediados por ondas internas.



Research papers

Influence of freshwater discharges and tides on the abundance and distribution of larval and juvenile *Munida gregaria* in the Baker river estuary, Chilean Patagonia

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ABSTRACT

Zooplankton time series collected with different temporal resolution and coverage were examined to characterize seasonal and diel patterns in the abundance of *Munida gregaria* larvae and juveniles in the Baker river estuary. Zoeae were more abundant in late winter and spring, coinciding with the season of lower sediment transport and higher primary production in the region. The occurrence of juveniles was exclusively in summer. There was a significant correlation between the abundance of zoeae and high-frequency temperature variability near the pycnocline over periods of 7–20 and 26–30 days prior to each plankton sampling. These time scales of correlation suggest that internal motions may be a proximal environmental cue for lunar rhythms in larval hatching, rather than directly causing the aggregation of larvae at the sampling area. To characterize shorter-term patterns in larval abundance and vertical distribution, stratified samples were collected every 3 h over a full late-spring day (November 2008) near one of the monitoring stations. Zoeae were significantly more abundant at 10–25 m depth ($p=0.039$), and changes in depth-integrated abundance of both zoea and megalopae were strongly associated with the tidal cycle. Together, these results suggest that the spatial structure and population dynamics of *M. gregaria* in this region may respond to the combined forcing of seasonal changes in freshwater inputs, tidally-driven processes such as lateral transport of larvae and juveniles, and internal-wave mediated changes in local conditions.

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1. Introduction

The retention of planktonic larvae in estuarine areas, or their migration into those environments, are critical for the population dynamics and geographic distribution of many benthic estuarine species (Norcross and Shaw, 1984; McConaughy, 1988). Larval retention or transport results from the interaction between larval behavior (Sulkin, 1984) and the heterogeneous estuarine flow field. Larvae can be retained in a mixed estuary by remaining near the bottom throughout the tidal cycle or near the surface during flood tides (Sponaugle et al., 2002). Tidal currents and the vertically-sheared flows characteristic of estuarine circulation are the main physical features that provide a means for planktonic

larvae to move into and out of estuaries (Cronin and Forward, 1982; Rothlisberg et al., 1983). Superimposed on this advective forcing, local salinity regimes impose physiological constraints that ultimately shape the spatial distribution of estuarine benthic species (Sanders et al., 1965; Carriker, 1967; Attrill and Thomas, 1996). As climate-change scenarios predict substantial changes in freshwater inputs to estuarine systems, circulation patterns are expected to change as well. Thus, it is important to identify the main processes and mechanism that determine the current patterns of larval transport and adult distribution, in order to understand the potential impact of future changes in estuarine circulation.

Chilean Patagonia is one of the most extended fjord regions in the world, spanning from 41.5° S (Reloncaví Fjord) to 55.9° S (Cape Horn), and comprising 240,000 km² of shoreline (Silva and Palma, 2008). Fjords and channels in this region receive freshwater discharges from rivers, surface runoff and groundwater flows fed by high rainfall (100–700 cm y⁻¹, MOP-DGA 1987), as well as glacier melting. Two major rivers in this region are the Baker and Pascua, both of which discharge water from glacial lakes and

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glacier melting into the large estuarine basin known as Baker Channel, situated in between the Northern and Southern Patagonian ice fields, the largest ice fields in South America. The Baker river is the largest river in the South American temperate forest biome (Rozzi et al., 2012) with a mean annual outflow of $1133 \text{ m}^3 \text{ s}^{-1}$ (DGA); it flows from Lake Bertrand and runs over 370 km along the eastern side of the Northern Patagonian ice field, to finally meet the estuary at the NE corner of the Baker Channel, near the town of Caleta Tortel. The Pascua River, with a mean annual flow of $753 \text{ m}^3 \text{ s}^{-1}$ (DGA), originates from Lake O'Higgins and runs over 67 km flows to reach its mouth near the Jorge Montt glacier, at the SE corner of the Baker Channel basin. This glacier experiences one of the highest calving fluxes ever recorded in Patagonia ($2.4 \text{ km}^3 \text{ y}^{-1}$, Rivera et al., 2012). As shown by recent estimates, the contribution of the Patagonian Icefields to sea-level rise has increased markedly over the twentieth century (Glasser et al., 2011).

The squat lobster *Munida gregaria* (Fabricius, 1793) (Decapoda, Anomura, Munididae) is widely distributed in coastal waters of southern South America as well as in the Southwest Pacific. In the SW Atlantic, it ranges from Uruguay (35°S) to Cape Horn (55°S), including the Falkland Islands. In the SE Pacific, it is found from Cape Horn to Chiloé Island (41°S) (Boschi et al., 1992). In the SW Pacific, it is found in Tasmania, eastern New Zealand, and sub-Antarctic islands (Zeldis, 1985). Its bathymetric distribution varies from sub-littoral to ca. 1100 m depth (Arntz et al., 1999). In the southern limits of its South American distribution, benthic *M. gregaria* aggregations can reach densities of ca. 30 ind m^{-2} (Tapella, 2002), and may constitute nearly 50% of macrobenthic biomass (Arntz and Gorny, 1996). Although while in the plankton it feeds on smaller crustaceans, micro- and macroalgae, as well as particulate organic matter (Diez et al., 2012), adult *M. gregaria* are primarily deposit feeders that provide a direct link between low trophic levels and top predators (Romero, 2003; Romero et al., 2004).

In Southeastern South America (Beagle Channel, Argentina) female *M. gregaria* carry eggs for 8–9 months in fall–winter, with larval hatching occurring in spring–summer, between October and January (Rodríguez and Bahamonde, 1986). Larvae go through 5 stages up to postlarval metamorphosis. *M. gregaria* has a juvenile pelagic phase, while adults are benthic and can perform vertical migrations into the water column (Zeldis, 1985). Based on observed distributions and abundance of larval stages during spring months in the fjords of Chilean Patagonia, it has been hypothesized that gravid females would migrate toward inner channels, where hatching and release of early larval stages would take place in winter months (León et al., 2008). Early larval stages would be dispersed toward outer, more oceanic waters, and the late-stage megalopae would concentrate near the mouth of these channels by late spring (León et al., 2008). It has been proposed that the mechanism by which juveniles return to the channels is associated with the landward subsurface flow that is characteristic of estuarine circulation. Details on the transition from this outer-channel distribution of megalopae to the benthic adult phase, and the role of estuarine waters in the reproduction and life cycle of this species in the Chilean fjord region, are still unclear.

The aim of this study was to characterize the seasonal and diurnal variability in abundance and distribution of planktonic larvae and juveniles of *M. gregaria* in the Baker River estuary, and to establish the relationship between these patterns and physical processes conducive to larval transport and redistribution. This is particularly important in a region that is undergoing changes in freshwater input regimes, which by affecting advective conditions in the estuary and associated fjords may substantially affect the spatial distribution and abundance of marine species whose life cycles are linked to estuarine systems.

2. Material and methods

2.1. Study area and sampling stations

Zooplankton samples and hydrographic observations were gathered from the estuarine area flanked by the town of Caleta Tortel on the east, and by the Steffen fjord on the west (Fig. 1). Three sampling stations located at ca. 1 km ('Baker', $47^\circ 47.78' \text{S}$ $73^\circ 35.77' \text{W}$), 4 km ('Center', $47^\circ 47.11' \text{S}$ $73^\circ 38.97' \text{W}$), and 6 km from the Baker river mouth ('Steffen', $47^\circ 47.25' \text{S}$ $73^\circ 40.20' \text{W}$) were sampled monthly. Mean depth along this transect is 200 m.

2.2. Data collection

To characterize the seasonal variability of hydrological and hydrographic conditions we used (i) outflow time series for the Baker and Pascua rivers, (ii) time series of sea level and water-column temperatures recorded near the Baker River mouth (Fig. 1), (iii) monthly measurements of surface temperature and salinity conducted at the 3 stations, and (iv) a set of CTD profiles collected near the river mouth (Baker station) in spring–summer months.

River outflow data spanning September 2008 through December 2011 were obtained from the Dirección General de Aguas (<http://www.dga.cl>) for two points along the Baker river basin (Angostura Chacabuco at $47^\circ 8.53' \text{S}$ $72^\circ 43.58' \text{W}$ and Colonia at $47^\circ 20.78' \text{S}$ $72^\circ 51.60' \text{W}$), and two points along the shorter Pascua river basin (Lago O'Higgins at $48^\circ 22.10' \text{S}$ $72^\circ 57.67' \text{W}$ and Quetru at $48^\circ 10.28' \text{S}$ $73^\circ 4.40' \text{W}$). A three-year record of sea level and water column temperatures was gathered from a mooring deployed since September 2008 near the Baker River mouth (Caleta Tortel, $47^\circ 49.13' \text{S}$, $73^\circ 32.22' \text{W}$) at ca. 20 m depth. The mooring was equipped with HOBO Pro temperature loggers (Onset Computer Corp., USA) at 4, 10, 14 and 18 m above bottom (mab), and a pressure sensor at 2 mab. Hydrographic conditions through the water column were characterized using a set of CTD profiles gathered in January, February, April, September, and October 2011. Finally, surface salinity was recorded monthly at the three sampling stations.

Zooplankton samples were collected monthly, from January 2010 to February 2012, at the three stations mentioned above (Fig. 1). Samples were collected by means of oblique tows from a depth of 25 m up to the surface, using a Bongo net with 300 μm mesh and 60 cm mouth diameter. Volume of water sampled by the net was estimated with a mechanical flowmeter (General Oceanics) attached to the net's mouth. Samples were preserved in buffered 5% formaldehyde, until laboratory sorting, identification, and enumeration of *M. gregaria* total zoea and juveniles.

2.3. Data analysis

Seasonal signals in the time series were characterized using harmonic analysis with a least-square fitting procedure (Emery and Thomson, 2001). High-pass filtering was used to remove low-frequency signals (periods $> 6 \text{ h}$) from the mid-water temperature records at 14 mab (ca. 6 m below the surface), thus enhancing high-frequency (HF) temperature variability that could be ascribed mostly to internal-wave activity in the area. Harmonic analysis of pressure data to identify the principal tidal constituents in the area was conducted using *t_tide* for MATLAB (Pawlowicz et al., 2002).

To characterize seasonal patterns in larval abundance, a mean annual cycle was produced based on monthly mean abundance of *M. gregaria* larvae and juveniles. Larval abundances were compared among seasons (spring–summer, fall–winter) and among sampling stations (Steffen, Center, Baker) using analysis of variance (ANOVA) whenever the homocedasticity and normality

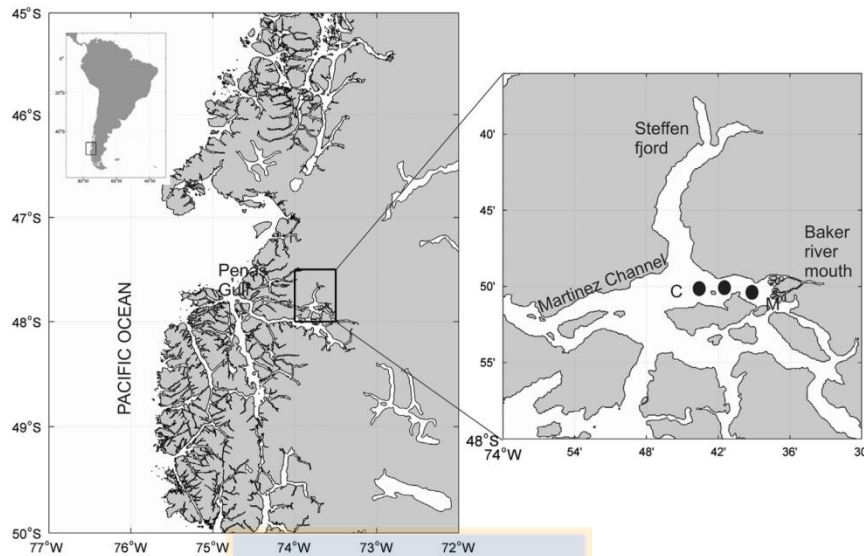


Fig. 1. Study area and location of the zooplankton sampling stations (circles), the mooring that gathered continuous records of temperature and pressure (M), and the CIMAR station where the 24-h study was conducted (C).

assumptions were met. Pairwise differences were tested using a Tukey test (Zar, 1999). Data were log-transformed when distributions did not meet the statistical assumptions.

Associations between larval abundance and environmental parameters (surface salinity, cumulative river outflow, high-frequency temperature variability) were explored through correlation analyses. High-frequency (HF) temperature variability at ca. 6 m below the surface (14 mab, depth corresponding to pycnocline, see below) was regarded as a proxy for internal wave activity, and quantified using a high-pass filter with a 6-hour cutoff period, which was aimed at removing temperature oscillations induced by diurnal and semi-diurnal tides. To test for correlations between larval abundance and HF variability prior to zooplankton sampling, the root mean square (RMS) of the HF temperature signal was computed for a number of increasingly long pre-sampling periods, from 1 to 30 days. Pearson correlation coefficients and their corresponding significance were calculated for each one of these periods. In this way, we assessed the temporal scales over which larval abundance and HF variability in the water column may be associated. We considered only summer months for making the correlation of juvenile abundance and environmental variables since juveniles are present in the plankton a shorter period of time than zoeae.

2.4. Diel vertical distribution and changes in abundance of *M. gregaria* larvae

To assess diel patterns in the vertical distribution of *M. gregaria* larvae, we analyzed depth-stratified samples collected over a 24-h cycle at a fixed station near the Steffen station (Fig. 1) during the CIMAR-14 oceanographic cruise, conducted in November 2008 onboard the R/V AGOR Vidal Gormaz. Zooplankton samples were collected from oblique stratified tows (depth strata: 0–10, 10–25, 25–50, 50–200 m) conducted every 3 h with a 1 m² mouth Tucker Trawl, with 300 µm mesh and equipped with a mechanical flowmeter (General Oceanic Environmental). Samples were preserved in buffered 5% formaldehyde. Together with each plankton

tow, hydrographic profiles that included dissolved oxygen were obtained from CTD casts (SBE-25, Seabird Electronics, USA) using Ocean Data View Software (Schlitzer, 2012). Temperature/Salinity diagrams were used together with contour plots to identify the main water masses present in the study area, and to visualize temporal changes in the vertical structure of the water column. Tidal constituents identified from the above-mentioned *t_tide* analysis were used to produce a hindcast prediction of tidal heights during this 24-h sampling period.

Larvae of *M. gregaria* were identified and enumerated as total zoea or postlarvae following Roberts (1973). Larval abundance data were log-transformed prior to statistical analyses, which were aimed at comparing abundances among developmental stages (zoea vs. megalopae), depth intervals, and daytime vs. nighttime samples. All comparisons were based on the non-parametric analysis of variance based on permutations described by Anderson (2001), where the test statistic pseudo-*F* was calculated as

$$F = \frac{SSA/(a-1)/SSW}{(N-1)},$$

This test statistic was used to conduct three sequential one-way analyses of variance, with developmental stage, depth interval, and day/night as random factors. Statistical significance was computed from 4999 permutations of the raw data method was utilized, the significance level chosen was 0.01%.

To evaluate the association between changes in vertical distributions and tidal fluctuations in the sampling area, we performed a nonlinear least-square regression analysis to fit abundance data to a sinusoidal model for sharply peaked oscillations (Batschelet, 1981):

$$Y = M + A \cos\left(\frac{2\pi t}{\lambda - \theta}\right) + v \sin\left(\frac{2\pi t}{\lambda - \theta}\right) + \varepsilon$$

where *Y* is the log-transformed abundance, *M* is the mean tidal height over the sampling period, *A* and *λ* are the amplitude and period of abundance fluctuations, respectively, *t* is sampling time,

θ is the acrophase angle, ν is a 'peakedness' parameter, and ε is a random error term. This approach has been used recently to describe cyclic variations in the abundance and distribution of coastal zooplankton (Yannicelli et al., 2006; Castro et al., 2011), and to assess periodicity in crustacean settlement data (Amaral et al., 2007). The regression coefficient r^2 was used as a rough criterion for goodness of fit and model selection.

3. Results

3.1. Hydrographic structure and variability

River outflow records showed a marked annual cycle for both rivers (Fig. 2), with maximum freshwater discharge in summer (February) and minimum values in early spring (October). Mean flows recorded for the Baker river in February and October were 1300 and 600 m³ s⁻¹, respectively (Fig. 2). The record from the monitoring station closest to the Baker river mouth (Colonia) showed very sharp short-term (1–2 d) increases in outflow of up to 4000 m³ s⁻¹ in a few hours (Supplementary material S1). The Pascua River flow also showed a well defined annual cycle with

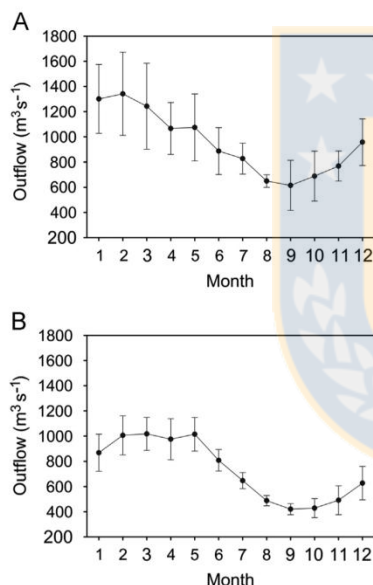


Fig. 2. Monthly means (i.e. climatologies, bars indicate standard deviation) computed for Colonia (a) and Quetru stations (b).

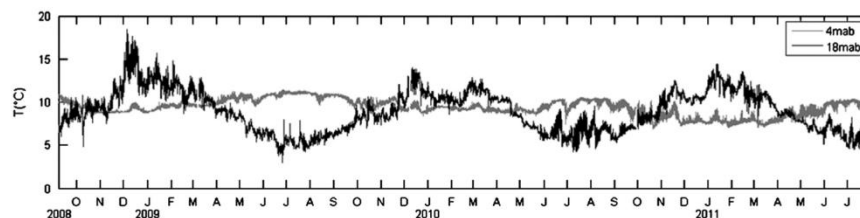


Fig. 3. (a) Variability of water column temperature at two different depths, shown as mab (meters above bottom) near the Baker river mouth.

maxima and minima that were consistent with the Baker series (Fig. 2), but overall lower values with no short-term increases.

Near-surface temperatures in the estuary (Fig. 3) were warmer than near the bottom in spring–summer (November–April), with ranges of 11–18 and 8.5–10 °C, respectively. In April–May a thermal inversion occurred, and near-surface waters (18 mab) were colder than those closer to the bottom (4 mab) until October–November (Fig. 3). Water temperature near the bottom varied over a much narrower range (4.5 °C) than near-surface waters (15 °C), where a stronger seasonal signal in temperature was evidenced by the much higher percentage of total variance explained by the fitted annual harmonic (Supplementary material S2). The high-pass filtered series of mid-water temperatures (14 mab) near the river mouth showed that high-frequency variability increased both in summer and winter months (i.e. times with maximum and minimum freshwater discharge), with the largest amplitude of HF fluctuations (ca. 4 °C) detected in late 2011 – early 2012 (Fig. 4).

Temperature, salinity, and density profiles obtained from CTD casts during 2011 (Fig. 5) showed a hydrographic structure that is consistent with the seasonal changes documented from the continuous records of river outflow and surface water temperatures. The strongest near-surface thermal gradient was observed in February, with a 8 °C drop from the surface down to ca. 15 m depth, and a thermal inversion between depths of 20 and 50 m (Fig. 5a). This thermal inversion was detected at similar depths in January, and much closer to the surface in September, i.e. during the low river outflow season (Fig. 5a). Changes in the halocline depth were also consistent with the observed changes in freshwater input to this area; it ranged from < 3 m in September to

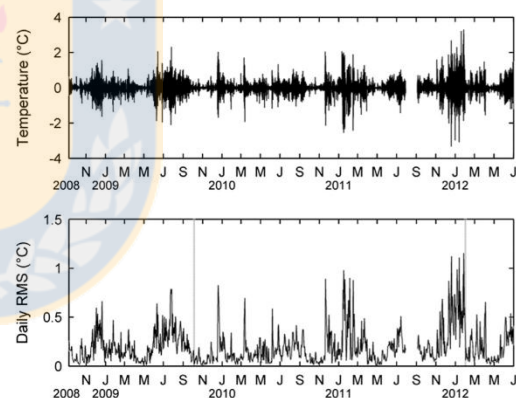


Fig. 4. High-pass filtered temperature at 14 mab (i.e. 6 m below the surface on average) and the root mean square (RMS) of this high-frequency signal computed over 24 h periods. Vertical dashed lines in bottom plot indicate period for which larval and juvenile abundance data were available.

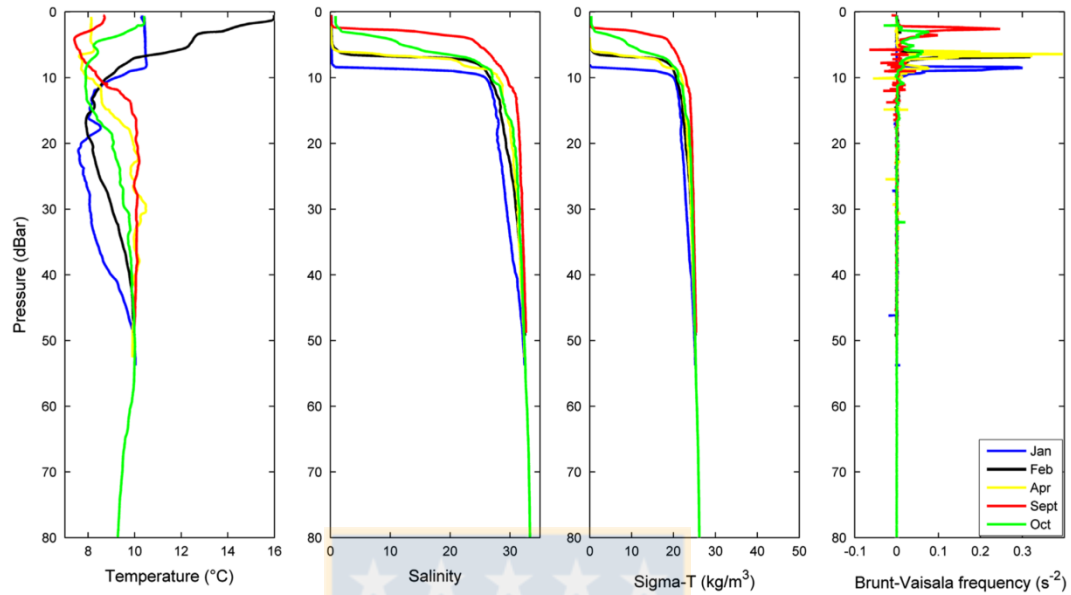


Fig. 5. Profiles of temperature, salinity, sigma-T and Brunt–Väisälä frequency for different months of 2011 at Baker station.

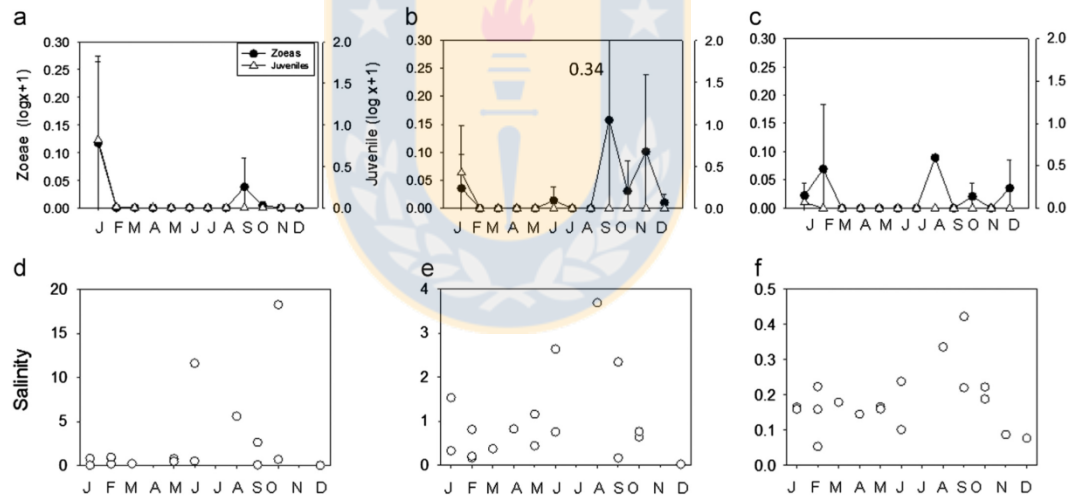


Fig. 6. Two-year composite annual cycle of *Munida gregaria* larvae and juvenile abundance at the three sampling stations: (a) Steffen, (b) Center, and (c) Baker, together with surface salinity measured on each sampling period (d–f). Numbers on the upper panels indicate out-of-range values.

ca. 10 m in January (Fig. 5b), when the freshwater discharge from the Baker river is close to its annual maximum (Fig. 2). Density profiles were nearly identical to the salinity profiles (Fig. 5c), confirming that density variability in this estuarine area is largely determined by changes in salinity, which in turn depend mostly on freshwater inputs. Profiles of Brunt–Väisälä frequencies showed that, as in the case of salinity and density, the layer of maximum stratification was closer to the surface in September, and deepest in January (Fig. 5d). They also showed that stratification was

strongest in late April 2011, when Baker river outflow was just pass its annual maximum (Fig. 2).

Surface salinity measured along the transect projecting seawards from the Baker River mouth was higher in late winter to early spring, and lower in summer and fall ($F_{1,54}=6.78$, $p=0.01$), which is consistent with the seasonal trends observed for river outflow. Surface salinities measured year round at the Steffen station (Fig. 6d) exhibited salinities that went from estuarine-fresh to pulses of estuarine-brackish water (11–21), whereas stations

Baker and Center (Fig. 6e, f) were typical of estuarine-fresh water (< 11). The mean annual surface salinity was significantly lower at the Baker station than at the Steffen station ($F_{2,54}=4.11$, $p=0.02$).

3.2. Seasonal and horizontal patterns of larvae distribution along the estuary

Zoeae of *M. gregaria* were found in very low numbers from late summer to early winter and increased in abundance between early spring and early summer, whereas juveniles were found only during summer months (Fig. 6a–c). Since there were no significant among-station differences in abundance of zoea ($F_{2,39}=1.27$, $p=0.29$), or juveniles ($F_{2,19}=0.49$, $p=0.61$), analyses of correlation

with environmental variability were performed using spatially-averaged abundances. Correlations between mean river outflow and zoeae/juveniles were not significant, although for the first 1–4 days the values were high and positive for juveniles and negative for zoeae (Fig. 7b). There was an apparent correspondence between changes in the abundance of zoeae and high-frequency temperature variability, quantified through weekly RMS calculations (Fig. 7a). Indeed, the spatially-averaged abundance of zoeae was significantly and positively correlated ($r_p=0.421$, $p=0.046$) with RMS computed over the 7 days preceding each zooplankton tow, whereas no correlation was found for juveniles. The change in correlation between zoea abundance and RMS values computed over periods of 1–30 days prior to each zooplankton sampling

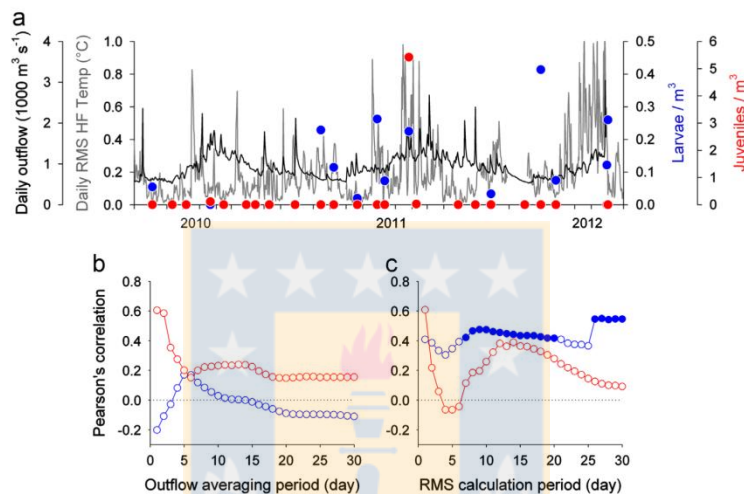


Fig. 7. (a) Monthly abundance of larval (blue) and juvenile (red) *Munida gregaria*, overlaid on daily time series of high-frequency temperature RMS (gray), and mean Baker river outflow (black). Bottom panels show the change in the correlation between larval/juvenile abundance and (b) time-averaged river outflow as well as (c) time-integrated HF temperature variability (RMS), as a function of pre-sampling period used to compute integrated environmental variability. Filled symbols indicate correlations that were significant at a level $\alpha=0.05$. (Correlations for juveniles, B and C, were calculated using summer months only). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

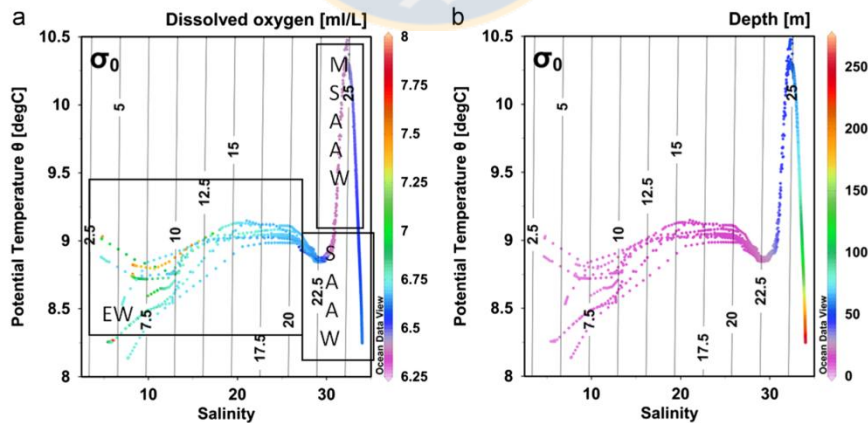


Fig. 8. Temperature–salinity diagrams from hydrographic data collected during the 24-hour sampling of November 2008. Colors correspond to (a) dissolved oxygen and (b) depth.

(Fig. 7c) showed that this association remains significant over periods of 7–20 days and 26–30 days prior to each sampling. There was no correlation between spatially-averaged abundance of juveniles and RMS (Fig. 7c).

3.3. Shorter-term changes in larval vertical distributions and hydrographic structure

During the 24-hour sampling of November 2008, salinities within the top 50 m of the water column were characteristic of estuarine waters, ranging from 5 to 30 (Fig. 8). Temperatures and salinities (32–33) observed between 50 and 100 m corresponded to Sub-Antarctic modified waters (MSAAW), whereas SubAntarctic waters (SAAW) were found below 200 m depth, with salinities of ca. 34.1 (Fig. 8b). Although the water column was well oxygenated, the lowest concentrations of dissolved oxygen (6.25 mL/L) and highest potential temperature (10.5 °C) were found at 50 m depth. The highest values of dissolved oxygen (8 mL/L) were associated with estuarine waters.

Zoeae and megalopae of *M. gregaria* were found throughout the 24 h, zoeae were more abundant at intermediate salinities of 25–30, and megalopae were distributed among a wider range of salinities (Fig. 9). There were no significant day/night differences in the vertical distribution of megalopae or zoeae ($F=0.347$, $p=0.75$ for megalopae, $F=0.227$, $p=0.86$ for zoea, Fig. 10), despite most megalopae occurred in the surface layer at night.

Depth-integrated abundance of zoeae and megalopae increased as the pycnocline shoaled during high tide (Fig. 11), which is consistent with the significant association between larval abundance and tidal height indicated by the nonlinear regression analysis. The fitted sinusoidal models showed high coefficients of determination for zoea ($R^2=0.7$) and megalopae ($R^2=0.72$), which

explained 49% and 52% of total variability of zoea and megalopae depth-integrated abundance, respectively (Fig. 11, Table 1).

4. Discussion

Our results document seasonal and tidal patterns in the abundance of *M. gregaria* larvae and juveniles near the Baker River mouth, and the potential forcing of this larval variability by freshwater inputs to this region. While juveniles were detected only in summer months, season characterized by the highest river outflow and higher surface temperatures, zoeae were more abundant in spring and their abundance was significantly correlated with high-frequency internal variability over temporal scales that suggest lunar periodicity in larval release. Combining monthly observations gathered over ca. 2.5 years with hourly observations over a 24-h cycle, it is possible to establish general patterns in larval abundance, and to formulate more specific hypotheses regarding the extent to which variable river discharges, both in terms of volume and quality, determine the spatial dynamics and inter-annual variability of *M. gregaria* populations.

4.1. Hydrographic structure and variability

Freshwater inputs to this estuarine area are largely explained by river discharges, and particularly by that of the Baker river (Gonzalez et al., in press). Both the Baker and Pascua rivers show coherent fluctuations in outflow, with maxima in summer that correspond with the warmest time of year and, consequently, the highest rates of snow and ice melting in the region. Transient and substantial increases in the Baker river outflow, recorded at the Colonia monitoring station, correspond well with events of sudden draining of the glacial lake Cachet 2, commonly referred to as GLOFs (Dussailant et al., 2010). Interestingly, these sudden increases in river outflow produce perturbations in the upper water column structure at the estuary, as documented by data from the thermistor line moored near the river mouth (data not shown), highlighting the impact that accelerated melting rates could have on local regimes of freshwater inputs to the estuary and to the entire Baker channel basin.

During summer, near-surface stratification of the water column is intensified by the increase in freshwater outflow from the rivers. According to previous knowledge of this region's hydrography (Sievers and Silva, 2008), the water masses identified at the Baker estuary during the 24-h sampling of November 2008 corresponded to Modified Subantarctic Water (MSAAW), which results from the mixing of SubAntarctic Waters and freshwater from multiple sources, and the less saline Estuarine Water (EW). The high-salinity, low-oxygen Equatorial Sub-Surface Waters (ESSW), which are often observed in continental shelf environments further north, were not detected at the sampling station during our November survey. It has been argued that

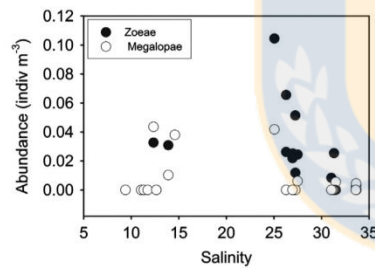


Fig. 9. Abundance of *M. gregaria* zoeae and megalopae as a function of salinity average over the depth range at which each zooplankton sample was collected during the 24-h sampling in November 2008.

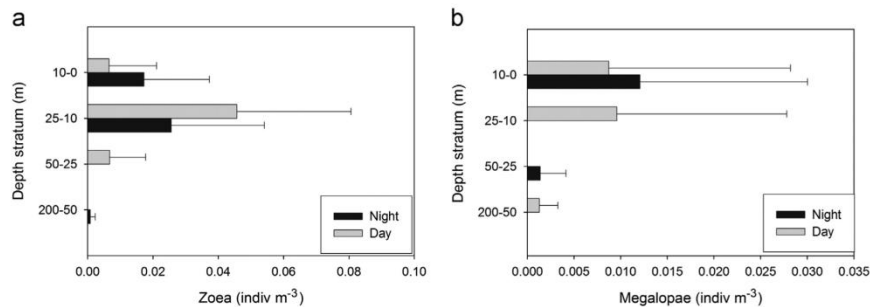


Fig. 10. Daytime vs. nighttime vertical distributions of *M. gregaria* zoea and megalopae during the 24-h sampling in November 2008.

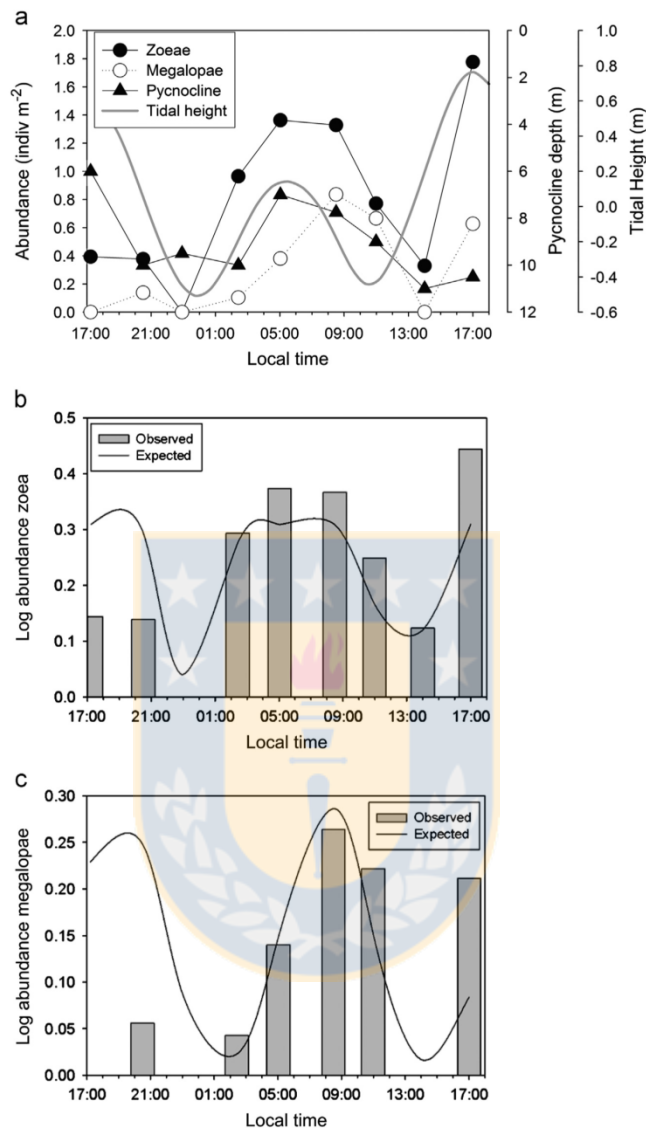


Fig. 11. (a) Depth-integrated abundance of *Munida gregaria* zoeae and megalopae, and pycnocline depth observed during the 24-hour sampling of 7–8 November 2008; the thick gray line shows predicted tidal height for the area. (b) Variations in depth-integrated abundance of *Munida gregaria* zoeae and (c) megalopae through the 24-h sampling period. Lines correspond to the tidal model fitted to each data set (see Methods).

the extent and relative shallowness of the Penas Gulf, and the large volumes of freshwater discharged by the Baker and Pascua rivers, would limit the intrusions of ESSW into the Baker Channel to periods with a particular set of oceanographic and meteorological conditions (Sievers et al., 2002; Palma and Silva, 2004; Aiken, 2012), which according to our observations would be more likely to occur during the 'drier' winter months. The occurrence of such intrusions and the impact they may have on the transport and/or retention of larval

stages within the Baker Channel are relevant and pending questions that warrant further study.

4.2. Seasonal and horizontal patterns of larvae distribution along the estuary

The finding of *M. gregaria* zoeae during winter and spring months in the Baker estuary is consistent with observations of

Table 1

Parameters of the sinusoidal function fitted to larval densities of *M. gregaria* during the 24 h sampling cycle. Data correspond to total zoea counts (all stages). λ is the period, θ is the acrophase angle, M is the mean value of the independent variable, A is the amplitude, R^2 is coefficient of determination, EV%: percentage of total variance explained by the model.

	λ (h)	θ (h)	M	A	R^2	EV%
Zoeae	13	6.24	0.152	0.156	0.7	49
Megalopae	13	4.01	0.152	0.138	0.72	52

early zoeae in winter months along the Aysen fjord (47°S), reported by León et al. (2008). The lower river discharges during late winter – early spring are expected to reduce sediment loads and, consequently, to reduce the high surface turbidity and light limitation that are found in the area through the rest of the year (Aracena et al., 2011). The timing of this drop in river discharge is consistent with an early spring maximum in phytoplankton abundance observed in northern Patagonia (Iriarte et al., 2007; Montero et al., 2011). It is thus likely that the wintertime increase in abundance of *M. gregaria* larvae is associated with lower sediment loads and a consequent increase in phytoplankton production. Further south in the Beagle Channel, early zoeae of *M. gregaria* occur in September, with abundance peaking in early November and some individuals found until January (Lovrich, 1999). This southward shift in the seasonal maximum of larval abundance may well be the result of latitudinal shifts in productivity patterns, as documented for Patagonia by Aracena et al. (2011).

The abundance of zoeae was positively correlated with high-frequency variability in mid water temperatures, and this correlation remained significant for periods of HF variability integration of 7–20 days and 26–30 days prior to each monthly zooplankton sampling. These time scales of significant correlation between larval abundance and HF internal variability, which we submit is a proxy for tidally-forced internal waves, suggest that internal motions may serve as a proximal cue for lunar rhythms in larval hatching, rather than directly affecting the aggregation or distribution of larvae over the sampling area. For brachyuran crabs, most semiterrestrial, intertidal and shallow subtidal crabs that live in warm temperate estuaries world-wide release their planktonic larvae near the times of nocturnal high tides on the larger amplitude tides in the biweekly or monthly cycles of tidal amplitude (Christy, 2011), however, the timing of hatching and of release of larvae by cold-temperate brachyuran and anomuran species has received little attention. This intriguing possibility requires direct testing in the field, with more frequent (daily) observations of larval abundance and stage composition as a function of lunar phase and HF temperature variability.

Although correlations between mean river outflow and zoeae/ juveniles were not significant, we observed that the values were high and positive for juveniles and negative for zoeae for the first 1–4 days. This is consistent with what we observed in terms of vertical distribution in the 24 h sampling, where we found that megalopae were preferentially distributed in a wider range of salinity, whereas zoeae appeared more tolerant to higher-salinity conditions.

The summertime presence of juvenile, with abundances reaching levels higher than those observed for earlier stages, may result from landward transport and retention aided by an enhanced estuarine deep circulation during the season of high river discharge. In open-coast environments, pelagic aggregations of juvenile *M. gregaria* have been associated with highly productive areas such as river plumes, coastal fronts (Rayner, 1935; Zeldis and Jillett, 1982), and areas with intense internal wave activity (Zeldis and Jillett, 1982; Bertrand et al., 2008). Productivity in the Baker

estuary ($91 \text{ mg Cm}^{-2} \text{ d}^{-1}$), however, is the lowest of available estimates for the Chilean fjord region between 41–55°S (Aracena et al., 2011), which is most likely due to the high load of glacial sediments in surface waters. This raises the question of which source of organic carbon sustains the aggregations of juvenile *M. gregaria* that reach the head of the Baker estuary each summer. Organic carbon of terrestrial origin may constitute up to 86% of particulate organic carbon (POC) in the Baker river plume, and account for a high percentage of tissue carbon in copepods sampled in the area (Vargas et al., 2011). Thus, the summertime aggregation of *M. gregaria* juveniles in the Baker river estuary could be a response to seasonal increases in river-borne POC, and could therefore be affected by future changes (natural or anthropogenic) in the local regimes of freshwater discharge.

4.3. Changes in larval *M. gregaria* vertical distribution and abundance during 24 h cycle

The fluctuations in vertical distribution and relative abundance of zoeae and juveniles observed during the 24-h sampling of November 2008 indicated that megalopae are preferentially associated to lower-salinity brackish waters, whereas zoeae appear more tolerant to higher-salinity conditions. This is consistent with previous observations in the region (León et al., 2008) that suggest an export of zoeae to open waters and a reinvasion of the channels and fjords by late stages.

Tidal cues are likely to play a key role in the life cycle of this species, as evidenced by the strong association with tidal height we observed in depth-integrated abundance of zoeae and megalopae, which is in good agreement with previously reported observations of zoeae in the Gulf of Ancud, 42° 10'S (Castro et al., 2011), where changes in the abundance of zoeae responded to semidiurnal tides and, additionally, exhibited diel patterns in their stage-specific vertical distribution. The lack of day/night differences in the vertical distributions of zoea and megalopae observed during our 24-h sampling could stem from a lack of vertical resolution, considering the much stronger vertical gradients in salinity observed at the Baker estuary. However, our results confirm that both early and late-stage larvae of *M. gregaria* are sensitive to tidal fluctuations, which together with salinity gradients may be the strongest environmental cue guiding their ontogenetic migration in this and other Patagonian fjords.

The observed tidal changes in depth-integrated larval abundance, in the absence of diel patterns in their vertical distribution, are most likely the result of lateral transport. However, vertical transport of larvae from deeper waters cannot be ruled out since total depth at the study site was 250 m and our plankton tows only spanned the top 200 m. Many studies indicate that vertical displacements of larvae may be strongly influenced by density structure in the water column (Tremblay and Sinclair, 1990; Rawlinson et al., 2004), and by the non-uniform distributions of phytoplankton and other source of food, often associated to density discontinuities (Viličić et al., 1989; Raby et al., 1994), and that strong salinity gradients may interfere with food availability cues (Sameoto and Metaxas, 2008). In our 24-h study, zoea abundance was highest within the 10–25 m layer, just below the strong halocline and pycnocline, suggesting that larvae remained within the layer with highest food availability and that hourly changes in their abundance resulted from lateral transport.

5. Conclusions

Larvae and juveniles of *M. gregaria* exhibited a highly seasonal pattern of abundance, with larvae occurring mainly in spring and juveniles exclusively in summer months. The higher abundance of

zoae in spring months might be associated to changes in phytoplankton biomass (and potentially composition) that should result from lower turbidity levels during the months of minimum river outflows. Over shorter time scales, a significant association was detected between zoae abundance and high-frequency thermal variability in the water column, which we use as a proxy for tidally-driven internal motions. The lagged association observed between larval abundance and HF variability (7–20 and 26–30 days prior to each set of zooplankton collections), suggests that internal waves may be providing a proximal cue for lunar rhythms in larval hatching, rather than directly promoting larval aggregation in the water column. Changes in depth-integrated abundance of zoae and megalopae during a 24-h sampling period in spring were associated with the tidal regime. These changes in larval *M. gregaria* abundance are probably caused by lateral transport of larvae. Overall, the results of this study suggest that seasonal and shorter-term changes in larval abundance in the Baker estuary are closely linked to environmental conditions modulated by seasonal changes in freshwater inputs and by tidal cues, both of which appear to affect the pace and spatial scale of larval development and juvenile migration into and out of this estuarine system.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.csr.2013.04.025>.

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4.3. Capítulo 3. Flujo superficial y subsuperficial de larvas de crustáceos a lo largo de un fiordo Patagónico durante la estación de máxima descarga del río.

Erika Meerhoff, Fabián Tapia, Marcus Sobarzo, Leonardo Castro

Resumen

El objetivo de este trabajo fue estimar el flujo de larvas de crustáceos en tres puntos a lo largo del complejo de fiordos Baker/Martínez –Patagonia chilena- durante la estación de máxima descarga del río. Se realizaron mediciones de zooplancton y corrientes en transectos perpendiculares al canal en tres sitios ubicados entre la desembocadura del río Baker y el Golfo de Penas, en el Pacífico sureste. Los resultados mostraron que en Febrero de 2013, la velocidad residual a lo largo del canal en los primeros 25 m de profundidad fue una circulación típica estuarina de dos capas. Cerca de la desembocadura del río Baker se observaron asimetrías transversales en flujos a lo largo del fiordo, estas asimetrías pueden ser importantes en el transporte de larvas. Dado que una larva que migra activamente depende de los flujos instantáneos a los cuales es expuesta durante sus migraciones verticales, los campos de velocidad instantánea obtenidos del ADCP se usaron para calcular los flujos instantáneos de larvas y posteriormente estos flujos fueron integrados para obtener estimaciones de flujos netos. Los nauplios de cirripedios fueron más abundantes en marea llenante (15.2 ± 8.8 indiv m^{-3} , media $\pm$ error estándar) que en vaciante (3.36 ± 0.95 indiv m^{-3}), sugiriendo que son transportados por la marea. Los estadios avanzados de nauplios de cirripedios y las cipris aumentaron su abundancia desde la estación externa hacia la estación interna. Cerca de la desembocadura del río Baker, el flujo neto superficial (0-25 m) mostró que los nauplios son transportados hacia la cabecera y las cipris son advectadas hacia el océano, mientras que las zoeas de *Munida gregaria* fueron advectadas hacia el océano, de forma consistente con investigaciones previas en la región. De este modo diferentes taxa y estadios de larvas de crustáceos responden de forma diferente a variaciones espaciales de pequeña escala en flujos a lo largo del fiordo durante la estación de máxima descarga del río.

Surface and subsurface flux of crustacean larvae along a Patagonian fjord during the maximum river outflow season.

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Please find attached a file containing a manuscript entitled "Surface and subsurface flux of crustacean larvae along a Patagonian fjord during the maximum river outflow season", by E.I. Meerhoff, F.J. Tapia, M.A. Sobarzo and L.R. Castro.

In this MS we examined zooplankton, hydrographic samples and currents taken during the maximum river outflow season along Baker river fjord, Chilean Patagonia, to determine the fluxes of crustacean larvae in three transects located along the fjord.

We found that Barnacle nauplii late stages and cyprids increased their abundance from a station closer to the ocean towards the inner station. Close to Baker river mouth, the net flux (surface-25 m depth) showed that barnacle nauplii were advected landward and cyprids were advected towards the ocean. The squat lobster *M. gregaria* zoeae were exported toward the ocean consistently with the literature. All authors have participated in the research and/or article preparation. I also include a list of four potential reviewers for this contribution.

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Surface and subsurface flux of crustacean larvae along a Patagonian fjord during the maximum river outflow season.

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Abstract

The objective of this study was to estimate the surface flux of crustacean larvae at 3 points along the Baker/Martinez fjord complex – Chilean Patagonia – during the season of maximum river discharge. Concurrent ADCP and zooplankton surveys were conducted at three across channel transects spanning 58 km along the fjord, in late February 2013. The results revealed a two-layer structure in along channel residual velocity within the top 25 m of water column, which resembled a typical estuarine circulation pattern. Near the river mouth, transverse asymmetries in along fjord flows and secondary circulation were found, which may be significant for larvae transport. Barnacle nauplii were more abundant during flood ($15.2 \pm 8.8 \text{ indiv m}^{-3}$, mean $\pm$ standard error) than during ebb tide ($3.36 \pm 0.95 \text{ indiv m}^{-3}$), suggesting they are tidally transported. Since the along-channel transport of vertically migrating larvae depends on the instantaneous flow fields to which they are exposed, larval abundance data were combined with velocity fields obtained from individual ADCP passes to produce instantaneous larval flux estimates. Near the Baker river mouth, the net flux estimates showed that barnacle nauplii are advected landward and cyprids seawards, respectively, whereas zoeae of the squat lobster *Munida gregaria* are exported from the fjord, consistently with previous findings, which may explain how different taxa and life stages within the meroplankton community respond differently to small scales spatial variations in flow along the fjord during the season of maximum river discharge.

Keywords: crustacean larvae, flux, fjord, larval retention, export

1. Introduction

Meroplankton dispersal depends mainly on the interaction between larval swimming behavior and the hydrodynamic regime, and secondarily on the duration of planktonic development. The variability of larval recruitment in the coastal ocean is related to the interaction of a series of physical factors, among which are winds (e.g. Roughgarden *et al.*, 1988; Wing *et al.*, 1995, 1998; Roegner *et al.* 2007; Morgan *et al.* 2009, 2011), tidal currents (Queiroga *et al.*, 2006) and coastal configuration (Shanks *et al.*, 2003; Palma *et al.*, 2006).

In estuaries, salinity gradients driven by freshwater inputs interact with tidal currents to produce circulation patterns that often result in net landward transport of sub-surface saline water and seaward transport of fresher surface water (Pritchard, 1953). This type of circulation may promote the retention of certain zooplankton within an estuary (Dyer, 1997), and is known to influence productivity, community composition, age structure, biomass and distribution of zooplankton in fjord systems (Basedow *et al.*, 2004). In fjords and deep estuaries (deeper than 20 m) stratification stays high through the tidal cycle (Valle-Levinson, 2010), maintained by the freshwater input. Mixing processes are central to gravitational circulation in estuaries because they are responsible for disturbing density gradients that establish the flux. Longitudinal fluxes are mainly advective while horizontal mixing and diffusion are important in the transversal section in fjords (Farmer and Freeland, 1983).

The retention of planktonic larvae in estuarine areas, or their migration into those environments, is critical for the population dynamics and geographic distribution of many benthic estuarine and marine species (Norcross and Shaw, 1984; McConaughy, 1988). The most commonly accepted model for estuarine invertebrate larval transport is the selective tidal stream transport (STST) which has been studied mainly in the Atlantic coast of North America and Europe (Forward *et al.*, 2001; Queiroga and Blanton, 2004). The best description of the bio-physical control of STST originated from a series of field and laboratory studies in crab megalopae, which are consistently more abundant in estuaries during nocturnal flood tides (Little and Epifanio, 1991; Queiroga *et al.*, 1994). This pattern originates from the combination of larval swimming inhibited by high light intensities and larval ascent triggered by increases in hydrostatic pressure and salinity, as well as enhanced turbulence, during flood tide.

During the in-coming phase of STST, larvae are located near the bottom during ebb tide and close to the surface during flood tide, with a net motion towards the head of the estuary. A similar pattern of net larval transport into estuaries and fjords, or retention in these systems has been described for the larvae of other invertebrates, such as barnacles in several northern-hemisphere estuaries, suggesting a vertical migration behavior (Bousfield, 1955; Martin and Foster, 1986; Lawson *et al.*, 2004; Macho *et al.*, 2010). Scaling comparisons indicate that retention of larvae is enhanced by fast development and in larger estuarine systems (Ketchum, 1954; Platt *et al.*, 1972).

In the extensive Baker/Martinez fjord complex, where the largest Patagonian rivers, Baker and Pascua, discharge up to 1400 and 1000 m³ s⁻¹ over a spring-summer day, recent studies have documented the seasonal variability in hydrography (Aiken, 2012; González *et al.*, 2013; Meerhoff *et al.*, 2013) and meroplankton community structure (Meerhoff *et al.*, submitted). Studies of circulation conducted thus far in this area, based on bottom-mounted ADCP measurements, have shown that the circulation corresponds to a typical estuarine two-layer system, and that maximum surface currents in summer could reach up to 20 cm s⁻¹ (Cáceres, 2007). However, circulation studies aimed at residual along-estuary circulation and its role as transport mechanism for meroplankton in the area are still lacking.

There is a growing knowledge base regarding distribution patterns of planktonic stages of both invertebrates and fish in Patagonian fjords and channels (Antezana, 1999; Mujica and Medina, 2000; León *et al.*, 2008; Bustos *et al.*, 2011; Landaeta *et al.*, 2013; Meerhoff *et al.*, 2013). However, little is known about the mechanisms that mediate the ocean-river transport of organisms and water properties in Patagonian fjords. Research on the dynamics of meroplankton transport and migration is highly relevant, since it may provide valuable insights on biophysical factors shaping reproductive patterns, rhythms of larval release, or the selection of certain estuaries as nursery areas for some species based on estimates of how much is exported and imported from and into the estuary at different times of the year. In this study, we aimed to assess the flux of crustacean larvae along the Baker/Martinez fjord during the season of maximum river discharge, when fjord circulation patterns are expected to be most influenced by freshwater inputs. Previous studies indicate that changes in hydrographic structure along this fjord, driven mainly by seasonal changes in river outflow, mediate changes in meroplankton community structure (Meerhoff *et al.*, submitted). Based on these observations and the available literature (León *et al.*, 2008), we expected the net flux of larval squat lobsters (*Munida gregaria*) to be seawards, and the net flux of larval barnacles to indicate retention in the estuary.

2. Material and methods

2.1 Study area

The Baker river basin (27000 km²) is located in Patagonia (46–48°S, 71–73°W), southern South America, in one of the most pristine and remote areas of the planet. Its hydrological regime is likely to undergo remarkable changes in the near future due to current climate trends and the potential development of hydroelectric power projects (Dussailant *et al.*, 2012). The basin comprises the second-largest lake in South America (lake General Carrera, surface area of ca. 1800 km²), and part of a major ice field (Dussailant *et al.*, 2012). The Baker and Pascua rivers are the main rivers of Chilean Patagonia, with mean annual outflows of 1133 m³ s⁻¹ and 753 m³ s⁻¹, respectively (DGA, Chile). Both drain water from glacial lakes and glacier melting into a large estuarine basin henceforth called the Martinez/Baker fjord complex, which comprises two main channels (Martinez and Baker). This extensive fjord basin, with depths that reach 400 m and a connection with the ocean that is constrained by the relatively shallow Penas Gulf, is located between the Northern and Southern Patagonian ice fields (47°–51°30' S, Fig. 1).

Shelf processes and their interaction with the Penas Gulf seem to explain seasonal exchanges of water and heat between this basin and the ocean (Aiken, 2012), driving fluctuations in subsurface temperature that may reach the head of this fjord complex (C. Moffat and F. Tapia, unpublished data). The tidal regime in this region is mixed with semi-diurnal dominance as the form factor $F = (K1+O1)/(M2+S2)$ is 0.36 (Ross *et al.*, 2014). The strong haline stratification observed consistently near the Baker river mouth (González *et al.*, 2013; Meerhoff *et al.*, 2013) favors the development and propagation of internal waves, some of which appear to be produced by semi-diurnal internal tides (Ross *et al.*, 2014).

2.2 Sampling design

To characterize the vertical structure of horizontal currents, 24-hour towed ADCP surveys were conducted along 3 transects in the Baker/Martinez fjord complex (see Fig. 1) during austral summer (25th to 28th February 2013). Transects were located at 10, 40, and 58 km from the Baker river mouth. A 307 kHz Workhorse ADCP (RD Instruments, USA) was used to conduct the surveys, during which

the downward-looking ADCP transducer was positioned at 1 m below the surface. Water velocity data were collected at 3 s intervals (pings) and averaged over 1-min ensembles.

To assess larval fluxes, depth-stratified zooplankton samples and hydrographic profiles were collected concurrently with the ADCP survey. Stratified sampling of zooplankton was carried out every 3 h over cycles of 24 h at the inner and outer transects, and over 12 h at the mid transect. Oblique tows of a closing Bongo net with 300 μm mesh and 60 cm mouth diameter were conducted from 25-m depth up to the base of the pycnocline, which ranged between 5 and 10 m depth, and from the pycnocline to the surface. Volume of water sampled by the net was estimated with a mechanical flow meter (General Oceanics) attached to the net's mouth. Samples were preserved in buffered 5% formaldehyde until sorting, identification, and enumeration of meroplanktonic groups in the laboratory.

Hydrographic profiles were obtained every 3 hours with an XR-620 RBR CTD (RBR, Canada) equipped with dissolved oxygen, fluorescence and turbidity sensors and recording data at a frequency of 6 Hz. Zooplankton and CTD profiling stations were located at both ends and in the middle of each transect. Time series contours to visualize temporal variability of hydrographic structure, and to compare among transects, were produced with Ocean Data View (Schlitzer, 2012).

A record of sea level height was obtained from a pressure sensor moored at ca. 20 m depth near the Baker River mouth (47°49.13'S, 73°32.22'W).

2.3 Data analysis

Harmonic analysis of pressure data to identify the principal tidal constituents in the area was conducted using the *t_tide* MATLAB toolbox (Pawlowicz *et al.*, 2002). Tidal constituents identified in the harmonic analysis were used to predict tidal heights during the sampling period.

Water velocity vectors were decomposed and rotated into along channel (*u*) and across channel (*v*) coordinates. Quality control of current profiles comprised the elimination of erroneous data, and standard criteria of goodness over 50%, flux < 100 $\text{m}^3 \text{s}^{-1}$ and error < 0.08 m s^{-1} . Profiles where bottom-track and GPS-derived velocities differed by >3 m s^{-1} were also discarded (e.g. Valle-Levinson *et al.*, 2007; Castillo *et al.*, 2012). A second quality-control criterion considered the correction of the direction, due to the fact that the magnetic compass of the ADCP is affected by magnetic fields

generated by the ship and local magnetic declination (Joyce, 1989; Trump and Marmorino 1997). To compute fluxes spanning the full water column, the uppermost velocity estimates – on average at 5 m below the surface – were extrapolated up to the surface. The assumption of constant velocity between the surface and uppermost measurement is conservative in terms of magnitude (Kirincich *et al.*, 2005), given that near-surface velocities are strongly influenced and enhanced by freshwater discharges, which were near their annual maxima at the time of our surveys. In terms of current direction, however, this extrapolation may distort the actual field of residual currents. Thus, hydrographic profiles collected at regular intervals during the ADCP surveys were used to test this assumption. When the first depth bin with usable ADCP data was centered at a depth above the pycnocline, it was considered likely that the direction (i.e. sign) of horizontal flows remained unchanged from that depth up to the surface.

Crustacean larvae were identified and enumerated as total Brachyuran and Anomuran zoeae, *Munida gregaria* zoeae (Roberts, 1973), barnacle nauplii and cyprids (Arenas, 1982). Larval abundance estimates (counts per unit volume of water sampled) were compared among strata, tidal phase (ebb or flood tide) and day-night through a non parametric analysis of variance, i.e. Kruskal-Wallis test (Zar, 1999).

In the Baker fjord, Ross *et al.* (2014) demonstrated that the baroclinic velocity showed largest semidiurnal amplitudes near the pycnocline, and from three modes obtained from the empirical orthogonal function analysis, two modes displayed a two- or three-layer flow structure with flow direction reversing at the pycnocline. This vertical change in amplitude and phase of current velocities implies that net horizontal displacement of an actively migrating larva depends to a large extent on the instantaneous flow fields to which it is exposed during the course of its vertical displacements (Queiroga and Blanton, 2004). Therefore, instantaneous larval fluxes were computed first by using depth-specific water transport estimates derived from instantaneous current-velocity fields produced by the ADCP survey. The instantaneous flux (number of larvae per second) of each larval taxon was calculated by multiplying the instantaneous depth-averaged velocity (from the ADCP; meters per second) by the instantaneous depth integrated larval concentration (number of larvae per cubic meter) and cross-sectional area of the fjord (square meter). Net fluxes of larvae over a 24-hour cycle were then computed as the summation of the mean ebb-tide and flood-tide fluxes.

3. Results

3.1 Hydrography

At the inner transect, low salinity values (<5) occurred at the surface layer down to 5-6 m. This low-salinity layer became thinner towards the outer transect, where it reached only 3 m depth (Fig. 2A). A seaward decrease in the relative contribution of low salinity waters was also evidenced deeper in the water column by the shoaling of the 30 isohaline from about 20 m at the inner transect up to 10-15 m at the outer transect, where an apparent internal wave occurred as suggested by the fluctuations in depth of the same isohaline. Surface temperature increased from the inner (12°C) to outer transect (13°C). Chlorophyll-a fluorescence and turbidity also showed a longitudinal gradient, with low fluorescence at the inner transect and maximum values of 0.56 mg m^{-3} at the outer transect (Fig. 2A). As for vertical gradients, fluorescence was highest in subsurface waters (e.g. 0.1 vs 0.05 mg m^{-3} at the inner transect) (Fig. 2A). Turbidity was highest at the inner transect, with values of ca. 100 NTU from the surface down to 10 m approximately (Fig. 2C). Turbidity in the low-salinity layer was an order of magnitude lower at the mid transect (3-10 NTU) than near the Baker river mouth, and dropped to 1-3 NTU at the outer transect.

3.2 Residual and instantaneous current fields

At the inner transect (i.e. near the Baker river mouth), along-channel residual velocities showed lateral asymmetries, within the top 25 m were directed landwards or seawards depending on which end of the transect was considered. Residual flows were directed landwards at the northern end (mean 1.4 cm s^{-1}), and were weakly seawards (mean -1.2 cm s^{-1}) in the middle and at the southern end of the transect (Fig. 3). At this transect, across-channel – or secondary – circulation was more energetic than along-channel (Fig. 3). Residual currents within the top 25 m were landwards at the middle transect. At the outer transect, the along channel residual velocity was directed seawards at the surface layer and landwards below the pycnocline, with a lateral effect on the currents. The vertical shift in direction of along-channel currents, detected in the outer and inner transects, was more apparent when progressive vector diagrams (PVD) were computed from instantaneous velocities at points arbitrarily chosen along each transect (Fig. 4). At the outer and middle transects, PVD trajectories showed patterns typical for estuarine circulation, with opposite directions at the surface and below the pycnocline. In the outer transect, surface PVD trajectories were oriented towards the ocean, while below it trajectories were oriented towards the head of the fjord. In the middle transect the PVD showed that the trajectories were oriented along the local channel axis. Maximum surface dispersal at the outer transect was ca. 8 km over a 24-h cycle (Fig. 4), which is consistent with the stronger surface currents measured at the

seaward end of our study area. At the inner station, surface PVD trajectories showed different directions depending on the side of the channel they were located. PVD in both strata indicated a net transport towards the North-Northeast on one side of the channel, and to the East on the other side (Fig. 4). In this inner transect the maximum dispersal distance estimated from surface PVD trajectories over a 24-h cycle was close to 10 km.

3.3 Crustacean larvae distribution

Crustacean larvae sampled from all three transects were numerically dominated by early and late larval stages of barnacles, commonly known as nauplii and cyprids, respectively (Fig. 5). Cyprids were more abundant at the inner transect, within the 0-10 m depth stratum. Abundance of *Munida gregaria* zoeae was low ($\leq 0.05 \text{ ind m}^{-3}$) at all three transects, whereas zoeae of other Anomuran species were slightly more abundant (0.09 ind m^{-3}) and were only found at the outer transect. Brachyuran larvae were more abundant in the surface stratum at the outer transect (Fig. 5). When counts of barnacle nauplii were separated into early and late nauplii (based on size and morphology criteria), opposite along-fjord patterns were observed. While the abundance of late nauplii increased from the outer to inner transect (20 to 40%), early nauplii were more abundant towards the outer transect (Fig. 6).

3.4 Short-term changes in larval vertical distributions

At the outer transect (Fig. 7) nauplii abundance remained high above the pycnocline from the morning ebb until the afternoon ebb tide, when they decreased in abundance. Cyprid abundance above the pycnocline increased during the afternoon flood tide and decreased during ebb tide. Below the pycnocline, nauplii were more abundant during the morning flood tide and decreased during the afternoon ebb tide. Abundance of Brachyuran larvae increased during flood tide and decreased during ebb tide. At the middle transect (Fig. 7), since only three sets of zooplankton tows were carried out during the 12-h survey, it was not possible to observe a clear pattern of changes in larval abundance. At the inner transect, the abundance of nauplii and cyprids above the pycnocline increased during the flood tide and decreased during the ebb tide (Fig. 7). Below the pycnocline, nauplii and cyprid abundance decreased towards the morning slack, then increased during the flood and decreased again in the afternoon ebb tide. Abundance of *Munida gregaria* larvae increased during the afternoon flood tide.

Considering the entire set of samples, nauplii were most abundant during flood tide (15.2 ± 8.8 indiv m^{-3} , mean $\pm$ standard error) than during ebb tide (3.36 ± 0.95 indiv m^{-3} , Table I). Cyprids were more abundant above the pycnocline (8.3 ± 5.8 indiv m^{-3}) than below the pycnocline (0.45 ± 0.21 indiv m^{-3} , Table I). We did not find night/day differences in vertical larval distribution (Table I).

3.5 Larval flux estimates

At the inner transect, a net landward flux of 2680 indiv s^{-1} was estimated for barnacle nauplii in the upper 25 m of water column, while a net seaward flux (-6072 indiv s^{-1}) was estimated for cyprids. While nauplii were always more abundant above the pycnocline, cyprids in this depth stratum were more abundant during ebb tide (Table II). Seaward net fluxes were also estimated for *Munida gregaria* zoeae and brachyuran zoeae (-61 and -49 indiv s^{-1} , respectively). Although juvenile *M. gregaria* were very low in abundance, their estimated flux was landward (results not shown).

At the middle transect, all estimates of net larval fluxes were landwards both in the surface and subsurface strata (Table II). At the outer transect, net flux estimates for barnacle nauplii and cyprids were seawards above the pycnocline and landwards below the pycnocline. Anomuran and Brachyuran zoea at the outer transect exhibited net landward fluxes at the surface, as a result of their increased abundance during flood tides (Table II, Fig. 3). Net fluxes estimated for *Munida gregaria* zoeae were seawards in both depth strata.

In summary, and within the 25-m layer spanned by our plankton survey (Table II), nauplii and cyprids at the inner transect exhibited opposite directions of net flux, indicating landward transport of nauplii and seaward transport of cyprids. At the outer transect, net flux estimates for nauplii and cyprids indicated landward transport in the subsurface layer and seaward transport in the surface layer. Net flux estimates for *M. gregaria* zoeae were seawards at both inner and outer transects. Despite some limitations of the sampling (e.g. incomplete cover of bathymetric range by the ADCP and loss of sight of the bottom in fjords, limited bathymetric range of zooplankton sampling), this work presents a novel approach to the assessment of plankton advective fluxes in Patagonian fjords, and our results show interesting patterns.

4. Discussion

The objective of this work was to determine the flux of crustacean larvae in the Baker/Martinez fjord complex during the maximum river discharge season, in February 2013. This is most important in an estuarine region that is undergoing changes in freshwater input regimes (Dussaillant *et al.*, 2012), which by affecting estuarine circulation may substantially modify the spatial distribution and abundance of species whose life cycles are linked to this estuarine system.

The abundance distributions of late nauplii and cyprids along Martinez channel, indicated transport of nauplii from the outer transect towards the inner transect. The estuarine circulation in Baker/Martinez fjord complex, at the outer transect, presented a typical flux towards the ocean in the surface and towards the head of the fjord at depth as a result of the dynamic balance between the pressure gradient and friction (Farmer and Freeland, 1983). At the outer transect, barnacle larvae and *M. gregaria* zoea appeared to be advected towards open waters. At the inner transect, near Baker river mouth the along channel circulation presented lateral asymmetries, and secondary circulation was also important.

4.1 Hydrography

The hydrographic results showed a salinity gradient with an increase in surface salinity from Baker river mouth towards the outer transect closer to Penas Gulf in the Pacific Ocean. Along-channel gradients in turbidity and chlorophyll-a fluorescence were also observed, with the highest turbidity near the Baker river mouth and a fluorescence maximum observed closest to Penas Gulf. In a recent contribution (Meerhoff *et al.*, submitted), we reported strong gradients in hydrographic conditions and meroplankton community structure during this February 2013 survey, which we ascribed to freshwater discharge. The influence of river discharges on salinity and density structure along the fjord were clearly visible as a shoaling of the pycnocline towards the outer transect.

4.2 Estuarine circulation along the Baker/Martinez fjord complex

The surface and subsurface circulation in Baker/Martinez fjord complex presented a typical estuarine circulation in the outer section, with net flux towards the ocean in the surface and towards the head of the fjord below the pycnocline as a result of the dynamic balance between the pressure gradient and friction (Farmer and Freeland, 1983). A third layer was observed at greater depth (results not presented), which was also directed towards the ocean. However, in the middle transect, residual currents were directed landwards above and below the pycnocline. One possible explanation for this

current pattern is that the ADCP measurements did not span the low-salinity surface layer, with the top velocity bin (4.5 m below the surface) located within the salty layer at all times.

Near the Baker river mouth, the along channel residual velocity showed two-layer circulation and lateral asymmetry. Secondary circulation was also very important in the upper 25 m of the water column. The progressive vector diagrams computed from instantaneous velocity sections showed that particles on one end of the transect describe a northward trajectory, whereas on the opposite end particles would move eastwards. This lateral asymmetry suggest that this section of the fjord may function as a retention zone, which is consistent with the higher abundance of late-stage barnacle nauplii and cyprids.

Transverse asymmetries in along-channel flows have been previously described (Valle-Levinson *et al.* 2003) and may be significant for larval transport as well as for larval settlement. For example, for larval settlement and subsequent recruitment of the crab *Carcinus maenas* in the Mira River Estuary, Portugal, Silva *et al.* (2006) found that within a curved region, megalopae preferentially settled on the left margin, probably due to weaker currents on this margin. Valle-Levinson *et al.* (2003) pointed out that the transverse structure of along-channel flows are produced by the earth's rotation effects, even in relatively narrow basins. The asymmetries disappear under strongly frictional (high Ekman number) conditions, thus illustrating the previously documented pattern of inflow in channels and outflows over shoals for typical estuaries. Valle-Levinson *et al.* (2003) also highlighted that transverse flows resemble a "sideways gravitational circulation" when frictional effects are apparent (Ekman number >0.1) responding to a transverse balance between pressure gradient and friction. These transverse flows reverse direction under very weak friction and reflect Coriolis deflection of along-estuary flows, that is, geostrophic dynamics. However, Friedrichs *et al.* (2013) indicate that transverse structure of along-channel velocity could be primarily due to simple density-driven circulation modified by bathymetry, as shown through analytical solutions for the James River estuary.

Near the Baker river mouth, lateral or secondary circulation was also very important. Lateral shear in channels with strong longitudinal density gradients produces strong lateral density gradients that also influence circulation patterns in tidal channels. In the case of flood currents, saltier water is confined to the deeper part of the channel, thereby imposing a lateral pressure gradient (Nunes and Simpson, 1985). This force drives a lateral, or secondary, circulation consisting of a surface flow converging toward the

center of the channel. At the bottom, the compensating flow diverges away from the center (Nunes and Simpson, 1985). It is through secondary flows that material is mixed across a channel and thus taking secondary flows into consideration is necessary to make estimates of dispersion in an estuary, and to determine the fate and transport of material discharged along an estuarine shore (Chant, 2010). Lateral mixing caused by secondary circulation may be an important mechanism driving dispersion in channels that are 100 to 1000 m wide (Chant, 2010), as is the case of the Baker/Martinez fjord complex, although there is scarce evidence to confirm the importance of transverse circulation as a relevant force affecting the transport of larvae (Eggleston *et al.*, 1998). Recently, Robins *et al.* (2012) demonstrated that strong secondary flows generated by estuarine axial convergent fronts can be important for larval dispersal and settlement, enhancing estuarine retention of natal populations for larvae that experience tidal stream transport and diel vertical migration (Robins *et al.*, 2012).

The peculiarities of the circulation near the head of the Baker/Martinez fjord may stem from the interaction of a complex bathymetry and multiple sources of freshwater besides the Baker river, such as the Steffen fjord located west of our inner transect. Recent work by Ross *et al.* (submitted) indicates that freshwater discharges from the Steffen Fjord could be a main driver of the circulation in this area.

4.3 Along fjord and short-term changes in larval vertical distributions

Barnacle larvae were the most abundant crustacean larvae during our surveys along Martinez Channel. The early planktonic stage of barnacles is most responsible for their dispersal or retention, because during this phase the hydrodynamic forcing on these larvae exceeds their swimming ability (Chia *et al.*, 1984). There was a consistent pattern observed among late nauplii and cyprids, both increasing their abundance from the outer to the inner section of the fjord.

The vertical distribution pattern of nauplii observed at the inner transect, increasing/decreasing above the pycnocline during the flood/ebb tide, and doing the opposite below the pycnocline, suggests a mechanism consistent with the "Selective tidal stream transport" model (Forward *et al.*, 2001), which prescribes a net displacement towards the head of the estuary. Our sampling design does not allow a complete test of this hypothesis given that plankton tows did not span the entire water column; however, considering the good correspondence between larval changes in abundance and tidal cycle in the inner zone (fig 7), we cannot rule out that such a mechanism may be at work in shallower sections

of the fjord. Vertical swimming behavior has also been identified as a critical factor for the dispersal of invertebrate larvae in open-coast waters (e.g. Largier, 2003; Pineda *et al.*, 2007; North *et al.*, 2008; Tilburg *et al.*, 2010). Tide-synchronized vertical migrations appear to be less common than diel migrations, but studies spanning invertebrates and fish indicate that larvae of most, if not all, species that inhabit estuaries during some part of their life cycle migrate in synchrony with the tidal cycle as a way to control their horizontal transport (Cronin and Forward, 1982; Queiroga *et al.*, 1997). An actively migrating larva does not depend on the net circulation but, rather, on the instantaneous flow fields to which it is exposed during the course its vertical movements (Queiroga and Blanton, 2004). Without exception, larval stages of species that occur in estuaries during at least part of their life cycle perform some type of tidal migration (Queiroga and Blanton, 2004).

The lack of day/night differences in vertical distribution of larval abundance in the Baker/Martinez fjord was not consistent with studies in other estuarine areas where, in general, larvae migrate deeper in the water column during the day to avoid visual predation (Lampert, 1989; De Robertis *et al.*, 2000; Forward, 2009; Ringelberg, 2010). The high surface turbidity observed along the fjord, and particularly near the Baker river mouth, suggest that light may be an important environmental cue for vertical migration, and that under low light conditions avoidance of visual predation during daytime hours may not be as critical for larval survival as in well-lit areas. The vertical migration behavior of invertebrate larvae may vary geographically according to regional-scale changes in hydrodynamics (Thatje *et al.*, 2003; Dellatorre *et al.*, 2014).

4.4 Flux of larvae along the Baker/Martinez fjord complex

The instantaneous along channel flux at the inner transect, integrated between 25 m depth and the surface was oriented landward for barnacle nauplii, and seaward for cyprids. This, together with the difference in abundance among nauplii stages along the channel, suggests that nauplii develop as they are transported from the ocean to the river mouth. Later, when they metamorphose into a competent cyprid stage (i.e. competent to settle onto adult habitats), they would be advected seawards.

At the outer transect, the instantaneous fluxes of nauplii and cyprids indicated advection towards the ocean above the pycnocline, and towards the fjord's head below the pycnocline. In the outer transect, Anomuran and Brachyuran zoea presented landward flux in the surface, because their abundance

increased in surface during flood tide, which indicates that these larvae are being tidally advected from the ocean towards inside the channel.

The results for *M. gregaria* zoea flux were consistent with those of León *et al.* (2008). They hypothesized that gravid females would migrate towards the interior channels, where hatching occurs in winter (León *et al.*, 2008). Early larval stages would be dispersed seawards, and megalopae would concentrate at the mouth of channels in late spring (León *et al.*, 2008). The mechanism by which juveniles return to the channels is associated with the landward subsurface flow that is characteristic of estuarine circulation. In this study we observed very low numbers of juveniles; however their fluxes (results not presented) were also positive, indicating that juveniles are entering to the estuary from the ocean, which is coincident with León *et al.* (2008) previous observations. Since *M. gregaria* juveniles have an important vertical swimming capacity, with swimming velocities up to 16 cm/s (Zeldis and Jillet, 1982), they probably can regulate their vertical positioning in the water column which allow them to move in different layers along a fjord. Alternatively, an exportation strategy of larvae offshore would be beneficial for this specie. The export strategy of *M. gregaria* young larvae could reduce inshore fish predation, expose the larvae to a more tolerable environmental variability or decrease the competition for food with benthic filter feedings in estuarine areas (Sponaugle *et al.*, 2002).

While *M. gregaria* appeared to export early larval stages from the fjord, flux estimates and the observed along-fjord change in stage structure suggest that barnacle larvae complete their development as they are advected towards the fjord's head, and to follow the opposite route once they molt into the competent cyprid stage. This was consistent with the distribution of adult barnacles observed along the fjord, with more abundant intertidal barnacles toward the ocean (authors personal observation). This pattern, together with previous studies of comparable estuarine systems (e.g. Bousfield, 1955; Macho *et al.*, 2010), suggests that the Baker/Martinez fjord – and probably other fjords in the Patagonian region – may function as a nursery area for barnacles. Estuaries are frequently cited as nursery areas due mostly to their high productivity (Mann and Lazier, 1991). However, two additional factors should be taken into consideration when examining the role of Patagonian fjords as nursery grounds for barnacles and other benthic invertebrates: strong along-fjord gradients in (1) turbidity and (2) size composition of phytoplankton. A recent study (Gyory *et al.*, 2013) found that an increase in turbidity may trigger hatching in the intertidal barnacle *Semibalanus balanoides*, and suggested the potential for turbidity to provide refuge against cannibalism and predation in the plankton. High turbidity is a permanent feature in surface waters near the head of the Baker/Martinez fjord (Marín *et al.*, 2013), due to the high loads

of glacial sediments in freshwater discharged by the Baker and Pascua rivers, as well as by the Steffen fjord (González *et al.*, 2013), and has been demonstrated determinant in the meroplankton distribution along the fjord (Meerhoff *et al.* submitted). This light limitation, combined with local nutrient conditions, explains the dominance of small-sized phytoplankton, with the smallest size fraction (i.e. picoplankton, $< 2 \mu\text{m}$) accounting for 45% of depth-integrated net primary production in this section of the fjord (González *et al.*, 2013). Feeding experiments conducted by Vargas *et al.* (2006) on the larvae of two intertidal barnacles from central Chile indicated that nauplii do feed preferentially on small-size phytoplankton ($< 5 \mu\text{m}$). Thus, the combination of turbidity refuge and small-size phytoplankton availability may have turned the Baker/Martinez and similar Patagonian fjords into particularly favorable nursery environments for barnacles and other benthic invertebrates. Future studies should assess the actual contribution of these factors to larval survival, as well as the effects that eventual changes in surface turbidity or phytoplankton size composition – driven by the imminent damming of the Baker and Pascua rivers – may have on the larval dynamics, renewal, and distribution of marine species in Patagonia.

Our results were obtained during the maximum river discharge season, and may not be interpolated to the minimum discharge season. During the last one, the estuarine circulation may be weaker than in February, as well as the patterns of ocean-fjord larval exchange in this system. Strong hydrographic gradients and clear differences in water-column conditions along this fjord, between these periods, were reported by Meerhoff *et al.* (submitted). The peculiarities of the circulation near the head of the Baker/Martinez fjord, such as lateral asymmetries and important secondary circulation may not occur during periods of low river and fjord discharge, future studies are needed to investigate this.

5. Conclusions

Although data obtained in this study presented some limitations, this work presents a novel approach to the assessment of plankton advective fluxes in fjords. To our knowledge, this is the first time that such an attempt is made in a Patagonian fjord, and hence these are the first estimates of zooplankton fluxes along the Martinez/Baker fjord complex. Our results imply that under the same circulation pattern, there are differences in the along-channel fluxes of the main crustacean larval groups. Barnacle larvae appear to complete their development as they are advected from the ocean to the fjord's head, and to follow the opposite route once they molt into the competent cyprid stage. This pattern is consistent with the pattern of adult barnacle abundance observed along the fjord, with higher intertidal barnacles

1 abundances toward the ocean (personal observation). Consistent with published data on larval
2 distribution along other Patagonian fjords (León *et al.* 2008), *Munida gregaria* zoea were advected
3 seawards, while juveniles presented landward flux. We found some peculiarities of the along-channel
4 flows detected with ADCP surveys and the (expected) canonical pattern of estuarine circulation, which
5 may be due to the complex bathymetry of the fjord and multiple sources of freshwater, such as the
6 Steffen fjord located west of our inner transect. Secondary circulation was important near the Baker
7 river mouth and together with transverse asymmetries in along estuary flows seems to produce
8 recirculation. This may be important from the socio economical point of view, particularly for the
9 selection of locations for wastewater discharges in towns at the head of the fjord, near the Baker River
10 mouth. Finally, given the current climate trends and glacial melt increases in Patagonian Ice Fields,
11 changes in freshwater discharge regimes may strengthen the estuarine circulation, as well as the
12 patterns of ocean-fjord larval exchange in this system.
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Fig. 1. Study area and location of the three transects where ADCP and plankton surveys were conducted. Numbers indicate the location, 1: outer transect, 2: middle, 3: inner transect, closer to Baker river mouth.

Fig. 2. Hydrographic 24-h time series at the three transects along Martinez Channel, A: outer transect, closest to the Penas Gulf; B: middle transect; C: Inner transect, closer to Baker river mouth (see Fig.1).

Fig. 3. Along- and across-channel residual velocity sections in Martinez Channel. At the inner and outer transect, distance = 0 corresponds to the northern end of the transect, whereas at the middle transect it corresponds to the northeastern end (see Fig. 1). Positive velocities are oriented landward, and negative velocities are oriented seaward. Zero velocity is indicated by a black contour. Salinity contours (5,15,25,30) are overlaid.

Fig. 4. Progressive vector diagrams from surface and sub-surface instantaneous velocities measured in Martinez Channel. Insets show maps with the position and orientation of the ADCP transect. Survey duration at outer, middle, and inner transect was 21.8, 12, and 24 hours, respectively. Two starting points were chosen, one on each half of the transect, in order to illustrate the lateral variability observed in residual currents.

Fig. 5. Mean abundance ($\pm$ standard error) of crustacean larval abundance above (surface) and below (subsurface) the pycnocline in each transect along Martinez Channel.

Fig. 6. Above-pycnocline (top) and below-pycnocline (bottom) distribution of early- and late-stage barnacle nauplii along Martinez Channel.

Fig. 7. Temporal variability in the abundance of decapod and barnacle larvae observed at each transect during the ADCP surveys in February 2013; the thick gray line shows predicted tidal height for the area. Outer transect was closest to the Penas Gulf, whereas inner transect was closest to the Baker river mouth.

Table I. Kruskal-Wallis test results for evaluating variation of larval abundance (significant values are marked with bold letters).

Table II. Instant flux (individuals/s) of crustacean larvae across the Baker/Martinez fjord complex during different tidal phases. Surface and subsurface flux of crustacean larvae during a tidal cycle across three transects at the Baker/Martinez fjord complex are also presented as well as total flux in the 0-25 m water column (positive sign indicates landward flux, negative sign indicates seaward).



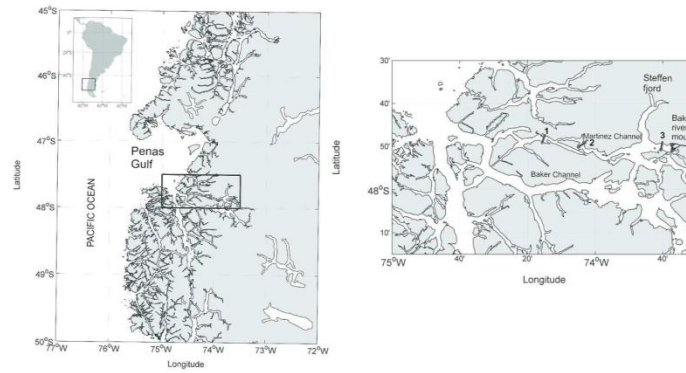


Fig. 1. Study area and location of the three transects where ADCP and plankton surveys were conducted. Numbers indicate the location, 1: outer transect, 2: middle, 3: inner transect, closer to Baker river mouth. 204x105mm (300 x 300 DPI)

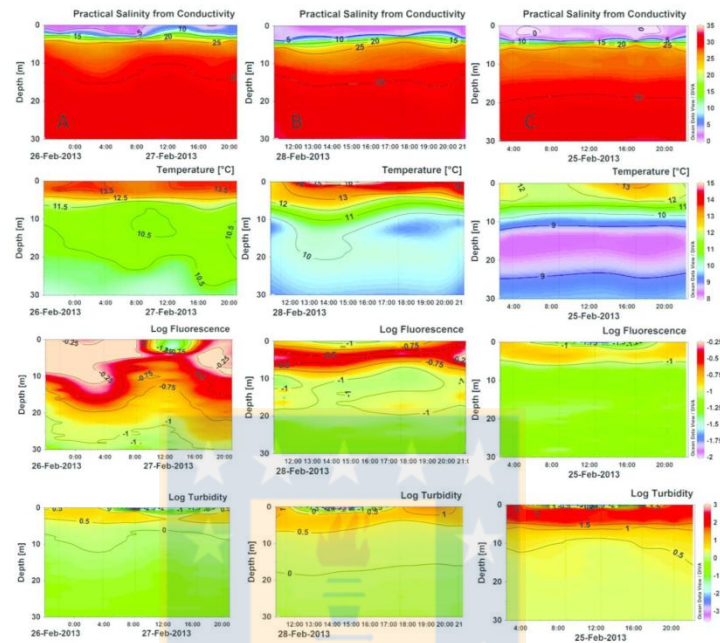


Fig. 2. Hydrographic 24-h time series at the three transects along Martinez Channel, A: outer transect, closest to the Penas Gulf; B: middle transect; C: Inner transect, closer to Baker river mouth (see Fig.1). 222x199mm (300 x 300 DPI)

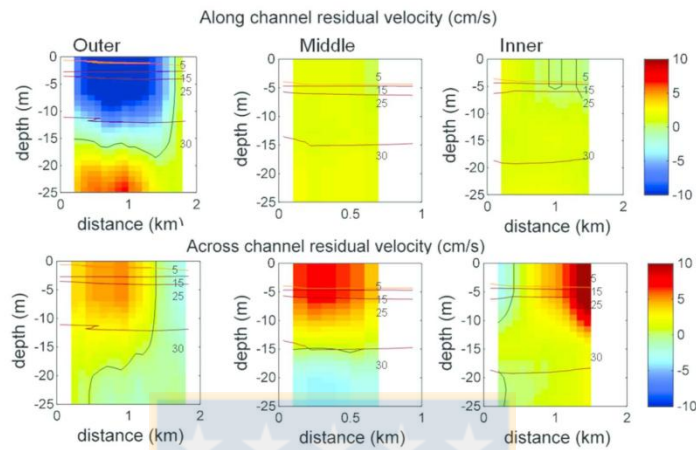


Fig. 3. Along- and across-channel residual velocity sections in Martinez Channel. At the inner and outer transect, distance = 0 corresponds to the northern end of the transect, whereas at the middle transect it corresponds to the northeastern end (see Fig. 1). Positive velocities are oriented landward, and negative velocities are oriented seaward. Zero velocity is indicated by a black contour. Salinity contours (5,15,25,30) are overlaid.

192x129mm (300 x 300 DPI)

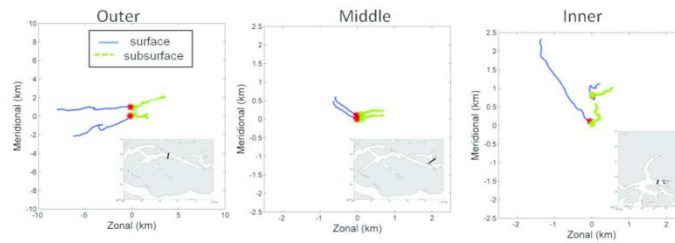


Fig. 4. Progressive vector diagrams from surface and sub-surface instantaneous velocities measured in Martinez Channel. Insets show maps with the position and orientation of the ADCP transect. Survey duration at outer, middle, and inner transect was 21.8, 12, and 24 hours, respectively. Two starting points were chosen, one on each half of the transect, in order to illustrate the lateral variability observed in residual currents

260x93mm (300 x 300 DPI)



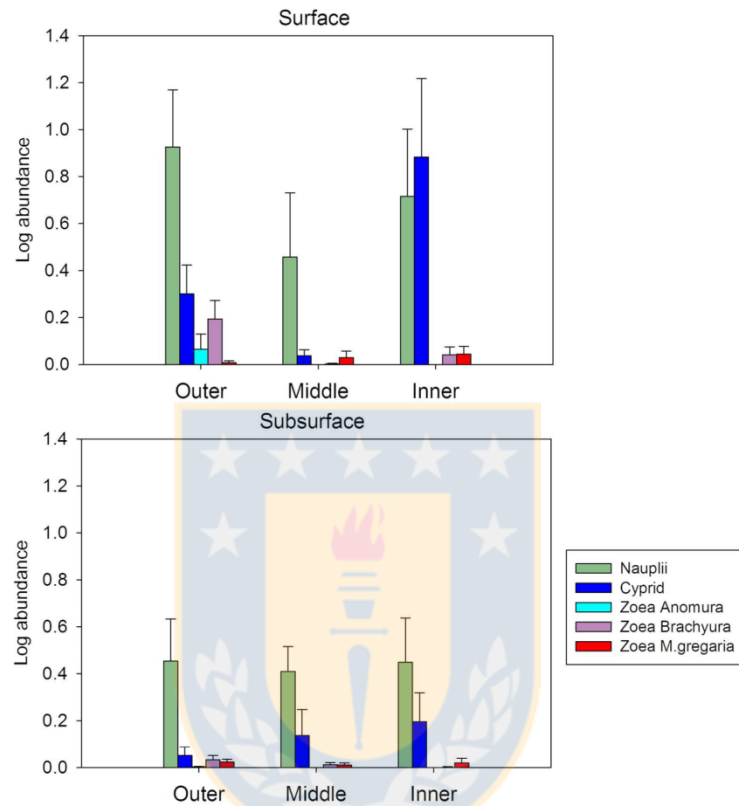


Fig. 5. Mean abundance ($\pm$ standard error) of crustacean larval abundance above (surface) and below (subsurface) the pycnocline in each transect along Martinez Channel.
201x225mm (300 x 300 DPI)

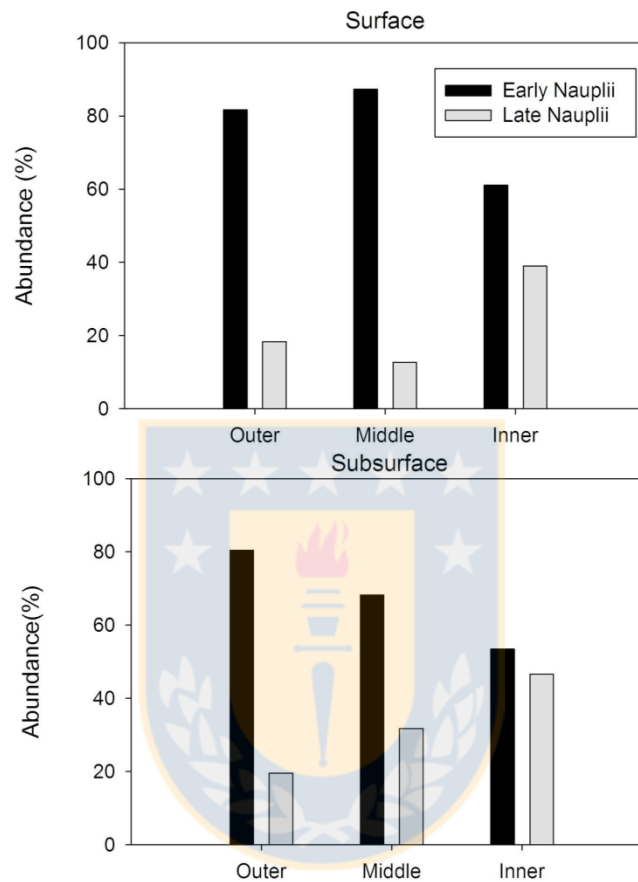


Fig. 6. Above-pycnocline (top) and below-pycnocline (bottom) distribution of early- and late-stage barnacle nauplii along Martinez Channel.
163x217mm (300 x 300 DPI)

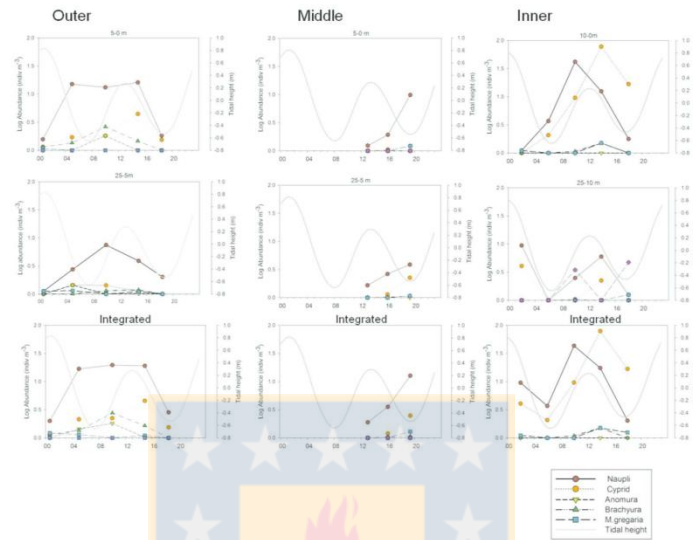


Fig. 7. Temporal variability in the abundance of decapod and barnacle larvae observed at each transect during the ADCP surveys in February 2013; the thick gray line shows predicted tidal height for the area. Outer transect was closest to the Penas Gulf, whereas inner transect was closest to the Baker river mouth.

Table I.

Factor	Barnacle larvae		Decapod larvae	
	Nauplii	Cyprids	All species	<i>M. gregaria</i>
Tidal phase	H=3.88	H=0.87	H=0.65	H=2.34
	p=0.04	p=0.35	p=0.42	p=0.12
Day/night	H=0.68	H=0.45	H=0.002	H=3.8
	p=0.41	p=0.5	p=0.96	p=0.05
Depth stratum	H=1.97	H=4.54	H=0.63	H=0.14
	p=0.16	p=0.03	p=0.42	p=0.71



Table II.

Transect	Strata	Tidal phase	Nauplii	Cyprids	Zoeae Anomura	Zoeae Brachyura	Zoeae M. gregaria
Inner	surface	ebb	-1213	-8060	0	-52	-61
		slack	1734	365	0	3	0
		flood	14	1041	0	0	0
		total surface	535	-6654	0	-49	-61
	subsurface	ebb	1821	573	0	0	0
		slack	17	0	0	0	17
		flood	306	8	0	4	0
		total subsurface	2145	582	0	4	17
	total 0-25 m		2680	-6072	0	-45	-44
Middle	surface	ebb	104	6	0	2	0
		slack	1578	39	0	0	39
		flood	-14	0	0	0	0
		total surface	1668	45	0	2	39
	subsurface	ebb	533	45	0	5	0
		slack	993	436	0	24	24
		flood	-103	0	0	0	0
		total subsurface	1423	481	0	29	24
	total 0-25 m		3091	526	0	31	63
Outer	surface	ebb	-6412	-757	0	-173	0
		slack	-93	-60	0	0	0
		flood	1792	80	133	212	-27
		total surface	-4713	-737	133	39	-27
	subsurface	ebb	-1986	-107	-42	-117	-75
		slack	-749	0	0	0	0
		flood	3627	237	0	79	-2
		total subsurface	892	130	-42	-38	-77
	total 0-25 m		-3821	-607	91	1	-104

5. DISCUSIÓN

El objetivo general de este trabajo fue caracterizar la composición y estructura espacial del meroplancton a lo largo del fiordo del río Baker y evaluar su asociación con cambios espaciales y estacionales en la estructura hidrográfica. Además, se evaluó el rol del río Baker como modulador de la hidrodinámica y transporte larval de invertebrados bentónicos en el fiordo del río del mismo nombre, en particular en larvas y juveniles de *M. gregaria*.

Los resultados permitieron caracterizar la variabilidad de las condiciones hidrográficas e hidrodinámicas del fiordo en función de cambios estacionales en la descarga del río Baker. Se determinó la existencia de fuertes gradientes hidrográficos a lo largo del fiordo, así como gradientes en la concentración de clorofila (fluorescencia) y turbidez.

La comunidad meroplanctónica observada a lo largo del fiordo del río Baker fue dominada por larvas de cirripedios, bivalvos, decápodos y gastrópodos. Se observó un claro cambio en la estructura comunitaria a lo largo del fiordo entre octubre y febrero, el cual fue principalmente debido a un cambio en la dominancia desde larvas de cirripedios a larvas de bivalvos. Además, los resultados documentan patrones estacionales y mareales en la abundancia de larvas y juveniles de *Munida gregaria* cerca a la desembocadura del río Baker, y el potencial rol de los aportes de agua dulce como forzantes de esta variabilidad larval. Mientras que los juveniles fueron detectados sólo en meses de verano, época caracterizada por la mayor descarga del río y mayores temperaturas superficiales, las zoeas fueron más abundantes en primavera y su abundancia estuvo correlacionada con la variabilidad de alta frecuencia en la temperatura cerca de la picnoclina.

5.1 Variabilidad de la estructura hidrográfica

Los aportes de agua dulce a este sistema estuarino corresponden principalmente a descargas de los ríos Baker y Pascua (Aiken 2012, González *et al.* 2013, Marín *et al.* 2013). Estas descargas de agua dulce parecen ser determinantes en la hidrografía e hidrodinámica del fiordo. Ambos ríos, Baker y Pascua, muestran fluctuaciones coherentes en la descarga, con máximos en verano que corresponden con la época más cálida del año y, consecuentemente, con las mayores tasas de derretimiento de hielo y nieve de la región (capítulo 2). Aumentos esporádicos y substanciales en la descarga del río Baker, registrados en aproximadamente 68 km río arriba de la desembocadura, en la estación Colonia del río Baker, se asociaron con

eventos de desagüe súbito comúnmente llamados GLOFs en el lago glacial Cachet 2, en la parte oriental del Campo de Hielo Norte (Dussaillant *et al.* 2010). Los desagües repentinos del lago Cachet 2 resultan en un aumento en la descarga del río Baker en 3-5 veces, mientras que la concentración de sedimentos en suspensión también aumenta 8 veces y la carga de sedimento 10-20 veces (Bastianon *et al.* 2012).

Durante el verano, la estratificación de la columna de agua cerca de la superficie se intensifica por el aumento en descargas de agua dulce de los ríos. Las masas de agua identificadas en el fiordo del río Baker durante el muestreo de 24 h de noviembre de 2008 (capítulo 2) correspondieron a Agua Subantártica Modificada (MSAAW), que resulta de la mezcla de aguas Subantárticas y agua dulce de múltiples fuentes, y agua estuarina (EW) menos salina. Estos resultados concuerdan con estudios previos de la hidrografía de esta región (Sievers & Silva 2008). Aguas de alta salinidad y bajo oxígeno, de tipo Ecuatorial-Subsuperficial (ESSW), observadas con frecuencia en ambientes de la plataforma continental más al norte, no fueron detectadas en el área de estudio durante el muestreo de noviembre. La longitud del fiordo, el hecho de que el Golfo de Penas sea relativamente somero, y los grandes volúmenes de agua descargados por los ríos Baker y Pascua, limitarían la intrusión de agua ESSW en el canal Baker a periodos con un conjunto particular de condiciones oceanográficas y meteorológicas (Sievers *et al.* 2002, Palma & Silva 2004, Aiken 2012), las cuales de acuerdo a estas observaciones ocurrirían más probablemente durante los meses “más secos” de invierno.

Los fuertes gradientes hidrográficos, y las diferencias detectadas en la hidrografía en los muestreos de Octubre 2012 y Febrero 2013 (capítulo 1), pueden ser atribuidos a cambios estacionales en la radiación solar y descargas de agua dulce. El gradiente de salinidad fue consistente con patrones generales observados para estuarios, con la salinidad superficial aumentando gradualmente hacia el océano, y un aumento de salinidad con la profundidad (Day *et al.* 2013). Para la temperatura, en ambos muestreos se detectó agua sub-superficial más cálida (20-80 m) cerca a la desembocadura del río Baker. El calentamiento de agua sub-superficial en este fiordo ha sido previamente reportado para el verano y otoño, y se ha hipotetizado que resulta de la intrusión de agua más cálida desde el Golfo de Penas (Aiken 2012). Si tales intrusiones ocurren de modo consistente, los patrones de transporte larval y

retención a lo largo del fiordo podrían ser influenciados por procesos oceánicos de mayor escala.

En octubre de 2012 y febrero de 2013, las concentraciones de oxígeno disuelto alcanzaron sus valores mínimos (4 ml/l) a 80 m de profundidad cerca de la desembocadura del río Baker, aunque el volumen de agua de bajo oxígeno parece haber aumentado en febrero (la isolinea de 4 ml/l alcanzó 40 km de distancia de la desembocadura en febrero, mientras que en octubre alcanzó 10 km de distancia), consistentemente con el máximo anual en la descarga del río (Aiken 2012, Meerhoff *et al.* 2013) y presumiblemente con un aumento en materia orgánica particulada de origen terrestre que ingresa al área estuarina. Menores concentraciones sub-superficiales de oxígeno en meses de verano podrían ser por remineralización de esta materia orgánica particulada, la que a 10 km de la desembocadura del río Baker puede llegar a 190 y 48 $\mu\text{g C l}^{-1}$ a 2 y 10 m de profundidad, respectivamente (Vargas *et al.* 2011).

Los valores de fluorescencia cercanos a cero observados en esta sección durante febrero de 2013 (capítulo 1) sugieren baja producción *in situ* de materia orgánica, y apoyan la idea de que gran parte de la materia orgánica particulada que alcanza aguas más profundas corresponde a aportes terrígenos transportados por el río.

El gradiente longitudinal de turbidez, observado tanto en octubre como en febrero, fue consistente con los resultados del modelo de Marín *et al.* (2013). Aunque este máximo de turbidez estuarino es común a muchos estuarios, su naturaleza difiere de la mayoría debido al origen glacial de los sedimentos en suspensión (Dowdeswell & Vásquez 2013) y su fuerte y persistente efecto en la atenuación de la luz y la producción primaria (Pizarro *et al.* 2005, Aracena *et al.* 2011).

5.2 Gradiente en la comunidad meroplanctónica a lo largo del fiordo

La comunidad meroplanctónica observada a lo largo del fiordo del río Baker estuvo dominada por larvas de cirripedios, decápodos, bivalvos y gastrópodos (capítulo 1) y fue diferente a la de otros fiordos Patagónicos ubicados más al sur (Defren-Janson *et al.* 1999) en los cuales abundan, además, larvas de erizos y briozoos. Sin embargo esta diferencia podría deberse a la utilización de diferentes tramas de malla de red de muestreo.

En octubre, los nauplios de cirripedios fueron más abundantes que cipris a lo largo del Canal Martínez, lo cual fue consistente con mayor fluorescencia cerca de la superficie en este

canal. Aunque la estructura de la comunidad meroplanctónica en octubre fue similar entre los canales Martínez y Baker, se observaron diferencias a lo largo del gradiente río-océano, con una agrupación de las estaciones más cercanas al océano, correlacionada con la concentración de clorofila-a (disponibilidad de alimento).

La estructura comunitaria en estaciones cercanas a la desembocadura del río Baker fueron explicadas por la estructura hidrográfica estuarina (temperatura y salinidad) bajo la picnoclina y por la turbidez sobre la picnoclina.

Los resultados mostraron un claro cambio en la estructura comunitaria a lo largo del canal Martínez entre octubre y febrero, el cual se debió principalmente a un cambio en la dominancia desde larvas de cirripedios a larvas de bivalvos. Por lo tanto, existe un patrón espacial de la comunidad meroplanctónica a lo largo del fiordo que no es constante en el tiempo.

Los cirripedios forman grandes agregaciones de adultos en costas rocosas y en estuarios tienen la capacidad de afectar la estructura comunitaria fuertemente a través de interferencia por espacio (Queiroga *et al.* 2007). La fase larval pelágica de los cirripedios es responsable de su dispersión o retención, porque durante esta fase el forzamiento hidrodinámico sobre las larvas excede su capacidad de nado (Chia *et al.* 1984). Factores como la tasa de hundimiento larval, la velocidad de nado, y la dirección y velocidad de las corrientes juegan un rol principal en su dispersión. Las larvas de cirripedios son un importante componente del meroplancton en aguas estuarinas de Patagonia. En su fase adulta, el cirripedio *Elminius kingii* es dominante en el bentos de fondos duros (Viviani 1963).

La abundancia de nauplios de cirripedios tendió a disminuir hacia la desembocadura del río Baker, mientras que la abundancia de cipris permaneció relativamente constante. La retención estuarina (Fig 4. Anexo I) de larvas de cirripedios ha sido descrita para especies como *Elminius modestus*, en numerosos estuarios del hemisferio Norte, sugiriendo comportamiento de migración vertical (Martin & Foster 1986, Lawson *et al.* 2004, Macho *et al.* 2010). Los nauplios fueron más abundantes en las estaciones cercanas al océano y sobre la picnoclina en ambos canales durante el muestreo de octubre de 2012, en asociación con mayores concentraciones de clorofila-a y presumiblemente, mayor disponibilidad de alimento para estas larvas. González *et al.* (2013) encontraron que en noviembre las estaciones oceánicas cerca del Golfo de Penas, exhiben una comunidad fitoplanctonica dominada por

diatomeas (ej. *Skeletonema* spp., *Leptocylindrus minimus*, *Thalassiosira* spp., *Chaetoceros* spp., y *Pseudonitzschia* spp.) que constituirían un alimento más adecuado para larvas de cirripedios que los dinoflagelados tecados que abundan hacia la cabeza del fiordo Baker. La disponibilidad de alimento adecuado es una condición clave para la eclosión larval en *Elminius kingii* (Jana 1978) y podría haber gatillado la liberación de nauplios encontrados durante el muestreo de octubre 2012. Por otro lado, para cirripedios del hemisferio norte se ha demostrado que la turbidez de cualquier origen, no sólo blooms de fitoplancton, puede gatillar la liberación de larvas, presumiblemente debido a que mayor turbidez podría disminuir la mortalidad por depredación o canibalismo de nauplios recién liberados (Gyory *et al.* 2013).

Los bivalvos producen grandes números de larvas planctotróficas que pasan varias semanas en la columna de agua antes de asentarse (Raby *et al.* 1994). En estuarios templados, el desove de bivalvos bentónicos es comúnmente gatillado por el aumento en la temperatura del agua (Ingle 1951). La dominancia numérica de larvas de bivalvos en febrero, cuando la temperatura cerca de la superficie alcanza su máximo anual, sugiere que este también es el caso para bivalvos en el fiordo del río Baker.

Junto con la temperatura del agua, la disponibilidad de alimento es uno de los principales factores que afectan los tiempos de desarrollo larval (Raby *et al.* 1994). El hecho de que las concentraciones de clorofila en verano fueran mucho menores que en primavera temprana y limitadas a las estaciones externas (capítulo 1) hace surgir la pregunta ¿de qué se alimentan estas larvas en el fiordo? Observaciones recientes en una estación cerca de la desembocadura del río Baker, han mostrado que más del 50% de la producción primaria neta corresponde al picoplancton y nanoplancton y que la producción secundaria bacteriana puede alcanzar el 70% de la producción primaria (González *et al.* 2013, Cuevas *et al.* enviado). Por otro lado, se ha demostrado que larvas de algunos bivalvos como la almeja *Crassostrea gigas* (Doulliet 1993) y *Pinctada fucata martensii* (Tomaru *et al.* 2000) pueden alimentarse de bacterias, las cuales en el primer caso pueden suplir hasta 50% de los requerimientos metabólicos de carbono (Doulliet 1993). Si las larvas de bivalvos en el fiordo del río Baker dependen de fitoplancton de pequeño tamaño y/o bacterias planctónicas como alimento principal para completar su desarrollo es una pregunta que necesita ser explorada.

5. 3 Patrones estacionales y horizontales de distribución de larvas de *M. gregaria* a lo largo del fiordo

Los resultados del capítulo 2 indican patrones estacionales y mareales en la abundancia de larvas y juveniles de *Munida gregaria* cerca de la desembocadura del río Baker, y el potencial forzamiento de esta variabilidad larval por aportes de agua dulce. Mientras que los juveniles fueron detectados sólo en meses de verano, estación caracterizada por la mayor descarga del río y mayores temperaturas superficiales, las zoeas fueron más abundantes en primavera y su abundancia se correlacionó con la variabilidad de alta frecuencia en la temperatura cerca de la picnoclina sobre escalas temporales que sugieren una periodicidad lunar en la liberación de larvas. Combinando observaciones mensuales durante 2,5 años con observaciones horarias sobre un periodo de 24 h, fue posible establecer patrones generales en la abundancia larval, y formular hipótesis más específicas respecto a la medida en que las descargas del río, variables en términos de volumen y calidad, determinan la dinámica espacial y variabilidad interanual de las poblaciones de *M. gregaria*.

La aparición de zoeas de *M. gregaria* durante meses de invierno y primavera en el fiordo del río Baker fue consistente con observaciones de zoeas tempranas en meses de invierno en el fiordo Aysén (47°S), reportadas por León *et al.* (2008). Se espera que la menor descarga del río durante fines del invierno y comienzo de primavera reduzca los aportes de sedimento y, consecuentemente, reduzca la turbidez superficial y limitación de la luz que se encuentran en el área el resto del año (Aracena *et al.* 2011). Esta disminución en la descarga del río es consistente con un máximo en la abundancia de fitoplancton observada en Patagonia norte al comienzo de primavera (Iriarte *et al.* 2007, Montero *et al.* 2011). Es probable, por lo tanto, que el aumento invernal en la abundancia de larvas de *M. gregaria* esté asociado con menor limitación de la luz en la columna de agua y un aumento en la producción fitoplanctónica. Más al sur, en el canal Beagle, las zoeas tempranas de *M. gregaria* aparecen entre septiembre y enero, con máximo de abundancia en noviembre (Lovrich 1999). Este cambio latitudinal en la época de máxima abundancia larval podría ser el resultado de cambios latitudinales en los patrones de productividad, como los documentados por Aracena *et al.* (2011). Los crustáceos decápodos de latitudes medias y altas exhiben patrones estacionales de reproducción y aporte larval, lo que les permite aprovechar las condiciones más favorables en ambientes cambiantes (Anger 2006).

Se pudo establecer que aumentos estacionales en la abundancia de larvas y juveniles de *M. gregaria* en el fiordo del río Baker se asocian a aumentos en el caudal del río. Aunque las correlaciones entre descarga media del río y abundancias de zoeas/juveniles no fueron significativas, observamos que los valores fueron altos y positivos para juveniles y negativos para las zoeas para los primeros 1-4 días. Esto es consistente con lo observado en términos de distribución vertical en el muestreo de 24 h: las megalopas aparecieron en un rango más amplio de salinidad, mientras que las zoeas parecieron restringidas a condiciones de mayor salinidad. De este modo, no se puede descartar que aumentos estacionales en la abundancia de larvas de invertebrados bentónicos, en el fiordo del río Baker, en particular larvas y juveniles de *M. gregaria* se asocien a aumentos en el caudal del río. Sin embargo, no se puede descartar que las megalopas tengan una mayor posibilidad de desplazamiento vertical que las zoeas, debido a su mayor capacidad de nado vertical, y por lo tanto pueden acceder a una gama más amplia de condiciones.

La presencia de juveniles cerca a la desembocadura del río Baker en verano, con abundancias mayores que las observadas para estadios tempranos, podría resultar de un transporte neto hacia la cabeza del fiordo y retención generada por la circulación estuarina profunda que se intensifica durante la época con mayor descarga del río. En ambientes de costa abierta, se han observado agregaciones pelágicas de juveniles de *M. gregaria* en áreas muy productivas como plumas de ríos, frentes costeros (Rayner 1935, Zeldis & Jillett 1982), y áreas con intensa actividad de ondas internas (Zeldis y Jillett 1982, Bertrand *et al.* 2008). Sin embargo, la productividad en el fiordo Baker ($91 \text{ mg Cm}^{-2} \text{ d}^{-1}$) es de las menores estimadas para la Patagonia chilena entre 41-55°S (Aracena *et al.* 2011), probablemente debido al alto aporte de sedimentos glaciales en aguas superficiales. Esto abre la pregunta de qué fuente de carbono orgánico sostiene las agregaciones de juveniles de *M. gregaria* que alcanzan la cabecera del fiordo cada verano.

Carbono orgánico de origen terrestre podría constituir hasta 86% del carbono orgánico particulado (POC) en la pluma del río Baker, y dar cuenta de un alto porcentaje del carbono en tejido de copépodos en esta área (Vargas *et al.* 2011). Así, la agregación de verano de juveniles de *M. gregaria* en el fiordo podría resultar de aumentos estacionales en POC aportado por el río, y podría por lo tanto ser afectado por futuros cambios (naturales o antropogénicos) en los regímenes de descarga de agua dulce. Alternativamente, la presencia de

ondas internas en el fiordo, asociadas a altas descargas del río Baker (Ross *et al.* 2014) podría promover aumentos esporádicos en la biomasa fitoplanctónica local, los que podrían sustentar las agregaciones de juveniles pelágicos de *M. gregaria*, o promover el transporte juveniles desde el océano hacia el interior del fiordo. Futura investigación se necesita para explicar cuál de los dos procesos es determinante.

5.4 Cambios en la distribución vertical de *M. gregaria* y abundancia durante un ciclo de 24 h

Las fluctuaciones en distribución vertical y abundancia relativa de zoeas y juveniles de *M. gregaria* observadas sobre un ciclo de muestreo de 24 h en noviembre de 2008 indicaron que las megalopas se asocian preferentemente con aguas salobres de menor salinidad, mientras que las zoeas parecen más restringidas a condiciones de mayor salinidad.

La marea probablemente juegan un rol clave en el ciclo de vida de estas especies, como fue evidenciado por la fuerte asociación con la altura mareal que se observó en la abundancia integrada de zoeas y megalopas, y que es consistente con observaciones previas de zoeas en el Golfo de Ancud, 42° 10'S (Castro *et al.* 2011). Cambios en la abundancia de zoeas en esta localidad respondieron a mareas semidiurnas y, adicionalmente exhibieron patrones diurnos en la distribución vertical por estadios. Los resultados confirman que ambos estadios tempranos y tardíos de *M. gregaria* son sensibles a las fluctuaciones mareales, las cuales junto con los gradientes de salinidad pueden ser los más fuertes inductores ambientales que dirigen su migración ontogenética en éste y otros fiordos patagónicos.

En ausencia de patrones diurnos en su distribución vertical, los cambios mareales observados en abundancia larval integrada, son probablemente un resultado de transporte lateral. Sin embargo, no se puede descartar el transporte vertical desde aguas más profundas debido a que la profundidad total en el sitio de estudio era 250 m y las redes de plancton solo cubrieron hasta los 200 m. En numerosos estudios se ha indicado que desplazamientos verticales de larvas pueden estar influenciados fuertemente por la estructura de densidad en la columna de agua (Tremblay & Sinclair 1990, Rawlinson *et al.* 2004), y por las distribuciones no uniformes del alimento, con frecuencia asociadas a discontinuidades de salinidad y/o densidad (Viličić *et al.* 1989, Raby *et al.* 1994, Sameoto & Metaxas 2008). En el estudio de 24 h, la abundancia de zoeas fue mayor dentro de la capa de 10-25 m de profundidad, justo debajo de la fuerte haloclina y picnoclina, sugiriendo que las larvas permanecieron dentro de

la capa con mayor disponibilidad de alimento y que cambios horarios en su abundancia resultaron de transporte lateral.

No fue posible determinar si existen diferencias entre la distribución vertical de larvas y juveniles de *M. gregaria* debido a que durante el muestreo estratificado de verano de 2013 los juveniles estuvieron presentes ocasionalmente. Por lo tanto no fue posible contrastar la segunda hipótesis vinculada a esta temática.

La falta de diferencias entre la distribución vertical de larvas de día y de noche no fue consistente con lo observado en otras áreas, donde las larvas migran hacia aguas profundas durante el día, supuestamente para evitar la predación visual (Lampert 1989, De Robertis *et al.* 2000, Forward 2009, Ringelberg 2010). Sin embargo, es probable que el riesgo de predación visual, en la cabecera del fiordo Baker, donde la turbidez es tan elevada, sea muy bajo como para representar una señal ambiental relevante.

5.5 Circulación estuarina y flujo de larvas en el fiordo del río Baker

La circulación en el Canal Martínez en los primeros 25 m de la columna de agua fue típicamente estuarina, con un flujo neto hacia el océano en la superficie y flujo hacia la cabecera del fiordo en profundidad, como resultado del balance dinámico entre el gradiente de presión y fricción (Farmer & Freeland 1983). Una tercera capa se observó a mayores profundidades (resultados no presentados) la cual también fluía hacia el océano.

Más allá de este patrón general, cerca de la desembocadura del río Baker se detectó una importante asimetría lateral en la velocidad residual a lo largo del canal, y circulación secundaria que también fue importante. Los diagramas de vector progresivo mostraron una trayectoria hacia el Norte en un lado del canal, y hacia el Este en el otro lado del canal, reflejando la asimetría lateral y sugiriendo que ésta podría ser una zona de retención larval, mediada por el patrón de circulación, lo que explicaría las mayores densidades para cipris y nauplios avanzados de cirripedios. Las asimetrías transversales en los flujos a lo largo del fiordo pueden ser significativas en el transporte larval así como en el patrón espacial del asentamiento. Un ejemplo de esto es lo observado para el asentamiento de megalopas y reclutamiento de juveniles del cangrejo *Carcinus maenas* en el fiordo del río Mira, Portugal,

(Silva *et al.* 2006) donde las megalopas se asientan preferentemente en uno de los márgenes, probablemente debido a menores velocidades de corriente.

Asimetrías transversales en flujos a lo largo de fiordos han sido descritas por Valle-Levinson *et al.* (2003). La estructura transversal de los flujos a lo largo del fiordo muestra los efectos de la rotación de la Tierra, incluso en sistemas relativamente angostos, produciendo asimetrías transversales en estos flujos. Las asimetrías desaparecen bajo fuertes condiciones friccionales (alto número de Ekman), ilustrando el patrón previamente documentado para estuarios típicos. Valle-Levinson *et al.* (2003) también señalan que los flujos transversales se parecen a la “circulación gravitacional lateral” cuando los efectos friccionales son aparentes (números de Ekman > 0.1) respondiendo a balances transversales entre el gradiente de presión y la fricción. Estos flujos transversales revierten la dirección bajo fricción muy débil y reflejan la deflexión por efecto de Coriolis de los flujos a lo largo del fiordo, o sea, dinámica geostrófica. Sin embargo, Friedrichs *et al.* (2013) señalan que la estructura transversal de la velocidad a lo largo del canal podría ser primariamente debido a la circulación forzada por densidad y modificada por la batimetría, como en el caso de las soluciones analíticas obtenidas para el estuario del río James en EE.UU.

Cerca de la desembocadura del río Baker, la circulación lateral también fue importante. El cizalle lateral en canales con fuertes gradientes longitudinales de densidad genera fuertes gradientes de densidad lateral, que también afectan los patrones de circulación en canales mareales. En el caso de corrientes de llenante, el agua más salada queda confinada a las partes más profundas del canal, imponiendo así un gradiente de presión lateral (Nunes & Simpson 1985). Esta fuerza dirige una circulación lateral, o secundaria, consistente de un flujo superficial que converge hacia el centro del canal. En el fondo, el flujo de compensación diverge del centro (Nunes & Simpson 1985). Existe poca literatura sobre la importancia de la circulación lateral para el transporte de larvas (Eggleston *et al.* 1998), lamentablemente el diseño de muestreo no permite concluir acerca del efecto de la circulación lateral en el transporte de larvas en el área de estudio.

La retención de larvas en estuarios es más efectiva cuando el desarrollo larval es rápido y en sistemas estuarinos de gran extensión (Ketchum 1954, Platt *et al.* 1972). Intuitivamente, la dispersión y pérdida del stock parental es probable en pequeños sistemas con alta descarga comparados con estuarios más grandes con largos tiempos de residencia. En ausencia de

comportamiento larval, la exportación desde los sistemas estuarinos es probable cuando el tiempo de desarrollo excede los tiempos de residencia hidráulica (Roegner 2000).

El flujo neto entre 25 m y la superficie en el transecto interno, cerca de la desembocadura del río Baker, fue hacia la tierra para los nauplios y hacia el océano para las cypriis. Esto junto con la distribución observada para los nauplios a lo largo del canal (capítulo 3), sugiere que las larvas tempranas de cirripedios son transportadas desde el océano hasta el área de la desembocadura del río Baker donde se desarrollarían, y que más tarde las cypriis son advectadas hacia el océano. Este patrón sugiere que los cirripedios podrían usar el interior del fiordo Baker como área de crianza (Fig. 5 Anexo I). Los hábitats estuarinos son frecuentemente citados como hábitats de crianza (Mann & Lazier 1991, Elliot & Hemingway 2002). Un hábitat se identifica como área de crianza si los peces o invertebrados juveniles ocurren en mayores densidades, sufren menor mortalidad por depredación, o tienen mayores tasas de crecimiento en este hábitat que en otros (Beck *et al.* 2001).

La aparente advección de zoeas de *M. gregaria* hacia el océano es consistente con los resultados de León *et al.* (2008), quienes hipotetizaron que las hembras grávidas migrarían hacia los canales interiores, donde ocurre la eclosión y liberación de las larvas en invierno. Los estadios larvales tempranos serían dispersados hacia aguas externas, más oceánicas, y la megalopa se concentraría en la boca de estos canales a fines de primavera (León *et al.* 2008). El mecanismo por el cual los juveniles regresan a los canales estaría asociado con el flujo sub-superficial hacia la tierra que es característico de la circulación estuarina. En este estudio, se observó un muy bajo número de juveniles de *M. gregaria*, sin embargo sus flujos (resultados no presentados) también fueron positivos, indicando que los juveniles estarían ingresando al fiordo desde el océano (Fig. 5 Anexo I).

Dado que el tiempo de desarrollo larval de *M. gregaria* es de unos 80 días (Pérez-Barros *et al.* 2007, Varisco 2013, en el Golfo San Jorge, Argentina) y que los juveniles de *M. gregaria* tienen una importante capacidad de nado vertical pudiendo mantener velocidades hasta 16 cm/s (Zeldis & Jillett 1982) que les permitiría moverse entre diferentes capas en un fiordo, una estrategia de exportación de larvas costa afuera sería beneficiosa para esta especie. Esta exportación podría reducir la mortalidad por depredación, exponer las larvas a variabilidad ambiental más tolerable y, ocasionalmente, disminuir la competencia por alimento con suspensívoros bentónicos en áreas costeras o estuarinas (Sponaugle *et al.* 2002). Además, en

esta área existen ondas internas de marea semidiurnas correlacionadas con pulsos de altas descargas del río (Ross *et al.* 2014), que podrían generar un significativo transporte de partículas (Lamb 1997, Vlasenko *et al.* 2005). Por lo tanto, es posible que la presencia en el fiordo de juveniles de *M. gregaria* en la época de máximo caudal del río, esté asociada a ondas internas, como ocurre en la costa de Nueva Zelanda (Zeldis & Jillett 1982). Lamentablemente el diseño de muestreo utilizado no permitió evaluar dicha hipótesis. Se espera que en el futuro próximo dicha hipótesis pueda ser contrastada.

Dadas las tendencias actuales de cambio climático y el aumento del derretimiento de glaciares en los campos de hielo de Patagonia (Glasser *et al.* 2011, Rivera *et al.* 2012), los cambios en la descarga de agua dulce podrían fortalecer la circulación estuarina al aumentar el gradiente de densidad. Además, bajo este escenario, junto con aumentos de descarga de agua dulce se esperaría un incremento en el aporte de sedimentos de origen glacial, el cual incrementaría la turbidez y tendría un impacto negativo sobre la productividad primaria en el fiordo. No es posible determinar a priori cómo el cambio climático afectaría la retención de larvas, conectividad y comportamiento larval. Por otro lado, bajo el escenario de construcción de represas en la cuenca del Baker, el efecto podría ser opuesto, disminuyendo el aporte de agua dulce hacia el fiordo y por lo tanto debilitando la circulación estuarina, además los sedimentos podrían quedar atrapados en las represas, disminuyendo la turbidez, y por lo tanto, podría aumentar la productividad primaria en el fiordo siempre y cuando haya disponibilidad de nutrientes.

Aunque los resultados obtenidos del estudio de corrientes con ADCP presentaron limitaciones, entre ellas una incompleta cobertura batimétrica y falta de señal en el fondo del fiordo, este trabajo es novedoso en el estudio de flujos advectivos de plancton en fiordos de Patagonia. Esta es la primera vez que se hace un acercamiento de este tipo en un fiordo Patagónico, y por lo tanto son las primeras estimaciones de flujos de plancton a lo largo del complejo de fiordos Martínez/Baker.

6. CONCLUSIONES

Fuertes gradientes horizontales y verticales en las condiciones hidrográficas y fluorescencia fueron observadas a lo largo del fiordo del río Baker a comienzos de primavera (octubre 2012) y fines de verano (febrero 2013). La fluorescencia fue relativamente baja comparada con valores de otros fiordos Patagónicos. Las concentraciones de clorofila-*a* fueron mayores en primavera en la zona centro del fiordo, y cuatro veces (ca. 4 mg/m³) el máximo del valor observado en verano (ca. 1 mg/m³), cuando los máximos de fluorescencia estuvieron limitados a estaciones más externas, cercanas al Golfo de Penas y ubicados a mayor profundidad en la columna de agua.

La comunidad de meroplankton consistió mayormente de larvas de cirripedios, decápodos, bivalvos y gastrópodos. Los cirripedios dominaron en primavera, cuando la descarga del río estaba en el mínimo, mientras que los bivalvos fueron más abundantes en verano, cuando la descarga del río estaba cerca de su máximo anual. La estructura comunitaria en primavera no difirió entre canales (Martínez y Baker), pero presentó una clara separación entre las estaciones externas y las cercanas a la desembocadura del río.

Nauplios y cipris fueron numéricamente dominantes cuando la salinidad era mínima por la descarga del río y la biomasa fitoplanctónica era mayor en relación a lo observado en verano. Larvas y juveniles de *M. gregaria* exhibieron un patrón estacional de abundancia muy marcado, con larvas apareciendo mayormente en primavera y juveniles exclusivamente en meses de verano. La mayor abundancia de zoeas en meses de primavera podría estar asociada con cambios en la biomasa (y potencialmente composición) de fitoplancton que debería resultar de menores niveles de turbidez durante los meses de mínima descarga del río.

La circulación en el fiordo del río Baker presentó un patrón estuarino típico, con flujo hacia el océano en superficie y hacia la cabecera del fiordo en profundidad como resultado del balance dinámico entre el gradiente de presión y fricción. Sin embargo, una tercera capa fue observada en profundidad, con flujo hacia el océano. Los resultados también mostraron asimetrías transversales en los flujos a lo largo de fiordo cerca de la desembocadura del río Baker; éstas pueden ser significativas para el transporte de larvas, porque estarían causando recirculación y/o retención en el lado Este del canal. Esta retención es también importante desde un punto de vista socio-económico y debería ser tomado en consideración para

eventuales proyectos de tratamiento de aguas de desecho, o para la instalación de emisarios submarinos.

Los resultados implican que bajo el mismo patrón de circulación, hay diferencias en los flujos de larvas de los principales grupos de crustáceos a lo largo del fiordo. Las larvas de nauplios de cirripedios parecen desarrollarse a medida que son advectadas desde el océano hacia la cabecera del fiordo, y realizar una migración opuesta durante el estadio cypis. Este patrón fue consistente con el patrón de abundancia de cirripedios adultos observado a lo largo del fiordo, con mayores abundancias hacia el océano (observación personal), aunque el patrón de los adultos puede estar mediado principalmente por la selección de hábitat y no necesariamente tiene que ver con el patrón de distribución de las larvas en la columna de agua. Por otro lado, de forma consistente con los resultados de León et al. (2008) en otros fiordos, las zoeas de *M. gregaria* fueron advectadas hacia el océano, mientras que los juveniles presentaron flujo hacia la cabecera del fiordo.

No se observaron diferencias en la distribución vertical de larvas entre el día y la noche. En este fiordo donde la turbidez es muy alta, no sería necesario para las larvas migrar hacia zonas profundas para evitar la depredación visual durante el día.

A modo global, los resultados de este estudio sugieren que cambios estacionales y de menor escala en la abundancia de larvas en el fiordo del río Baker están estrechamente relacionados con las condiciones ambientales, que están moduladas por cambios estacionales en aportes de agua dulce y por oscilaciones de alta frecuencia cerca a la picnoclina probablemente relacionadas a ondas internas, ambos parecen afectar el ritmo y escala espacial del desarrollo larval y migración juvenil hacia y desde este sistema estuarino.

Los resultados encontrados para la distribución de larvas de cirripedios dejan abierta la pregunta de si nauplios de cirripedios en el fiordo del río Baker dependen de fitoplancton de pequeño tamaño y/o bacterias planctónicas como alimento principal para completar su desarrollo, ya que resultados de observaciones recientes en una estación cerca de la desembocadura del río Baker, han mostrado que más del 50% de la producción primaria neta corresponde al picoplancton y nanoplancton y que la producción secundaria bacteriana puede alcanzar el 70% de la producción primaria (González et al. 2013, Cuevas et al. enviado).

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ANEXO I



ANEXO I.

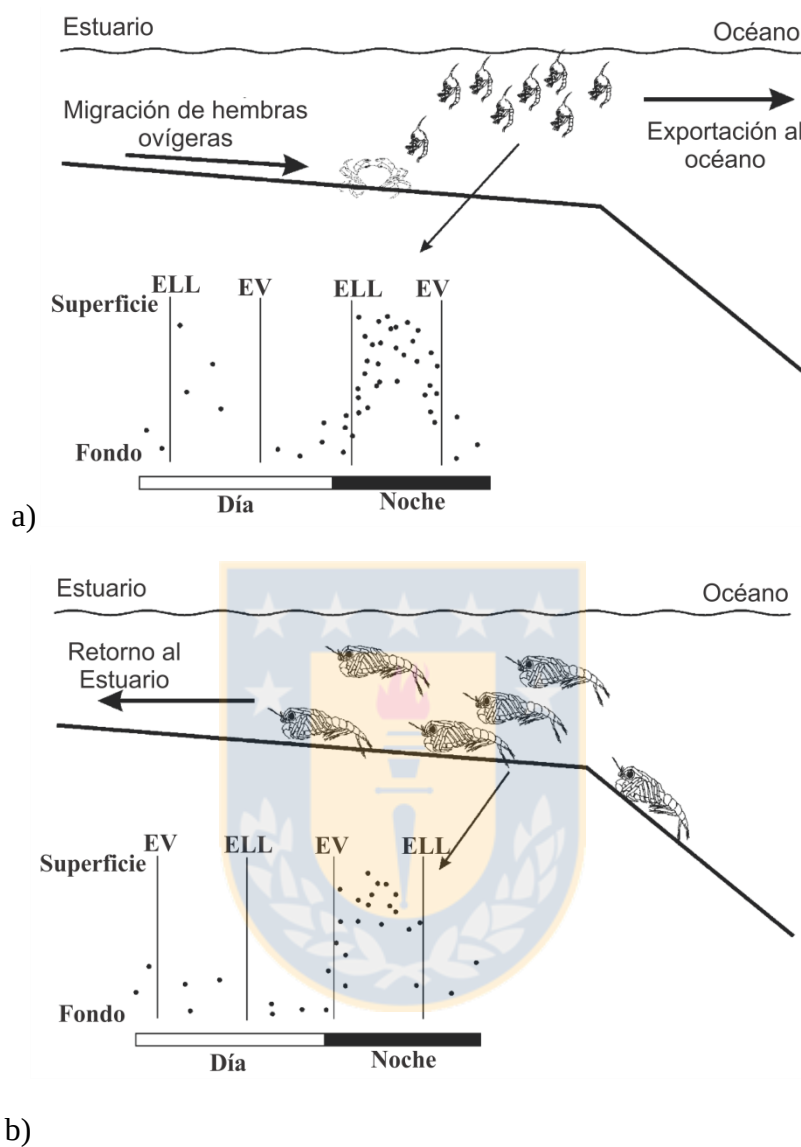


Figura 1. Exportación de la primera zoea desde estuarios (a) seguida por retorno de la megalopa (b). La gráfica de abajo representa cambios en la posición vertical de los estadios larvales durante los ciclos mareales y diarios. La posición más alta a lo largo de la columna de agua es alcanzada durante la vaciante en la fase exportación (a) y durante llenante en la fase de re-invasión (b). El portúnido *Carcinus maenas* es un representante de este tipo de comportamiento. (EV= estoa vaciante, ELL= estoa llenante, modificado de Queiroga y Blanton 2005).

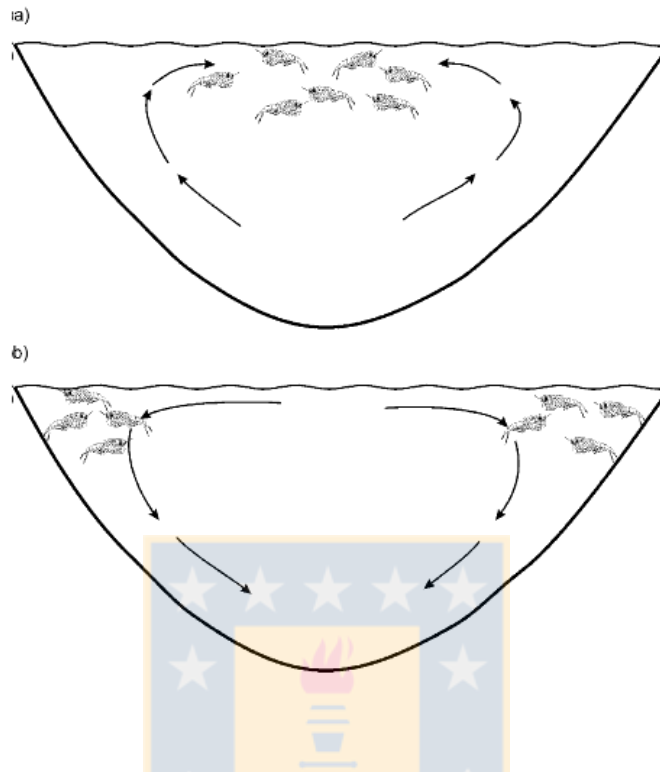


Figura 2. Efectos de la circulación secundaria en la advección de larvas en un estuario. Cada panel es una sección transversal de un estuario hipotético. Debe haber un gradiente de densidad axial (salinidad) lo suficientemente fuerte para que la circulación secundaria sea significativa. Corriente llenante (a) causa circulación secundaria, que concentra las larvas en el eje, donde el flujo hacia la tierra es más fuerte. Corriente vaciante (b) causa la circulación secundaria reversa, que concentra las larvas en los bordes del estuario, donde el flujo hacia el océano es relativamente débil. El resultado neto de este proceso es que las larvas viajan hacia tierra más que hacia el océano. Este mecanismo constituye otro ejemplo de transporte mareal selectivo, pero su importancia no ha sido documentada (tomado de Queiroga y Blanton 2005).

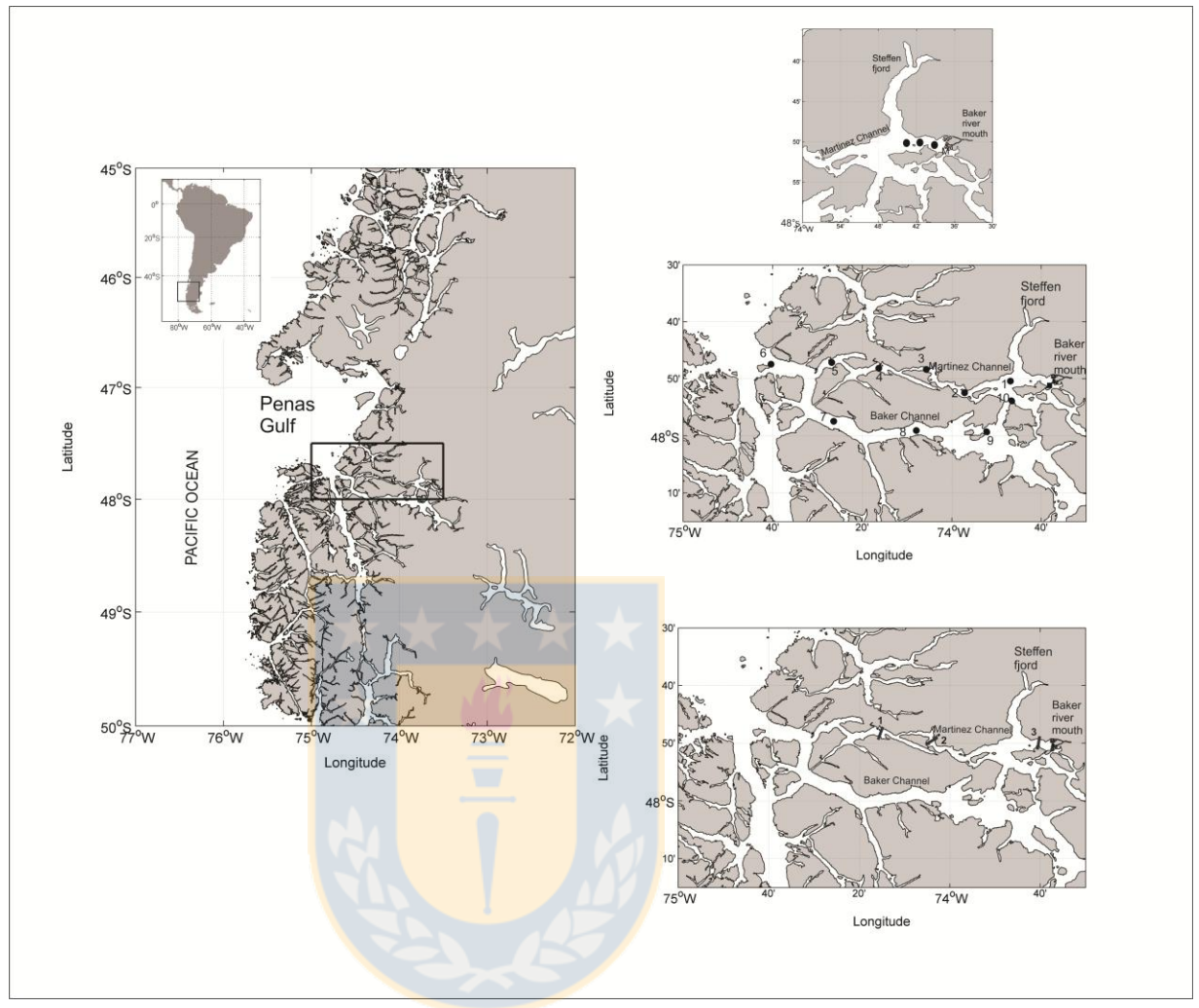


Figura 3. Mapa del área de estudio con las estaciones de muestreo. Panel superior derecho, de izquierda a derecha: estaciones Steffen, Centro y Baker de muestreo mensual de zooplancton, ubicación del anclaje de termistores. Panel del medio: estaciones de muestreo a lo largo del Canal Martínez y Baker. Panel inferior: ubicación de los transectos en donde se realizó muestreo con ADCP remolcado y zooplancton durante Febrero de 2013.

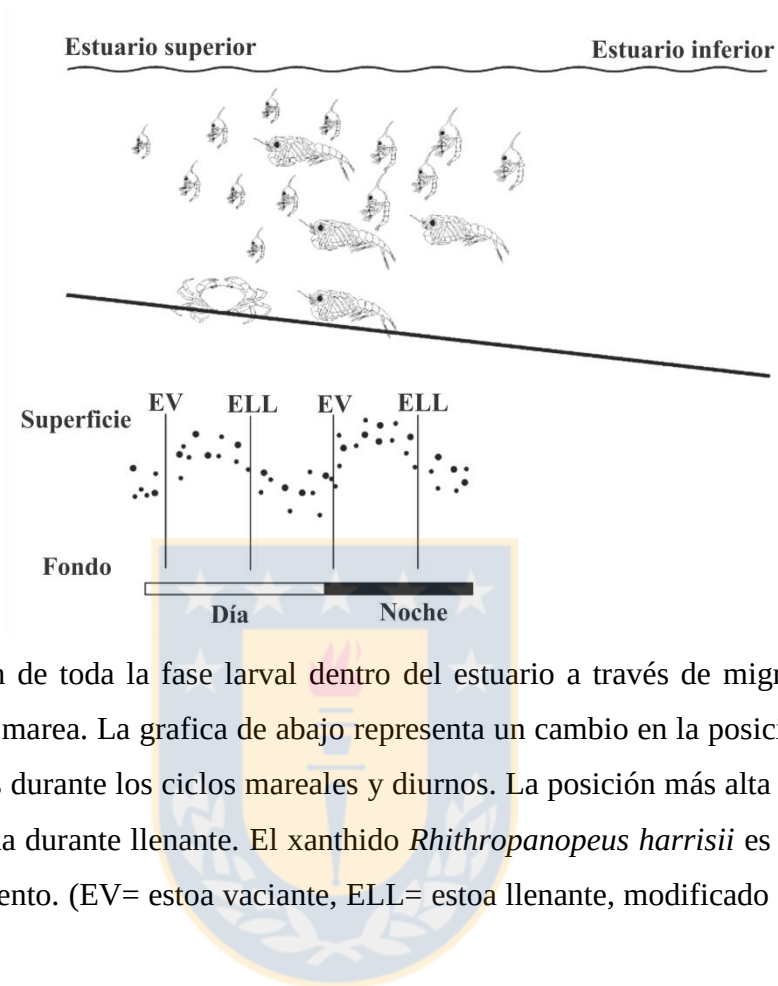


Figura 4. Retención de toda la fase larval dentro del estuario a través de migración vertical sincronizada con la marea. La grafica de abajo representa un cambio en la posición vertical de los estadios larvales durante los ciclos mareales y diurnos. La posición más alta en la columna de agua es alcanzada durante llenante. El xanthido *Rhithropanopeus harrisii* es representativo de este comportamiento. (EV= estoa vaciante, ELL= estoa llenante, modificado de Queiroga y Blanton 2005).

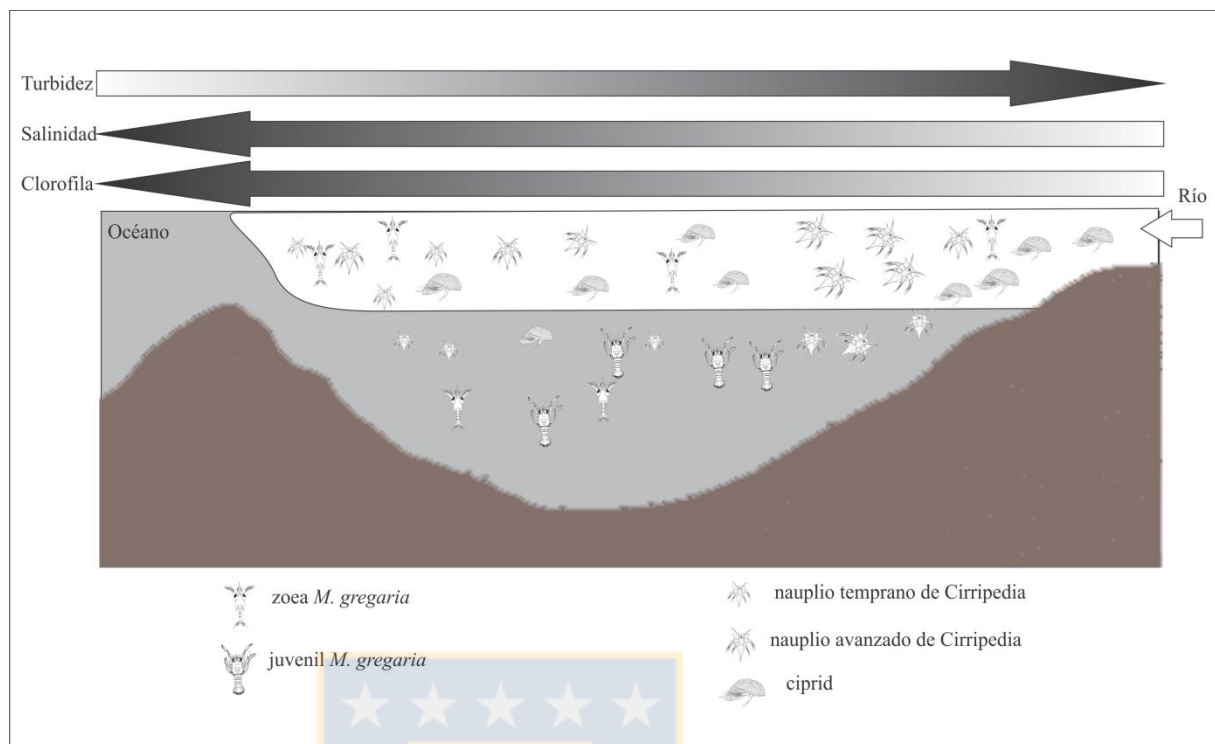


Figura 5. Diagrama conceptual de la distribución de larvas y juveniles de *Munida gregaria* y larvas de cirripedios a lo largo del fiordo Baker durante la época de mayor descarga del río (Febrero).