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**Acoplamiento entre abundancia larval en el plancton y el
asentamiento submareal e intermareal de invertebrados
bentónicos en bahía de Totoralillo Norte, Región de
Coquimbo**

Tesis para optar al grado de Magister en Ciencias con mención en
Oceanografía

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La Tesis de “*Magíster en Ciencias mención Oceanografía*” titulada “*ACOPLAMIENTO ENTRE ABUNDANCIA LARVAL EN EL PLANCTON Y EL ASENTAMIENTO SUBMAREAL E INTERMAREAL DE INVERTEBRADOS BENTÓNICOS EN BAHÍA DE TOTORALILLO NORTE, REGIÓN DE COQUIMBO*”, de la Srta. CRISTINA ANDREA STUARDO STUARDO 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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A mí querida Familia.

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Resumen

“Acoplamiento entre abundancia larval en el plancton y el asentamiento submareal e intermareal de invertebrados bentónicos en bahía de Totalillo Norte, Región de Coquimbo”

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Una fase crítica en el ciclo de vida de muchos invertebrados bentónicos marinos es el transporte larval hacia la costa. Sin embargo, la llegada de larvas a la costa no siempre con lleva un asentamiento exitoso, debido a numerosos factores físicos y biológicos que inducen mortalidad en las larvas o impiden su asentamiento. En este trabajo investigamos la asociación entre el asentamiento de larvas de invertebrados y su abundancia en el plancton costero en la Bahía de Totalillo Norte, localizada en una zona se surgencia en Chile central ($29^{\circ}29'S$ $71^{\circ}19'W$). Se realizaron una serie de observaciones de abundancia de larvas planctónicas de cirripedios, decápodos, bivalvos y gastrópodos y de su asentamiento en colectores intermareales y submareales durante un periodo 10 días a fines de primavera (noviembre-diciembre) de 2013. También se examinó la influencia de la variabilidad del viento local en el asentamiento submareal, intermareal y abundancia de larvas en la bahía. Los resultados muestran que las tasas de asentamiento de todas las especies fueron más altas en el submareal que en intermareal. Las altas tasas de asentamiento submareal y abundancia de larvas en el plancton fueron consistentemente observadas en el extremo norte de la bahía. Si bien el asentamiento intermareal y submareal no estuvieron correlacionados en todos los grupos taxonómicos examinados, hubo una correlación positiva y significativa entre el asentamiento submareal y la abundancia de larvas planctónicas en decápodos y gastrópodos. La variabilidad diaria del asentamiento intermareal no se correlacionó con la variabilidad del viento local. En cuanto al asentamiento

submareal, la influencia del forzamiento del viento pareció diferir entre taxa y sitios. El asentamiento submareal de decápodos se correlacionó positivamente con el forzamiento del viento hacia la costa, mientras que, aparentemente los vientos hacia el ecuador tienen un efecto negativo en el asentamiento submareal de gastrópodos. El aparente desacople entre el asentamiento intermareal y la abundancia de larvas en plancton cercano a la costa es consistente con investigaciones previas en zonas costeras similares, y destaca las limitaciones de inferir un mecanismo de transporte larval basado únicamente en observaciones de asentamiento intermareal. Por otro lado, los resultados contrastantes entre taxa con respecto a la correlación entre el asentamiento submareal y el viento costero revelan la importancia de las diferencias taxonómicas en las capacidades de natación de las larvas y su respuesta conductual a la compleja hidrodinámica cerca de la costa.



Abstract

“Coupling between larval abundance in the plankton and the subtidal and intertidal settlement of benthic invertebrates in the bay of Totalillo Norte, Region of Coquimbo”

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Larval transport to near-shore environments is a critical phase in the life cycle of many marine benthic invertebrates. However, onshore delivery of larvae not always translates into their successful settlement, due to numerous physical and biological factors that induce larval mortality or preclude settlement. Here we investigated the association between the settlement of invertebrate larvae and their abundance in the nearshore plankton of Totalillo Norte bay, located in the upwelling region of central Chile (29°29'S 71°19'W). Planktonic larvae of barnacles, decapods, bivalves, and gastropods, and their settlement on intertidal and subtidal collectors were surveyed daily over a 10-day period in the late austral spring (November-December) of 2013. The influence of local wind variability on the subtidal settlement, intertidal settlement and planktonic larval abundance across the bay was also examined. Our results show that settlement rates of all species were higher in the subtidal than in the intertidal across the bay. The highest rates of subtidal settlement and abundance of planktonic larvae were consistently observed at the bay's northern tip. While intertidal and subtidal settlement were uncorrelated for all taxonomic groups, there was a significant positive correlation between the subtidal settlement and planktonic larval abundance in decapods and gastropods. Daily variability of intertidal settlement was not correlated with local wind variability. As for subtidal settlement, the influence of wind forcing appeared to differ across taxa and sites. Subtidal settlement of decapods was positively correlated with onshore wind forcing, whereas the

equatorward wind appeared to have a negative effect on the subtidal settlement of gastropods. The apparent decoupling between intertidal settlement and larval abundance in the near-shore plankton is consistent with previous work on similar coastal areas, and highlights the limitations of attempts to infer larval delivery mechanism based solely on intertidal settlement observations. On the other hand, the contrasting results regarding subtidal settlement vs. wind correlations reveal the importance of taxonomic differences in the swimming abilities of larvae and their behavioral response to complex near-shore hydrodynamics.



1. INTRODUCCION

1.1. Ciclos de Vida Complejo

La mayoría de los organismos que habitan el intermareal poseen un ciclo de vida complejo; esto quiere decir que luego de la fecundación, sea interna como el caso de los cirripedios, o externa como en los mitílidos, se liberan a la columna de agua miles y hasta millones de larvas planctónicas. Estas larvas pueden permanecer por días, semanas o incluso meses en el plancton (Shanks et al. 2003), periodo en el cual experimentan altas tasas de mortalidad debido a inanición, depredación y canibalismo (Thorson 1950, Morgan 1995). Además de los factores biológicos que influyen en la abundancia larval en el plancton, también se deben considerar los factores físicos que influyen sobre la distribución espacial de las larvas, principalmente en términos de su distancia a la costa una vez que alcanzan un estadio competente para asentarse en el bentos. Esto va a depender en gran medida de las corrientes predominantes, de la duración del periodo de desarrollo larval en el plancton, y del comportamiento natatorio de las larvas en relación a la variabilidad hidrodinámica en aguas cercanas a la costa (Shanks et al. 2003, Shanks y Shearman 2009). Una vez alcanzado el estadio competente para asentarse, los patrones de asentamiento y posterior reclutamiento de estos organismos están fuertemente influenciados por factores físicos que determinan el transporte larval hacia la costa y, en el caso de organismos intermareales, a través de la zona de rompiente (Navarrete et al. 2015, Shanks et al. 2017). Por ello, la distribución espacial de numerosas especies de invertebrados bentónicos está determinada por la secuencia de interacciones físico-biológicas que determinan la sobrevivencia larval en el plancton, el transporte larval, y los patrones espaciales y temporales de asentamiento (Thorson 1950, Menge 1991, Navarrete et al. 2008, Pfaff et al. 2015). En este contexto, la abundancia de larvas competentes en el plancton de aguas costeras, a menudo referida como “suministro larval”, y los patrones espacio-temporales de asentamiento son aspectos clave para entender la dinámica y estructura espacial de poblaciones bentónicas costeras.

1.2. Suministro y Asentamiento Larval

La renovación de las poblaciones bentónicas se puede entender como una secuencia de tres etapas. Primero, el suministro larval, definido como la densidad de larvas competentes en la cercanía de hábitats de asentamiento (Harrold et al. 1991). Segundo, el asentamiento larval, que es la transición desde el plancton al ambiente bentónico, y que requiere de un sustrato adecuado. Por último, el reclutamiento, entendido como la adición de individuos a la población asentada y que implica la sobrevivencia por un determinado periodo post-asentamiento (Harrold et al. 1991, Caley et al. 1996).

El asentamiento larval sobre colectores instalados en el intermareal ha sido ampliamente utilizado como *proxy* del transporte de larvas competentes hacia la costa (e.g. Hatton 1938, Shanks 1983, Roughgarden et al. 1988, Wing et al. 1995, Pineda 2000). Sin embargo, el número de larvas que se asienta en un determinado tiempo sobre una determinada área del intermareal no necesariamente refleja la abundancia de larvas planctónicas competentes en el plancton cerca de la costa (Rilov et al. 2008, Hoffmann et al. 2012, Navarrete et al. 2015). Este aparente desacople entre el suministro larval y el asentamiento larval en ambientes intermareales resulta de la interacción entre diversos factores físicos y biológicos que afectan el transporte y/o sobrevivencia de larvas competentes en aguas muy cercanas a la costa (Young & Gotelli 1988, Pineda et al. 2010). Por ejemplo, el desacople se puede generar por diferencias en “timing” entre el desarrollo larval en el plancton y la ocurrencia de fenómenos físicos que determinan su transporte en el eje perpendicular a la costa (Hoffmann et al. 2012), o por efecto de las condiciones de turbulencia en la zona de rompientes, previo al arribo de una larva al ambiente intermareal (e.g. Navarrete et al. 2015).

Es posible que el grado de acople o desacople entre suministro y asentamiento larval varíe espacialmente debido a cambios en los factores físicos que dominan el transporte larval cerca de la costa, lo que podría generar diferencias espaciales incluso a escala de unos pocos kilómetros. Por ejemplo, debido a la variabilidad espacial de la interacción del viento con la topografía y batimetría costera, en bahías de pequeño tamaño es posible encontrar diferencias espaciales consistentes en el asentamiento larval de cirripedios (Bonicelli et al. 2014b).

1.3. Mecanismos de Transporte Larval

El transporte en los ejes paralelo y perpendicular a la costa es asimétrico, pues las corrientes a lo largo de la costa son más energéticas que en el eje perpendicular (Largier 2003). Sin embargo, es el transporte perpendicular a la costa el que permite el transporte y posterior asentamiento de larvas en hábitats intermareales (Pineda et al. 2010). Por ello, identificar los procesos que median el transporte larval en este eje es de gran relevancia para entender los factores que determinan el suministro de larvas al ambiente intermareal, y posteriormente el reclutamiento de invertebrados bentónicos (Tapia & Navarrete 2010). Los procesos físicos involucrados en el transporte larval hacia la costa abarcan un amplio espectro de escalas temporales y espaciales; desde surgencia y subsidencia inducidas por variaciones sinópticas del viento (e.g. Lagos et al. 2005, Narváez et al. 2006, Lagos et al. 2007), a transporte inducido directamente por el viento (Bertness et al. 1996, Kaplan et al. 2003, Tapia et al. 2004), eventos de transporte inducidos por ondas internas (Vargas et al. 2004, Ladah et al. 2005) y transporte mediado por el oleaje (Shanks et al. 2010, Navarrete et al. 2015). También es relevante la influencia que puede tener la descarga de un río, si éste se encuentra cerca de zonas de asentamiento de invertebrados (Piñones et al. 2005). La importancia relativa de estos procesos físicos puede cambiar de una región a otra (Epifanio & Garvine 2001) o entre diferentes épocas del año en una misma región.

1.4. Zona de Estudio

Las bahías son excelentes casos de estudio para entender cómo la variabilidad espacial en los mecanismos que median el transporte larval determinan el arribo y posterior asentamiento de éstas en hábitats intermareales, debido a que en una pequeña escala espacial presentan abruptos cambios en la orientación de la costa y por consecuencia se puede observar una variedad de combinaciones en forzantes físicos y respuestas biológicas. Estudios previos en bahías pequeñas (escalas de 1-10 km) han demostrado que cambios en la dirección y en la intensidad del viento pueden causar variaciones en el patrón espacial de asentamiento de invertebrados intermareales (Bertness et al. 1996, Tapia & Navarrete 2010, Bonicelli et al. 2014b).

La heterogeneidad espacial del asentamiento larval puede resultar de un transporte heterogéneo de larvas al intermareal, dado por la variabilidad espacial en condiciones hidrodinámicas cerca de la costa (e.g. Ladah et al. 2005), incluyendo cambios en la importancia relativa de la zona de rompiente como última barrera hidrodinámica antes del arribo y asentamiento de larvas sobre el intermareal. Finalmente, se ha propuesto que el patrón de asentamiento está mayormente relacionado a la disponibilidad de sustrato para el asentamiento en el intermareal (Pineda & Caswell 1997, Rilov et al. 2008). Discernir entre cuál de estas hipótesis es correcta resulta difícil si sólo se cuenta con observaciones de asentamiento en el intermareal, como es el caso de numerosos estudios publicados hasta la fecha (e.g. Caffey 1985, Satchell & Farrel 1993, Lagos et al. 2005, Tapia & Navarrete 2010). Para resolver estas interrogantes es necesario realizar observaciones simultáneas de asentamiento intermareal, asentamiento submareal, abundancia larval en el plancton y su relación con variables físicas tales como la magnitud y dirección del viento, temperatura superficial, y estratificación de la columna de agua.

Dado este contexto, el objetivo de este trabajo fue estudiar el acoplamiento entre suministro y asentamiento costero a partir de observaciones de asentamiento submareal, intermareal, larvas en plancton costero y viento local en una bahía de la costa de Chile centro-norte, la Bahía de Totalillo Norte (BTN) en la Región de Coquimbo. El foco de la investigación estuvo en evaluar la conexión entre asentamiento y la disponibilidad de larvas en el plancton, así como el efecto de la variabilidad del viento local sobre las condiciones físicas de aguas cercanas a la costa y sobre la variabilidad en abundancia o asentamiento de larvas. Las hipótesis abordadas apuntan a la secuencia de interacciones físico-biológicas que determinan la dinámica del asentamiento larval y las posteriores estructuras poblacionales de invertebrados bentónicos en estos sistemas.

2. HIPOTESIS Y OBJETIVOS

2.1. Hipótesis

H1: El asentamiento larval de invertebrados bentónicos en el intermareal se relaciona positivamente con el asentamiento en el submareal.

H2: El asentamiento en el submareal se correlaciona positivamente con la abundancia de larvas en el plancton.

H3: El incremento en stress del viento favorece la llegada de larvas a la costa.

2.2. Objetivo general:

Estimar el acoplamiento entre el asentamiento submareal e intermareal de invertebrados bentónicos y su relación con la abundancia de larvas en el plancton, además de evaluar si existe una relación con el viento dentro de una bahía.



2.3. Objetivos específicos:

- 2.3.1. Determinar la variabilidad diaria en la tasa de asentamiento de invertebrados bentónicos en el intermareal y submareal de la Bahía de Totalillo Norte.
- 2.3.2. Caracterizar la abundancia larval de invertebrados bentónicos intermareales en el plancton de la Bahía de Totalillo Norte.
- 2.3.3. Caracterizar el viento predominante en la Bahía de Totalillo Norte.
- 2.3.4. Evaluar el acople o desacople del asentamiento intermareal, submareal y la abundancia planctónica de larvas de invertebrados bentónicos con el viento en la Bahía de Totalillo Norte.

3. MATERIALES Y METODOS

3.1. Área de estudio

Se realizó un muestreo intensivo en la bahía de Totalillo Norte (BTN) (29°29'S 71°19'W), región de Coquimbo (Figura 1), durante un periodo de 10 días, entre el 30 de noviembre y 9 diciembre de 2013. La BTN es una bahía semi-expuesta orientada al noroeste, con una extensión de 3 km medida entre sus extremos y profundidades que varían entre 5 m en el extremo sur y 50 m en el extremo norte, además posee una pequeña isla cercana al extremo sur de la bahía, que restringe la conexión e intercambio de agua con mar abierto. Las temperaturas superficiales fluctúan entre 15 y 18°C en primavera-verano (López et al. 2012). La línea de costa presenta diferentes grados de exposición al viento, y comprende tanto sustrato rocoso como dos playas arenosas: Temblador y Totalillo Norte, en los extremos norte y sur de la bahía, respectivamente.



3.2. Obtención de datos

3.2.1. Variables ambientales

Se obtuvieron registros de temperatura del agua mediante data loggers HOBO Temp (Onset Computer Corp., USA) instalados a distintas profundidades por medio de anclajes desplegados en tres puntos de la bahía. Las profundidades de instalación de sensores correspondieron a 1, 7, 10, 14 y 20 metros sobre el fondo (Figura 1). Los sensores tienen una precisión de $\pm 0,2$ °C y registraron la temperatura a intervalos de 10 min, por un periodo de 10 días.

Los datos de magnitud y dirección del viento en la zona fueron obtenidos desde una estación meteorológica ubicada en el extremo sur de la BTN (Figura 1), a 5 metros sobre el nivel medio del mar.

3.2.2. Muestreo biológico

Para caracterizar la variabilidad temporal y espacial del asentamiento larval en los grupos más representativos de invertebrados bentónicos (decápodos, cirripedios, mitílidos y gastrópodos), se utilizaron colectores instalados tanto en la zona intermareal baja como en el submareal de ambos extremos de la bahía (Figura 1), en sitios denominados Temblador y Totoralillo Norte en los extremos norte y sur de la bahía, respectivamente. Los colectores utilizados fueron del tipo “tuffy”, que corresponden a esferas de malla plástica. Este tipo de colector ha sido utilizado en numerosas investigaciones en la costa de Chile, Estados Unidos y Sudáfrica (e.g. Menge et al. 1994, Narváez et al. 2006, Porri et al. 2006, Navarrete et al. 2008), lo que permite comparar las observaciones con información ya existente. En el intermareal fueron adosadas al sustrato mediante un tornillo de acero inoxidable. Las cuatro réplicas instaladas en cada sitio fueron retiradas y reemplazadas cada 24 horas, generalmente cerca de las 9 AM hora local (UTC-3).

Para evaluar el asentamiento larval en ambientes submareales, se utilizó el mismo tipo de colector (tuffy) adosado a racks que se instalaron a 1 m bajo la superficie y 1 m sobre el fondo (ca. 20 m bajo la superficie) en líneas ancladas en ambos extremos de la bahía (Figura 1). Los colectores fueron recuperados y reemplazados mediante buceo cada 24 horas, aproximadamente a las 9 AM hora local.

Para estimar la abundancia de larvas en el plancton, cada dos días se realizó un muestreo de zooplancton en una grilla de 7 estaciones dispuestas a lo largo y en dirección perpendicular a la bahía (Figura 1). En cada estación se realizaron arrastres oblicuos con una red bongo de 300 μm de trama y 50 cm de diámetro de boca, desde 20 m hasta la superficie. Además, en cada estación se realizaron arrastres horizontales con una red epineustónica, sobre una distancia aproximada de 150 metros y una velocidad promedio de 1,6 nudos. Adicionalmente, en ambas redes se instalaron flujómetros (General Oceanics, USA) para conocer el volumen de agua filtrada por estas. .

Todas las muestras de zooplancton fueron preservadas en alcohol al 70% y analizadas en laboratorio bajo microscopio de disección. Las larvas fueron enumeradas e inicialmente asignadas a grupos mayores (ej. cirripedios, decápodos, bivalvos, gastrópodos). En algunos

casos fue posible identificar las larvas a nivel de especie, como los decápodos *Cyclograpsus cinereus* y *Taliepus dentatus*, y el gastrópodo *Concholepas concholepas*.

3.3. Análisis de la información

3.3.1. Estimación de stress de viento

A partir de la magnitud y dirección del viento medidas por la estación meteorológica, se calcularon las componentes meridional (norte-sur) y zonal (este-oeste) del viento, y se identificó el ángulo de máxima variabilidad (11,9° con respecto al Norte). Este ángulo fue utilizado para rotar el sistema de coordenadas y obtener las componentes paralela (v) y perpendicular (u) del vector de viento. De acuerdo a este nuevo sistema de coordenadas (ver Figura 1), los valores positivos en la componente v representan viento soplando en dirección Noreste (hacia el extremo norte de la bahía), mientras que los valores positivos en la componente u representan viento en dirección Sureste (hacia la playa de Totoralillo Norte). Se utilizó la magnitud del viento V (m s^{-1}) para calcular el stress del viento τ (N m^{-2}) según Large y Pond (1981).

$$\tau = \rho * cd * V \quad [1]$$

donde ρ es la densidad promedio del aire, y cd es el coeficiente de arrastre estimado a 5 metros sobre el nivel del mar, donde se ubicaba la estación meteorológica. Una vez calculado el módulo del stress de viento, se obtuvo las componentes paralela y perpendicular del vector de stress de viento, para luego calcular series diarias de stress acumulado a lo largo de cada eje, integrando sobre las 24 horas previas a los tiempos de recuperación de los colectores.

3.3.2. Temperatura de la columna de agua

Desde las mediciones de temperatura obtenidas por los sensores instalados en los anclajes, se obtuvo series de tiempo horarias para cada profundidad en los tres puntos dentro la BTN. Una vez obtenidas estas series de tiempo de temperatura, se realizaron análisis de densidad espectral, para detectar en qué frecuencias las series mostraron la mayor energía. Posteriormente, para cada profundidad y anclaje se calculó el día promedio de temperatura, considerando todo el periodo de muestreo. Con estos resultados, se obtuvo una serie de mapas

de contorno que permitieron comparar la variabilidad diurna en la estructura térmica de la columna de agua entre los tres puntos de la bahía en que se instaló anclajes.

3.3.3. Análisis de correlación

Se llevó a cabo un análisis de correlación entre las series de tiempo de asentamiento larval sobre colectores, tanto del intermareal como del submareal, y la variabilidad temporal en el gradiente de temperatura, intensidad del viento y stress del viento. Previamente, para cada serie de tiempo se calcularon coeficientes de autocorrelación en función del desfase k en el tiempo, de acuerdo a,

$$R_{xx} = \frac{1}{N-k} \sum_{i=1}^{N-k} (x_i x_{i+k}) \quad [2]$$

donde $k = 0, 1, \dots, M$ (Emery & Thomson 1998).

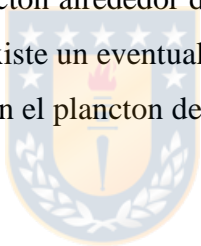
Cuando los autocorrelogramas así construidos indicaron niveles significativos de autocorrelación en una serie, ésta fue removida calculando la primera diferencia de las series, es decir $[x_n - x_{n-1}]$. Este método es frecuentemente utilizado para remover la tendencia de series de tiempo geofísicas de corta duración. Finalmente, para evaluar la significancia estadística de las diferencias en asentamiento de cada tipo de larva entre colectores superficiales y de fondo, o entre colectores en los extremos norte y sur de la bahía a una misma profundidad, se realizaron pruebas t de una cola,

$$t = \frac{\bar{x} - \bar{y}}{\sqrt{\frac{s_x^2}{n} + \frac{s_y^2}{n}}} \quad [3]$$

donde \bar{x} e \bar{y} son los promedios de abundancia larval en cada grupo, s_x y s_y son las desviaciones estándar de cada grupo de observaciones y n corresponde al número de días con observaciones de asentamiento en ambos grupos. Se utilizaron los datos transformados a $\log(x + 1)$ con el fin de cumplir con los supuestos de normalidad y homogeneidad de varianza, los que fueron

examinados en cada caso usando las pruebas de Lilliefors (Conover, 1999) y Levene (Zar, 1996), respectivamente. Debido a las diferencias en distribución vertical descritas para los diferentes grupos estudiados, las hipótesis estadísticas puestas a prueba difirieron según el grupo. En el caso de las larvas cypri de cirripedios y larvas de gastrópodos, se puso a prueba la hipótesis de que el asentamiento en el fondo es mayor que en la superficie, mientras que para las larvas de decápodos se planteó la hipótesis opuesta.

Para evaluar la asociación entre el asentamiento de larvas en colectores submareales y su abundancia en el plancton, se calcularon correlaciones de Pearson entre las tasas de asentamiento y las abundancias estimadas en el plancton un día antes. Se realizaron transformaciones logarítmicas a los datos ($\log(x + 1)$), para cumplir con los supuestos de normalidad y homogeneidad de varianza. Este análisis se realizó por separado para la abundancia estimada a partir de la red bongo y de la red epineustónica. El cálculo de correlaciones entre asentamiento y abundancia se repitió para diferentes grados de integración espacial en las observaciones de plancton alrededor de cada anclaje submareal, esto con el fin de determinar a qué escala espacial existe un eventual acople entre el asentamiento larval en el submareal y la abundancia de larvas en el plancton de la bahía.



4. RESULTADOS

Acoplamiento espacial y taxonómico entre el asentamiento intermareal y la abundancia de larvas en el plancton en una bahía pequeña.

Stuardo, C., Tapia, F.J., Bonicelli, J., Palma, A. Spatially and taxonomically variable coupling between settlement and planktonic abundance of invertebrate larvae in a small bay.

(enviado a Journal of Experimental Marine Biology and Ecology JEMBE)

Resumen

Por décadas, se ha utilizado el asentamiento de larvas de invertebrados en colectores intermareales como un *proxy* de suministro de larvas competentes a la costa. Sin embargo, evidencia reciente de varias regiones costeras sugiere que el acoplamiento entre asentamiento y suministro larval podría ser una excepción más que una regla. Aquí usamos diferentes observaciones de asentamiento y abundancia de larvas en el plancton a lo largo de una bahía en el norte de Chile para comprobar (1) si las fluctuaciones diarias de asentamiento cambian con la disponibilidad de larvas en el plancton, y (2) bajo qué condiciones el asentamiento intermareal podría ser un buen *proxy* para la abundancia o asentamiento de larvas más allá de la zona de rompiente. Durante 10 días en la primavera de 2013, se registró diariamente el asentamiento de larvas de cuatro grupos de invertebrados bentónicos (cirripedios, gastrópodos, decápodos y bivalvos) mediante colectores instalados en el intermareal y submareal en ambos extremos de la bahía, mientras que el plancton fue muestreado cada 2 días con redes epineustónica (superficie) y bongo (0-20 m). Se obtuvo registros continuos de la velocidad del viento y temperatura de la columna de agua en tres puntos de la bahía.

La temperatura en la columna de agua mostró un marcado ciclo diurno, con un ligero calentamiento superficial en la tarde, y un gradiente en la temperatura superficial a lo largo el día, que se correlacionó positivamente con el stress del viento en la costa. El asentamiento varió ampliamente entre taxa, sitios y profundidades de muestreo. Con excepción de las larvas cipris de cirripedios, las tasas de asentamiento fueron siempre más altas en los colectores submareales, donde las megalopas de decápodos fueron dominantes (80% de los conteos totales). No se encontraron larvas de bivalvos ni zoesdecápodos en los colectores intermareales. En los colectores submareales, el asentamiento de megalopas cerca de la superficie fue

significativamente mayor que cerca del fondo en ambos extremos de la bahía, aunque en el extremo norte el asentamiento fue siempre mayor en ambas profundidades. Las larvas de bivalvos representaron el 10% de los conteos totales de larvas encontradas en los colectores submareales, con mayores tasas de asentamiento en el extremo norte de la bahía. Las tasas de asentamiento de gastrópodos fueron similares entre extremos de la bahía, tanto en el intermareal como cerca del fondo en el submareal. Las larvas cypriis de cirripedios fueron numéricamente dominantes en los muestreos con redes bongo y epineustónica. Las larvas de gastrópodos y megalopas aparecieron en ambos tipos de muestreos, pero los gastrópodos fueron más abundantes en el estrato de 0 – 20 m, mientras que las megalopas fueron consistentemente más abundantes en el neuston. Se encontró un escaso número de larvas de bivalvos en los muestreos de plancton.

Las correlaciones entre el asentamiento y la abundancia de larvas en el plancton no fueron consistentes entre sitios ni entre profundidades o grupos taxonómicos. El asentamiento intermareal de cirripedios en el extremo norte de la bahía, y el asentamiento cerca del fondo del submareal en el extremo sur, se correlacionaron positivamente con su abundancia integrada a través de la bahía. El asentamiento intermareal en el extremo sur de la bahía estuvo fuertemente correlacionado con el asentamiento submareal cerca del fondo en el extremo norte de la bahía. Se observó una correlación positiva, aunque no significativa, entre el asentamiento submareal de decápodos en el extremo norte de la bahía (ambas profundidades) y la abundancia de larvas en el plancton (0 – 20 m) integrada a través de la bahía.

En conjunto, estos resultados muestran que las observaciones de asentamiento submareal son un mejor *proxy* del suministro larval que aquellas realizadas en el intermareal, y que la profundidad más adecuada para las observaciones depende del grupo taxonómico de interés. En cuanto a la distribución espacial de las observaciones, ésta debiese tener en consideración la configuración de la costa en relación a los principales forzantes físicos. Lograr una comprensión general de cómo cambia el acoplamiento intermareal-submareal-plancton en función del taxón y las condiciones físicas (exposición, forzamiento del viento, batimetría local) es un desafío pendiente. Tal comprensión es clave para evaluar hasta qué punto las tendencias en el reclutamiento de invertebrados marinos resultan de cambios en el plancton, o de cambios en las condiciones que afectan el asentamiento.

Palabras claves: Asentamiento larval, suministro larval, acoplamiento, intermareal-submareal, norte de Chile.

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Journal of Experimental Marine Biology and Ecology

Spatially and taxonomically variable coupling between settlement and planktonic abundance of invertebrate larvae in a small bay

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ABSTRACT

For decades, the settlement of invertebrate larvae on intertidal collectors has been used as a proxy for the supply of competent larvae to shore. However, recent evidence from various coastal regions suggests that a coupling of settlement and supply might be an exception rather than the rule. Here we use a set of concurrent observations of settlement and planktonic larval abundance along a small bay (ca. 3 km) in northern Chile to test (1) whether daily fluctuations in settlement map temporal changes in larval availability, and (2) under which conditions intertidal settlement could be a good proxy for the abundance or settlement of larvae beyond the surf zone. Settlement of four major larval groups (barnacles, gastropods, megalopae, bivalves) was monitored daily with intertidal and subtidal collectors deployed at both ends of the bay, whereas plankton tows with epineustonic (surface) and Bongo nets (0-20 m) were conducted every other day for 10 days, in the austral spring of 2013. Wind velocity and water-column temperature at 3 points along the bay were continuously monitored.

Water-column temperatures exhibited a strong diurnal cycle, with a degree of afternoon surface heating, and along-bay gradient in surface temperatures, that were positively correlated with onshore wind stress. Settlement varied greatly among taxonomic groups and sites/depths. Except for barnacle cyprids, settlement rates were always higher on subtidal collectors, where crab megalopae were numerically dominant (80% of total counts). Megalopae and bivalves were absent from intertidal collectors. In the subtidal, megalopae settled at significantly higher rates on near-surface collectors at both ends of the bay, although north-end settlement was always higher at both depths. Bivalve larvae accounted for 10% of total counts in subtidal collectors, and settled at higher rates at the north end of the bay. Gastropods settled at similar rates on intertidal and near-bottom subtidal collectors, with no apparent differences in settlement across the bay.

Barnacle cyprids were numerically dominant in both epineustonic and Bongo net samples. Gastropod larvae and crab megalopae were found in both types of samples, but gastropods were more abundant within the 0-20 m layer and megalopae were consistently more abundant in the neuston. Bivalves were almost absent from plankton samples. Associations between settlement

observations, and between settlement and planktonic abundance, were not consistent among sites, depths, or taxonomic groups. Intertidal settlement of barnacle cyprids at the north end of the bay, and near-bottom subtidal settlement at the south end, were positively correlated with their epineustonic abundance integrated across the bay. Intertidal settlement at the south end was strongly correlated with near-bottom subtidal settlement at the north end. Subtidal settlement of crab larvae at the northern end of the bay (both depths) was positively, though not significantly, correlated with their planktonic abundance (0-20 m layer) integrated across the bay.

Together, these results show that if settlement observations are to be used as a proxy for the supply or availability of larvae in the plankton, the best choice of depth depends on the taxonomic group of interest, whereas the best choice of shore location depends on the configuration of the coast and advective conditions in the study area. Achieving a general understanding of how the intertidal-subtidal-plankton coupling changes as a function of taxon and physical conditions (exposure, wind forcing, local bathymetry) is a pending challenge. Such understanding is key to assess the extent to which recent trends in recruitment of marine invertebrates result from changes in the plankton, or from changes in the conditions that affect settlement.

Keywords: Larval settlement, larval supply, coupling, nearshore, northern Chile

1. INTRODUCTION

Understanding recruitment and its variability is essential to understand the dynamics of marine populations (Thorson, 1950). This is particularly challenging in the case of benthic species that are geographically widespread and whose life cycle includes a planktonic phase that is susceptible to transport mediated by currents (Gaylord and Gaines, 2000; Pineda et al., 2007; Roughgarden et al., 1988). Complex patterns of larval transport in coastal waters (Largier, 2003; McManus and Woodson, 2012; Siegel et al., 2008) combined with varying rates of mortality in the plankton (Morgan, 1995; Rumrill, 1990; White et al., 2014) often decouple local abundance of adults from the supply of competent larvae to a given site (Gaines et al., 2007).

Upon settlement on benthic habitat, biotic and abiotic sources of post-settlement mortality may substantially modify the abundance and spatial distribution of specimens that will eventually reach sexual maturity and effectively contribute to population renewal (Gosselin and Qian, 1997; Thorson, 1966). Thus, the spatial structure, renewal, and persistence of marine populations depend on a combination of factors that include larval survival and transport during planktonic development, larval supply to suitable habitat, settlement conditions, and post-settlement survival.

For many coastal invertebrates that are either sessile or have limited mobility as adults (e.g. mussels, barnacles, sea urchins, crabs), the dominant view over the past decades has been that their recruitment depends to a large extent on the supply of competent larvae to suitable habitats (Pineda et al., 2010; Roughgarden et al., 1988). Various swimming behaviors displayed by larval invertebrates in the plankton interact with physical phenomena that influence advective conditions in nearshore waters, and determine patterns of along- and cross-shore larval transport (Largier, 2003; McManus and Woodson, 2012; Nickols et al., 2015; Pineda et al., 2007). Upon successful completion of planktonic development, the (relatively) few larvae that survive to reach a competent stage must traverse the distance that separates them from suitable settlement habitats. Multiple mechanisms have been proposed as critical for the cross-shelf translocation required to go from nearshore plankton to onshore settlement. For instance, the relaxation of upwelling winds has been often proposed to underlie mesoscale patterns of onshore transport

and intertidal settlement (e.g. Farrell et al., 1991; Narváez et al., 2006; Wing et al., 1998). At smaller scales, the onshore transport or nearshore retention of larvae appear to be mediated by more localized and directional phenomena such as the sea breeze, surface waves, and internal waves (e.g. Hendrickson and MacMahan, 2009; Navarrete et al., 2015; Shanks et al., 2015; Walter et al., 2014; Woodson et al., 2007).

Many studies conducted over the past decades, and aimed at determining how and which of these phenomena drive larval supply to coastal habitats, have relied on observations of larval settlement on intertidal substrate or artificial collectors as a way to obtain a proxy for larval supply (e.g. Barth et al., 2007; Gaines and Roughgarden, 1985; Hatton, 1938; Navarrete et al., 2008; Pineda, 1994a; Shanks, 2009, 1986; Tapia and Navarrete, 2010). In all of these studies, it has been assumed – implicitly or explicitly – that the number of larvae reaching the shoreline at a given site is a reflection of their abundance in the nearshore plankton (Pineda et al., 2010). In other words, it has been assumed that what settles at the shoreline is a representative sample of what is available in the plankton at a given time and that, by observing settlement and its spatial-temporal variability, something can be inferred about the variability in larval supply to the shoreline and the physical processes that determine it (Pineda, 2000; Pineda et al., 2010). However, a growing number of studies conducted more recently indicate that the number of larvae settling at a given site does not necessarily represent the abundance – or even the presence – of those larvae in the nearshore plankton (Navarrete et al., 2015; Rilov et al., 2008), whereas others have shown that the coupling of settlement and supply is strongly dependent on the site, taxon, and even tidal height at which the comparisons are made (Dudas et al., 2009; Hoffmann et al., 2012). Defining the scales, taxa, and physical conditions for which larval supply and settlement can be considered as coupled processes is a challenge that warrants further investigation, considering the need to better understand the constraints that current and future physical variability in the coastal ocean may impose on the structure and dynamics of marine communities.

Recent studies conducted in small bays that are embedded in upwelling systems show that large differences in settlement rates may appear consistently over distances of a few kilometers (e.g. Bonicelli et al., 2014b; Hoffmann et al., 2012; Pfaff et al., 2011). Small bays provide an

excellent setting to study the scale of settlement-supply coupling, given the changes in topographic and hydrodynamic conditions that may be found over short distances. Recent studies around a small bay in central Chile have shown that spatial-temporal patterns of barnacle settlement can be explained by inter-annual and intra-seasonal fluctuations in the strength and orientation of coastal winds relative to the shoreline (Bonicelli et al., 2014b; Tapia and Navarrete, 2010). Spatial heterogeneity in larval settlement (e.g. Ladah et al., 2005) may also result from spatially-heterogeneous onshore transport, probably influenced by spatial changes in the relative importance of the surf zone as a final hydrodynamic hurdle to be cleared (Navarrete et al., 2015; Rilov et al., 2008; Shanks et al., 2015). However, intertidal settlement observations are not sufficient to achieve a mechanistic understanding of the near field physical-biological interactions that finally determine the pattern of larval arrival and settlement on the shoreline. Fluctuations in settlement must be examined jointly with information on larval presence and abundance in the nearshore plankton, as well as physical forcing that may modify patterns of larval transport and onshore delivery. In this contribution, we attempt to clarify the connection between the settlement of invertebrate larvae and their abundance in the plankton by examining concurrent observations (physical and biological) conducted along a small bay of northern Chile. Additionally, we examine the effect of day-to-day changes in wind forcing on thermal conditions along the bay, on the abundance and distribution of planktonic larvae, and on the spatial pattern of larval settlement.

2. MATERIALS AND METHODS

The study was conducted in Totoralillo Norte Bay (TNB), located at 29.5°S on the northern Chile coast (Fig. 1a), over a 10-day period during late austral spring (29 November - 9 December 2013). This is a semi-exposed NW facing bay that spans ca. 3 km between its northern and southern tips, with depths that range between 5 and 50 m (Fig. 1b). A small island and the associated shallows near its southern tip constrain the actual mouth of the bay to ca. 1.5 km (Fig. 1b), which is likely to limit water exchange with open waters. Surface water temperatures range between 15 and 18°C in spring-summer (Tapia et al., 2014). The shoreline exhibits different degrees of exposure to wind and wave action, and comprises both hard substrate and sandy beaches at both ends of the bay.

2.1. Environmental data

Wind speed and direction records were obtained from a weather station installed on a pier near the bay's southern tip (Fig. 1b), at ca. 5 m above mean sea level. To assess the consistency of local winds with regional patterns, wind records for three other coastal sites located within 30-100 km of the TNB (Fig. 1a) were obtained from CEAZA's meteorological service (www.cezamet.cl).

Continuous records of water temperature at different depths were obtained with strings of HOBO U22 temperature loggers (Onset Computer, USA) deployed at 3 different locations in the bay (Fig. 1). Loggers were positioned at 1, 7, 14 meters above the bottom (mab) at the north mooring; at 1, 7, 10, 15, 21 mab at the center mooring; and at 1, 7, 10, 15, 23 mab at the south mooring. All loggers were programmed to record temperature at 10 min intervals. Additionally, HOBO U20 pressure sensors (Onset Computer, USA) were attached to each mooring at 1 mab.

2.2. Biological sampling

To characterize the temporal and spatial variability of settlement in the most representative groups of benthic invertebrates (barnacles, gastropods, decapods, bivalves), collectors made of plastic mesh Tuffy® (see Navarrete et al., 2015 and references therein) were deployed in the intertidal and subtidal at both ends of the bay (Fig. 1). To monitor subtidal settlement, collectors were attached to lines moored at ca. 20 m depth on each end of the bay (Fig. 1b), and recovered/replaced daily by a diver. Sets of 4 replicate collectors were deployed at two depths on each mooring: 1 m below the surface and 1 m above the bottom. Intertidal settlement was also monitored at both ends of the bay, where collectors were attached to rock benches at mid-low intertidal height using stainless steel screws affixed to the rock with plastic anchors. Four replicates were deployed at each site as well. Tuffys were first deployed on 29 November, and replaced each morning at 9 AM local time (UTC-3) until 9 December.

To estimate the abundance of larvae in the plankton, and to characterize their spatial distribution and temporal variability, a grid of 7 stations arranged along and across the bay (Fig. 1b) was

sampled every other day. At each station, oblique tows were conducted from 20 m depth up to the surface, using a Bongo net with 50 cm diameter mouth and 300 μm mesh. Concurrently, an epineustonic net with 100 by 50 cm rectangular mouth and 210 μm mesh was towed over ca. 150 m at an average speed of 1.6 knots. Volume of water filtered on each plankton tow was estimated with a mechanical flowmeter (General Oceanics, USA) attached to the net's mouth.

All zooplankton samples were preserved in 70% ethanol and sorted in the laboratory under a dissecting microscope. Invertebrate larvae were enumerated and classified into major taxonomic groups (e.g. cirripedia, decapoda, bivalvia, gastropoda). In some cases it was possible to identify larvae to the species level, such as the crabs *Cyclograpsus cinereus* and *Taliepus dentatus*, and the gastropod *Concholepas concholepas*. Larval counts were standardized as number of individuals in 100 m^3 .

2.3. Data analysis

From the records of wind speed and direction gathered by the meteorological station, zonal and meridional components were obtained and used to compute the main axis of wind variability, which corresponded to 12° east of geographic north and roughly along the main axis of the bay (see Fig. 1b). Wind vectors were rotated into this new coordinate system, and used to compute alongshore (v) and cross-shore (u) components of the wind. In this new coordinate system, positive values of v corresponded to wind blowing towards the northern tip of the bay, whereas positive values of u corresponded to wind blowing onshore. Wind stress was computed following Large and Pond (1981), and used to produce daily series of cumulative stress for each wind component.

Temperature records retrieved from moored loggers were time-averaged to produce hourly time series at each depth. As a proxy for a time series of thermal stratification, surface-to-bottom differences were computed. Additionally, temperature records from all depths were used to produce a time series of depth for the 14°C isotherm at each mooring location. To conduct this procedure, heights above the bottom of temperature loggers were converted into meters below

the surface using the mean depth recorded at each mooring from pressure sensor data. Depth of the 14°C isotherm at each time step of the series was found using linear interpolation.

Diurnal harmonic functions (i.e. period 24 h) were fitted to near-surface temperature records using a least-square procedure (Emery and Thomson, 1998). Residuals from this fit summed over the afternoon hours for each day were used as a proxy for overheating due to aperiodic physical forcing. Given the short duration of this study, diurnal changes in surface temperature due to solar heating alone were expected to be consistent from day to day. Deviations from a diurnal harmonic should occur when surface temperatures were affected by factors other than solar heating, i.e. cloud cover, strong wind. Overheating was assessed as the residuals from a diurnal harmonic fit summed over the 12:00-21:00 window for each day, and correlated with cumulative wind stress computed over the 12:00-18:00 window. Linear correlation was used to test for associations between thermal structure of the water column and wind forcing in the bay. Daily changes in cumulative wind stress were compared with indices of (1) thermal stratification, (2) horizontal gradients in near-surface temperatures, and (3) overheating of near-surface water (see above).

Maps of larval abundance estimates derived from each plankton tow were produced for each survey. As an index of spatial heterogeneity, log-transformed larval counts from all 7 stations were used to compute the coefficient of variation for each day with plankton observations. The potential relationship between heterogeneity in the distribution of plankton and daily variability in wind forcing was assessed using a linear correlation analysis.

Correlation analyses were also used to test for associations between cumulative wind forcing and the abundance of planktonic larvae integrated across the bay, or their settlement on subtidal and intertidal collectors. Horizontal (north vs. south) and vertical (surface vs. bottom) differences in subtidal settlement rates were also analyzed as a function of physical variability in the bay. To determine the statistical significance of vertical and horizontal differences in subtidal settlement, paired-sample tests were used to compare settler counts in surface vs. bottom collectors at each end of the bay, as well as between ends of the bay for a given depth. When normality assumptions were not met, and data transformations failed to produce

normally-distributed residues, a Wilcoxon signed-rank test was used instead of the paired-sample t test.

Finally, to examine the coupling between subtidal settlement and the abundance of larvae in the plankton, correlation coefficients were computed between settlement rates and the planktonic abundance estimates obtained the day before. This analysis was performed separately for plankton data from tows of the Bongo and epineustonic nets. The computation of correlation coefficients was done repeatedly, using plankton abundance values obtained by integrating data over an increasingly larger spatial range, i.e. sequentially adding stations located farther from the settlement collectors. This approach was followed in order to allow for the fact that settlement on collectors over a 24-hour period may not necessarily reflect instantaneous planktonic abundance near the collectors at the time of sampling, but still bear some relationship with abundance integrated over some spatial scale.

3. RESULTS



3.1. Environmental time series

Wind patterns recorded at TNB were consistent and coherent with those observed at 3 other coastal sites in the region (see Fig. 1a), located at distances that ranged between 22 km (Islote Pajaros) and 100 km (Pt. Lengua de Vaca). Although all correlations were positive and significant, wind at TNB was most highly correlated ($r=0.81$, $p<0.001$) with that measured at Pt. Choros (30 km NW), which in turn was most highly correlated ($r=0.84$, $p<0.001$) with Islote Pajaros (22 km SW of TNB).

Wind exhibited a strong diurnal pattern along its main axis (Fig. 2a-b), which explained 90% of wind variability during the study and was roughly aligned with the bay's longitudinal axis (see Fig. 1). Wind along the perpendicular axis (i.e. cross-shore) showed no clear periodicity (Fig. 2b), although it tended to blow onshore during the afternoon hours and to be calm at night (Fig. 2a and 3a). Together, these diurnal patterns amounted to the wind blowing N-NE during the day and S-SW (i.e. into the bay) at night. On average, diurnal winds reached maximum velocities at

5-6 PM, whereas nocturnal winds were strongest at ca. 3 AM (Fig. 3a). On top of this diurnal pattern of variability, there was a synoptic-scale change in wind conditions over the course of our study, consisting mainly of stronger nighttime winds blowing into the bay during three consecutive nights (Fig. 2a, 2-4 December).

Temperature records from all three moorings revealed a dominance of diurnal variability near the surface (Fig. 2c-d), and a stronger influence of semi-diurnal fluctuations near the bottom (Fig. 2e-f). Diurnal changes in surface temperature across the bay were attenuated during the 3-day period with stronger nighttime wind blowing into the bay, which apparently prevented the nocturnal cooling of surface waters typically seen for this bay (Fig. 3b-d), and for coastal waters in general. Near-bottom temperature variability, on the other hand, was enhanced during the same period (Fig. 2e).

Thermal structure of the water column revealed strong thermal stratification, which increased in the afternoon hours at all 3 moorings, and which was always strongest at the most exposed northern site (Fig. 3b-d). A clear diurnal pattern in thermal structure of the water column was driven by the afternoon warming and late-night cooling of near-surface waters. A horizontal gradient in surface warming was apparent along the bay, with consistently warmer temperatures at the northern site. Also, the warm surface layer was consistently thicker at the northern site, and progressively thinner at the center and south moorings (Fig. 3b-d). This can be seen more clearly when the depth of the 14 °C isotherm is compared among moorings (Fig. 3b-d).

The percentage of temperature variability explained by a diurnal harmonic increased towards the north mooring, and was greater near the surface at all three locations. The diurnal harmonic explained 29.1%, 40.5%, and 48.0% of near-surface temperature variability at the south, center, and north mooring, respectively. Near-bottom temperatures showed substantially less influence of a diurnal cycle, with under 10% of temperature variability explained by a diurnal harmonic. Afternoon overheating of near-surface waters at the three moorings was positively correlated with cumulative onshore wind stress over the morning and afternoon hours (9 AM – 6 PM), and more strongly so at the center mooring ($r=0.92$, $p=0.0004$). Finally, daily changes in the

horizontal gradient of near-surface temperatures along the bay, i.e. between the north and south mooring, were positively correlated with cumulative onshore wind ($r=0.98$, $p=0.001$).

3.2. Larval settlement

There were clear differences in timing and rate of settlement among taxonomic groups, as well as among sites and depths (Fig. 4). With the exception of barnacle cyprid larvae (Fig. 4a,e), settlement rates were always higher on subtidal collectors, especially for crab megalopae (Fig. 4c,g). Megalopae were the most abundant group of larvae found in the subtidal collectors (80%), whereas bivalve, gastropod, and barnacle larvae accounted for 10%, 6%, and 4% of total counts, respectively. Bivalve settlers and crab megalopae were absent from intertidal collectors.

Barnacle cyprids accounted for 76% of total intertidal settlers. Subtidal settlement of cyprids did not exhibit bottom-surface or north-south differences over the duration of this study. The second most abundant group settling on intertidal collectors were gastropods (22%), which settled at constant and similar rates on intertidal and near-bottom subtidal collectors (Fig. 4b,f). With the exception of one day with two counts at the northern site, there was no settlement of gastropods on near-surface subtidal collectors.

Crab larvae (megalopae) found in subtidal collectors corresponded mostly to the brachyurans *Cyclograpsus cinereus* (70%) and *Taliepus dentatus* (23%). At both ends of the bay, megalopae settled at higher rates near the surface than near the bottom (one-tailed tests, $p=0.008$ and $p=0.012$ for north and south end, respectively), and overall were significantly higher at the northern mooring (one-tailed Wilcoxon test, $p=0.016$ and $p=0.004$ for bottom and surface settlement, respectively).

Unlike crab larvae, subtidal settlement of mussels was greater near the bottom (one-tailed paired t test, $p=0.014$) at the bay's northern end (Fig. 4d,h). Settler counts near the surface at the southern mooring were too low to conduct a proper statistical comparison between surface and bottom settlement for bivalves. The across-bay comparison of bottom settlement for mussels

showed significantly higher settlement rates at the northern end of the bay (one-tailed paired t test, $p=0.020$).

Wind stress integrated over the 24-hour periods of collector deployment appeared to have a consistent effect on the settlement of two of the four types of larvae considered in this study. Subtidal settlement of megalopae at the northern end of the bay increased on days with stronger onshore winds, and reached minimum values when the cross-shore wind component was weakest. This positive correlation ($r=0.747$, $p=0.033$) was specific for the near-bottom subtidal settlement of megalopae (Table 1 and Figure S1). At the same location and depth, settlement of bivalves was negatively correlated with cross-shore wind stress ($r=-0.859$, $p=0.006$). Maximum rates of bivalve settlement were found when the onshore wind was weakest, and settlement rates dropped to near-zero when the cumulative onshore wind stress surpassed values of ca. 0.3 Pa (Figure S1). A third significant correlation was found for intertidal settlement of cyprids at the bay's southern tip and alongshore wind stress (Table 1). However, an examination of the corresponding scatterplot indicated that the strong correlation was due to an anomalous observation rather than to a consistent relationship (Figure S1).

3.3. Larval abundance in the plankton

Barnacle cyprids were the most abundant group found in the neuston (Fig. 5a-e), reaching ca. 200,000 individuals per 100 m³ and concentrated at the northern section of the sampling grid at the beginning of the study (Fig. 5a). By the third day, cyprid abundance had decreased by two orders of magnitude, and the distribution had shifted to the southern, inner section of the bay (Fig. 5b). On subsequent days, cyprids became less abundant and mostly concentrated inside the bay (Fig. 5c-e). Coefficients of variation computed as an index for spatial heterogeneity ranged between 0.38 and 1.34 for these larvae. Gastropod larvae were substantially less abundant in the neuston than cyprids (<200 indiv./100 m³), and exhibited more heterogeneous spatial distributions (see coefficients of variation in Fig. 5). Almost half of the collected gastropod larvae (46.4%) corresponded to the commercially important muricid *Concholepas concholepas* commonly known as 'loco'. The abundance of gastropod larvae was less variable from day to day than for cyprids, and their distribution was mostly concentrated at the northern

section of the sampling grid (Fig. 5f-j). Neustonic megalopae were even less abundant than gastropod larvae (<30 indiv./100 m³), exhibited a relatively homogeneous distribution across the bay (Fig. 5k-o), and were numerically dominated by the brachyuran *Pisoides edwardsi* (19.3%) and the anomuran *Emerita analoga* (24.7%). Mussel larvae were found in the neuston only on two instances (unidentified veliger stages), and in very low numbers compared to the other taxa (Fig. 5p-t).

Cyprids collected within the top 20 m with a Bongo net were more abundant than those collected from the neuston (Fig. 5a-e and 6a-e), exhibited more homogeneous spatial distributions (coefficients of variation ~ 0.2), and appeared more consistently contained within the bay than those found in the neuston. A similar vertical pattern was observed for gastropod larvae, which were always more abundant within the top 20 m than in the neuston (Fig. 6f-j), and were numerically dominated (98.9%) by the muricid *Concholepas concholepas*. As for their spatial distribution, it varied from being concentrated mostly at the northern section of the bay during the first half of the study to a more homogeneous distribution during the second half (Fig. 6f-j). Megalopae in the 0-20 m depth range were less abundant than in the neuston and exhibited a less homogeneous distribution across the bay (Fig. 6k-o). On most days, megalopae were concentrated at 2-3 of the 7 stations of the sampling grid, and there was no clear numerical dominance of a particular group. Finally, bivalve larvae in the 0-20 m water column were absent in all but one sampling day (6 December, Fig. 6s), at which time they were concentrated at the southern, more protected end of the bay.

When temporal changes in spatial heterogeneity were compared with cumulative wind stress computed along the two main axes, a strong negative correlation was found for gastropods sampled with the Bongo net and alongshore wind ($r=-0.92$, $p=0.027$). This suggests that gastropod larvae within the top 20 m of the water column are more homogeneously distributed when the wind blows more strongly towards the bay's north end. No other group of larvae exhibited a relationship between their spatial distribution and wind forcing (Table 2). Finally, there were no significant correlations between temporal changes in the planktonic abundance of larvae – integrated along the sampling grid – and cumulative wind forcing (see Table S1).

3.4. Coupling of settlement and larval abundance

In general, intertidal settlement was decoupled from subtidal settlement – both near the surface and near the bottom – at both ends of the bay (Table 3). The exception to this pattern was the strong positive correlation ($r=0.892$, $p=0.007$) between the settlement of cyprids at the south end of the bay and near-bottom subtidal settlement at the north end. Cyprids were the only group for which intertidal settlement was correlated with planktonic abundance, with strong positive correlations ($r>0.97$, Fig. 7a) between intertidal settlement at the north end of the bay and epineustonic abundance integrated over distances of 0.6 to 2.2 km (i.e. beyond the single plankton station that was closest to the intertidal site). Although intertidal settlement of cyprids at the southern end of the bay also exhibited positive correlations with epineustonic abundance integrated over distances of 0.5 to 1.9 km ($r>0.8$, Fig. 7c), correlations were not statistically significant.

As for the coupling of subtidal settlement and planktonic abundance, near-surface settlement of cyprids at the north end of the bay exhibited high but non-significant positive correlations with epineustonic abundance (Fig. 8a). Correlations were high ($r>0.96$) and significant between near-bottom settlement of cyprids at the south end of the bay and epineustonic abundance integrated over distances of 1.6-2 km (Fig. 8d). Near-bottom subtidal settlement of gastropods was negatively/positively correlated with planktonic abundance at the north/south end of the bay, although none of the correlations were significant (Fig. 8b,e). Finally, subtidal settlement of megalopae at the north end of the bay was positively correlated with planktonic abundance estimated from both nets and across the range of distances used for abundance integration (Fig. 8c). Correlations were higher for Bongo net estimates, and were similar between near-surface and near-bottom (Fig. 8c). However, none of these correlations were significant. Subtidal settlement of megalopae at the south end of the bay exhibited a less consistent pattern of correlation with planktonic abundance estimates, and only near-surface settlement appeared strongly correlated with Bongo-derived abundances at scales of 0.5 to 1.5 km (Fig. 8f).

4. DISCUSSION

Historically, the assumption has been made that temporal patterns of larval settlement are correlated with the fluctuations in larval supply to shoreline habitats, and that supply is a function of larval availability (i.e. abundance) in the nearshore plankton (Pineda, 2000; Pineda et al., 2010). These putative connections, however, are anything but simple and general. First, for a competent larva to move across the surf zone and finally reach the shoreline, its behavior must interact with the coastal physical phenomena that mediate cross-shelf transport of water and suspended material: wind, surface waves, and internal motions (Bonicelli et al., 2014b; Liévana MacTavish et al., 2016; Navarrete et al., 2015; Pineda, 1991, 1994b, 2000). Such transport is highly directional, strongly influenced by factors such as local topography, bathymetry, and shoreline orientation. Considering that all of these factors are susceptible to change in space, and especially around a bay, it follows that the function connecting planktonic larval abundance (i.e. availability) and larval supply must vary in space, and over scales that may be as small as the bay in which our study was conducted. Furthermore, swimming behavior relative to onshore-moving hydrodynamic features is critical for the transport of larvae to settlement habitats (Helfrich and Pineda, 2003; Pineda, 1994b; Scotti and Pineda, 2007). Since vertical distribution and swimming capabilities of invertebrate larvae differ substantially among taxonomic groups (Chia et al., 1984; Pineda, 1999, 1994b), a function that links nearshore planktonic abundance and settlement is thus expected to be taxon-dependent.

Upon arrival to the shoreline, swimming behavior of competent larvae prior to settling also differs among taxonomic groups. In addition to the classical work illustrating how polychaete and barnacle larvae may explore the substrate prior to attaching permanently (Butman, 1987; Pawlik et al., 1991), recent papers have widened the array of swimming responses that competent invertebrate larvae may display when exposed to nearshore turbulence. Gastropod larvae may switch from hovering to diving behavior when exposed to a scale of turbulence similar to that produce by the interaction of tidal currents with aggregations of adults of the same species (Fuchs et al., 2007, 2004; Fuchs and DiBacco, 2011). Larvae of intertidal mussels, on the other hand, have been hypothesized to respond to surf zone turbulence by sinking and remaining at the sediment–water interface, where the final stretch of their onshore transport is

mediated by wave action (Navarrete et al., 2015). Finally, the availability of suitable substrate has been shown to affect the settlement rate per unit area of some intertidal species (Pineda and Caswell, 1997; Von Der Meden et al., 2012), and could further distort the supply-settlement relationship for some taxa.

Numerous papers have documented and analyzed temporal variability of intertidal settlement, both in Chile and elsewhere (e.g. Hoffmann et al., 2012; Pineda, 1994a; Porri et al., 2006; Tapia and Navarrete, 2010). However, only a few articles have shown concurrent observations of settlement on the intertidal and subtidal, together with observations on planktonic abundance of the same larvae (Dudas et al., 2009; Pfaff et al., 2015; Rilov et al., 2008). Although comparatively our observations span a brief period during a single settlement season, they do show spatial and taxonomic discrepancies that are consistent with recent work conducted under similar oceanographic conditions (Pfaff et al., 2015).

Together, our results show that whether subtidal or intertidal settlement are a better proxy for the availability of larvae in the plankton depends on the taxon and coastal configuration of the study area. Settlement observations indicate that even in a small bay there can be consistent spatial differences in settlement patterns, both horizontally (north vs. south end of the bay) and vertically (near-surface vs. near-bottom). To some extent, these spatial and taxonomic differences in settlement patterns are determined by local-scale effects of diurnal wind forcing on the cross-shelf transport of surface waters, which appeared to modify the vertical structure of water-column temperatures along the bay.

Thermal stratification across the TNB is affected by local wind forcing in a fashion that is consistent with previous observations in bays of similar size (Bonicelli et al., 2014a), and that suggests onshore transport and retention of warm surface waters (Kaplan et al., 2003; Tapia et al., 2004). The daily overheating of surface waters, regarded as a proxy for the piling up of surface waters against the shoreline, was positively and strongly correlated with onshore wind stress. A strong positive correlation with onshore wind stress was also observed for near-bottom subtidal settlement of megalopae at the bay's northern end. Since megalopae were always more concentrated at the epineuston than within the 0-20 m depth layer, the strong correlation between

their near-bottom settlement and onshore wind forcing could be an indication that wind-driven onshore transport interacts with the vertical distribution of megalopae. Unfortunately, the lack of depth-stratified plankton tows in our surveys does not allow a test of this hypothesis.

The relationship between temperature structure within the bay and wind stress suggests that wind influences the spatial distribution and/or abundance of planktonic larvae in the bay, and potentially the spatial pattern of settlement, as observed in previous work such as Bonicelli et al. (2014b). Although we found no correlation between bay-scale integrated planktonic abundance and wind stress along either component (Table S2), the spatial distribution of some larvae was apparently affected by wind forcing. Gastropod larvae sampled with the Bongo net within the top 20 m exhibited spatial coefficients of variation that were negatively correlated with alongshore wind stress ($r=-0.920$, $p=0.027$), which explained 90% of wind variability during our study and, for this section of the Chilean coast, is strongly diurnal (Muñoz, 2008). Considering the intensification of coastal winds documented for a number of upwelling regions (García-Reyes et al., 2015; García-Reyes and Largier, 2010), and their implications for larval transport over scales of tens to hundreds of kilometers (Aiken et al., 2011), the effect of more intense diurnal wind forcing on the nearshore distribution and supply of competent larvae to littoral habitats is a topic that warrants further investigation.

Up to this point, there has been an emphasis on the use of settlement information as a proxy for patterns of transport and scales of dispersal in the coastal ocean (*sensu* Pineda et al., 2007). Exploring these questions has clear value in terms of ecological knowledge. However, establishing the relationship between changes in the abundance of larvae in the plankton and their settlement on a given surface is also of great interest for certain commercial activities, such as aquaculture in coastal areas. For instance, the mussel aquaculture industry in southern Chile is not based on culturing competent larvae in hatcheries. Rather, their production of mussels depends entirely on the collection of “seeds”, i.e. competent larvae, by collectors deployed throughout the Inner Sea of Chiloe region. Drops in the collection of mussels seeds in recent years have been linked to a change in the abundance of planktonic abundance, which in turn have been attributed to a change in the variability of chlorophyll-a (Lara et al., 2016). Little is known, however, about the potential effect that other environmental changes in the region (e.g.

wind patterns, freshwater inputs, water-column stratification) may have on the vertical distribution and swimming behavior of larvae, which may affect the relationship between planktonic abundance and “effective supply” to the collecting structures. Such knowledge would allow tackling questions such as “what is the threshold concentration and set of hydrographic conditions that warrant the deployment of collectors for productive purposes?”. In summary, our results support the notion that a connection between settlement and supply depends strongly on the taxonomic group and location/depth of interest. The widely used intertidal settlement is often decoupled from day-to-day changes in planktonic larval abundance, likely due to small-scale physical constraints such as local bathymetry, wave exposure, and substrate type. If settlement observations are to be used as a proxy for the supply or availability of larvae in the plankton, the best choice of depth depends on the taxonomic group of interest, whereas the best choice of shore location depends on the configuration of the coast and advective conditions in the study area. Achieving a general understanding of how the intertidal-subtidal-plankton coupling changes as a function of taxon and physical conditions (exposure, wind forcing, local bathymetry) is a pending challenge. Such understanding is key to assess the extent to which recent trends in recruitment of marine invertebrates result from changes in the plankton, or from changes in the conditions that affect settlement.

5. ACKNOWLEDGMENTS

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7. FIGURE LEGENDS AND TABLES

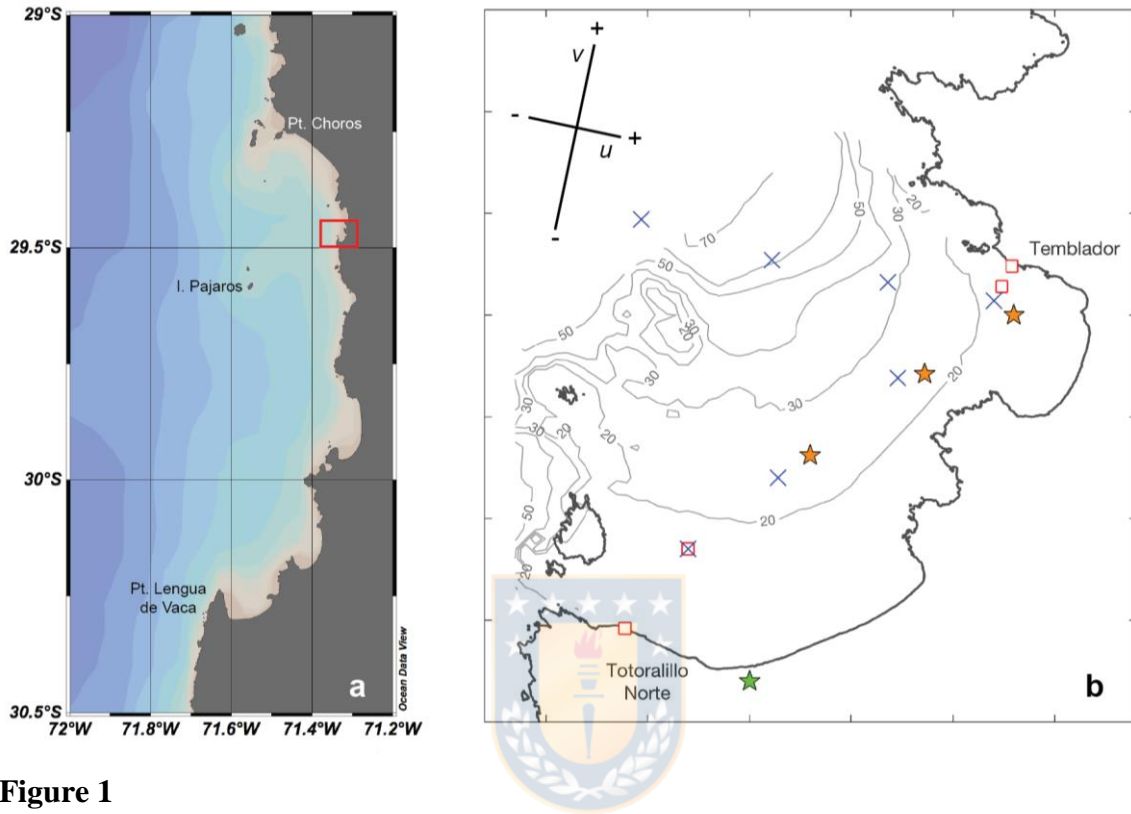


Figure 1

(a) Location of Totoralillo Norte Bay in central-northern Chile, and (b) detailed view of the bay and its bathymetry, indicating the location of wind measurements (green star), temperature moorings (orange stars), subtidal and intertidal settlement collectors (red squares), and plankton sampling (blue crosses). The black lines on the upper left corner of (b) show the coordinate system used to rotate wind vectors to obtain alongshore (v) and cross-shore (u) wind velocities. Sites labeled in (a) correspond to wind monitoring stations from the CEAZAmet service (www.ceazamet.cl). Bathymetry data courtesy of Andes Iron.

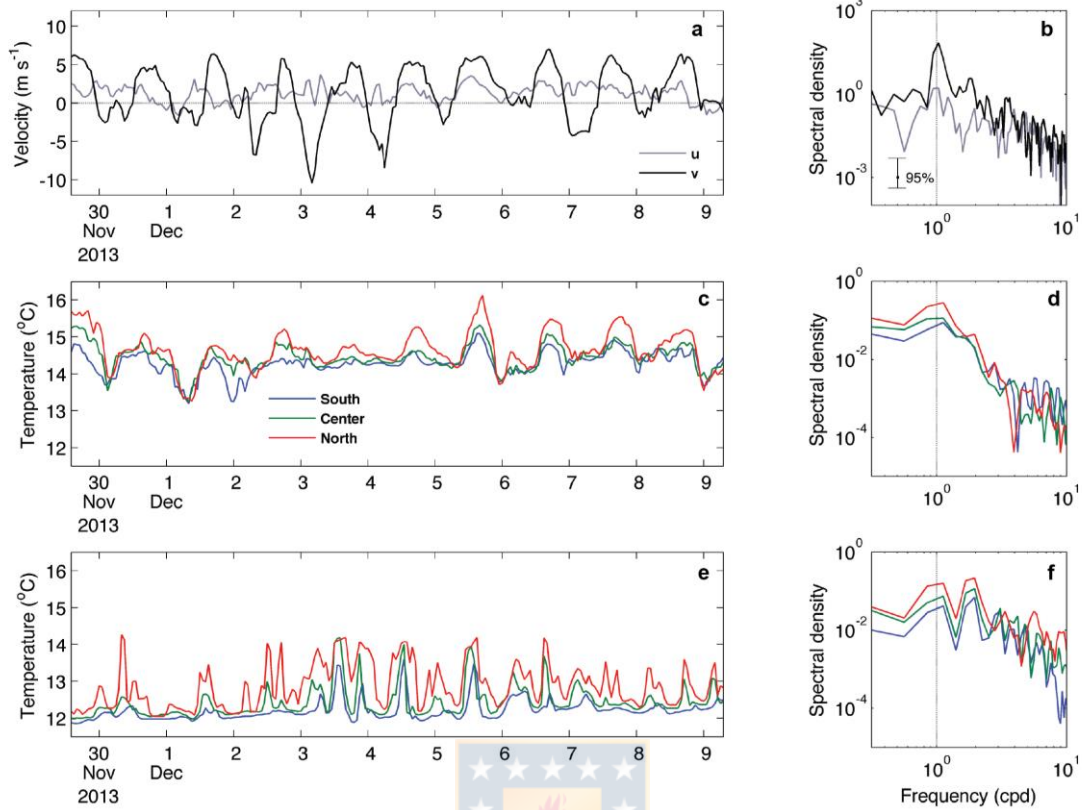


Figure 2

Time series and spectral diagrams for hourly records of wind velocity gathered at the TNB peer (a-b), and water temperatures recorded at the surface (c-d) and bottom (e-f) of the three moorings. Alongshore (v) and cross-shore (u) wind components are shown in black and grey, respectively. The vertical dashed line on the right-hand panels correspond to diurnal periods (i.e. frequency of 1 cycle per day).

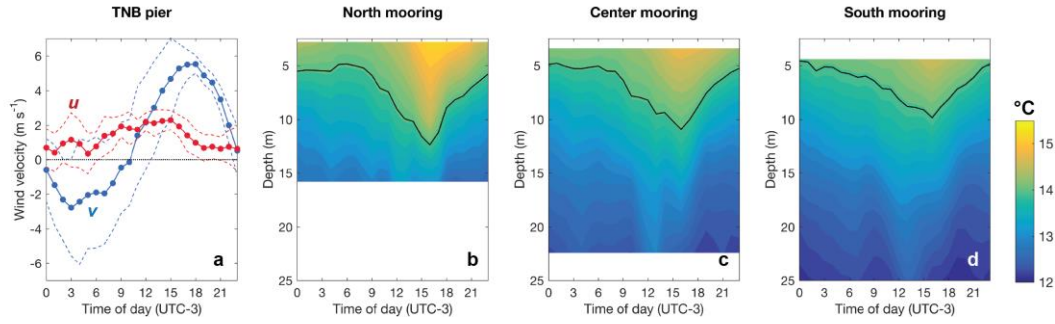


Figure 3

Canonical day of wind velocity components (a) and thermal structure at the north (b), center (c), and south (d) moorings. Black contour corresponds to the 14 °C isotherm.

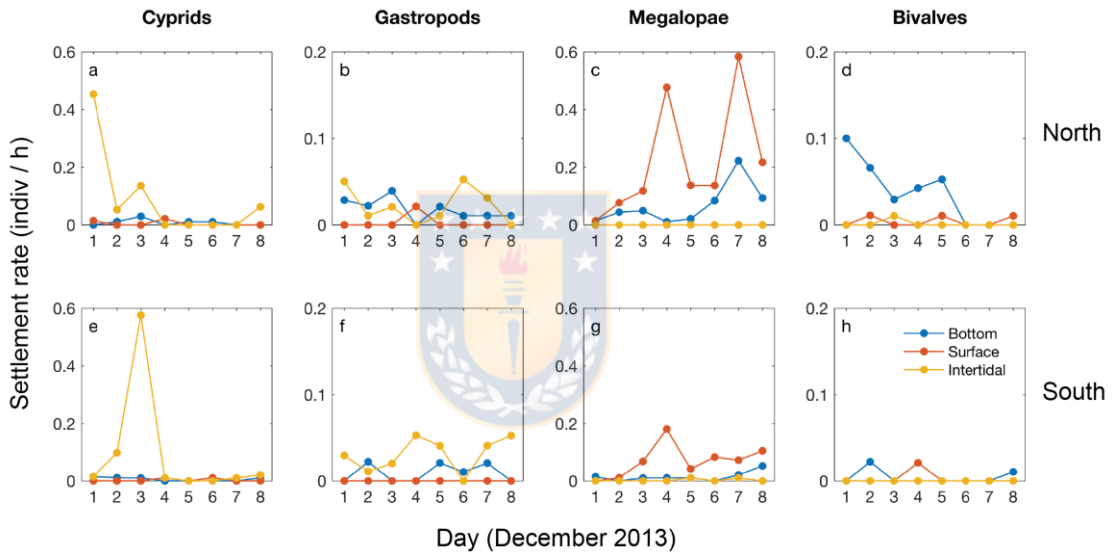


Figure 4

Daily fluctuations in the rate of larval settlement on intertidal and subtidal collectors deployed at the northern (left) and southern (right) ends of Totoralillo Norte Bay in December 2013. Values correspond to the mean count of larvae per collector, divided by deployment time. Note that y-axis scales for gastropods and bivalves are 1/3 of the scales shown for cyprids and megalopae.

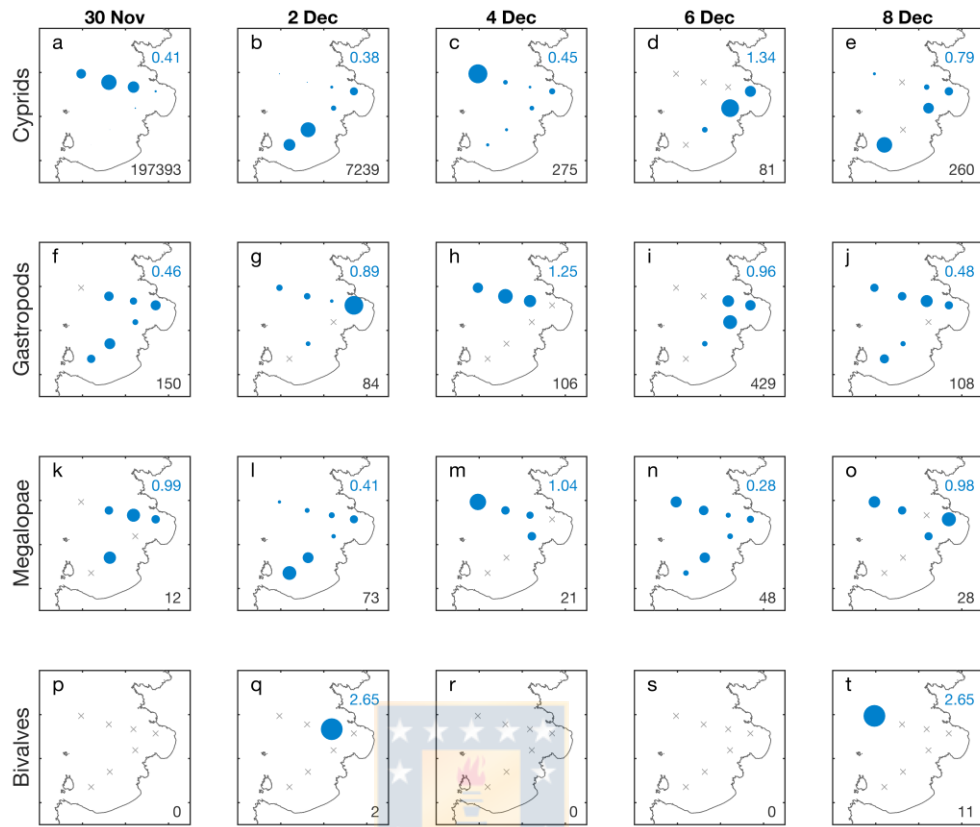


Figure 5

Temporal variability in the daytime spatial distribution of larval invertebrates in the neuston (epineustonic net) of Totoralillo Norte Bay during late spring 2013. The size of circles is proportional to the fraction of total abundance recorded on each day for each taxonomic group. Crosses indicate absence. Numbers on the top-right corner correspond to coefficients of variation computed for the log-transformed abundance ($\log_{10}(x+1)$) of each group on each sampling day. Numbers on the bottom-right corner correspond to total abundance (ind/m^3) computed for each day, i.e. integrated across all 7 sampling stations.

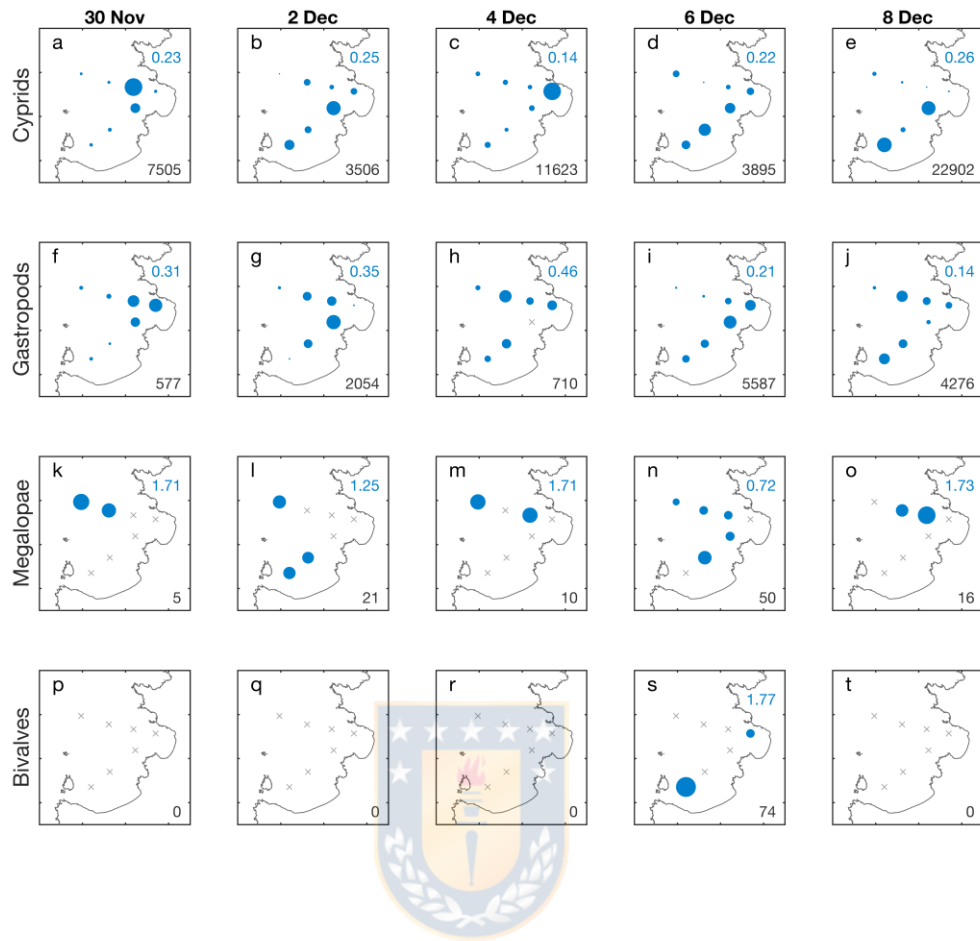


Figure 6

Temporal variability in the daytime spatial distribution of larval invertebrates within the top 20 m (Bongo net) across Totoralillo Norte Bay during late spring 2013. The size of circles is proportional to the fraction of total abundance recorded on each day for each taxonomic group. Crosses indicate absence. Numbers on the top-right corner correspond to coefficients of variation computed for the log-transformed abundance ($\log_{10}(x+1)$) of each group on each sampling day. Numbers on the bottom-right corner correspond to total abundance (ind/m^3) computed for each day, i.e. integrated across all 7 sampling stations.

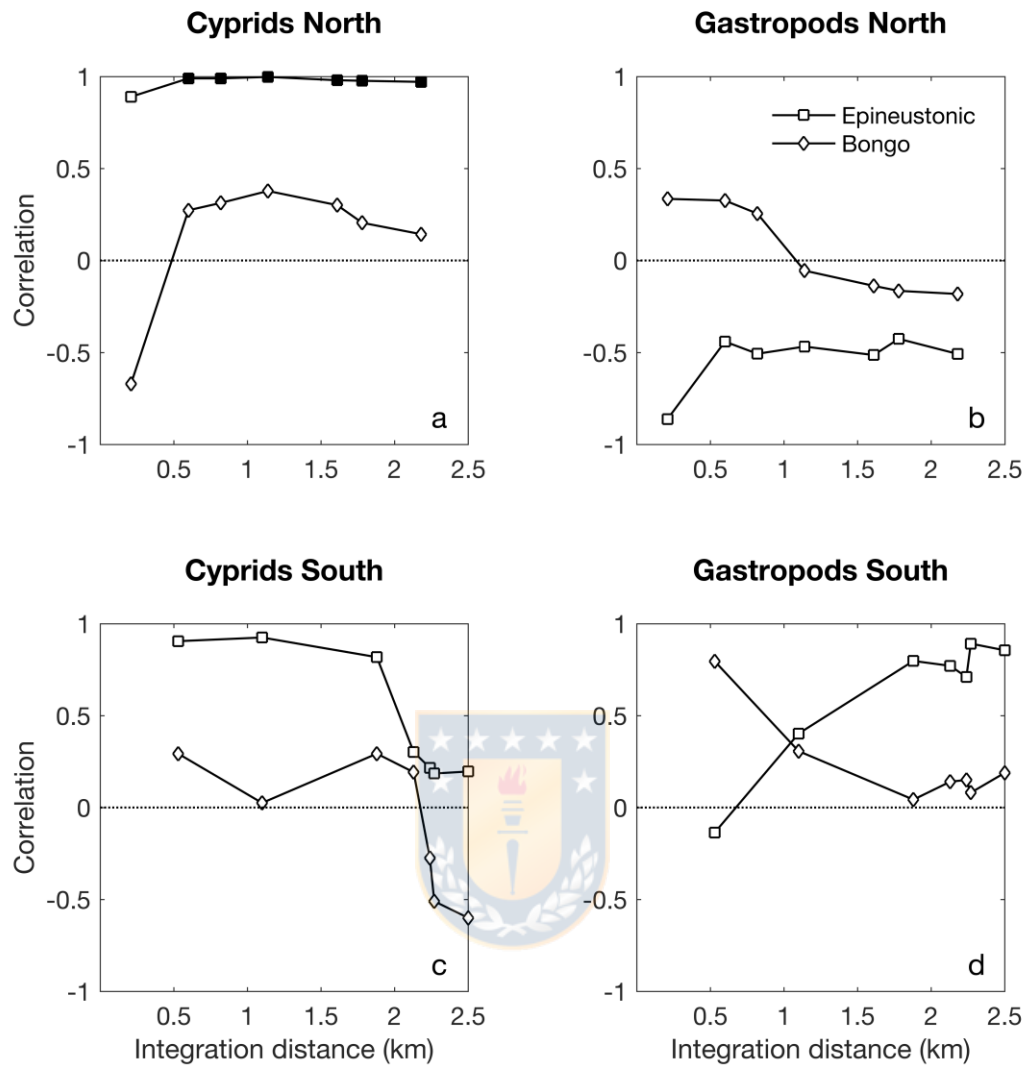


Figure 7

Correlations computed for intertidal settlement versus larval abundance in the plankton integrated over a range of spatial scales. Symbols represent the two different types of plankton net utilized in this study. Correlations at the shortest distance on the x-axis correspond to correlations between settlement at a given collector and larval abundance at the nearest plankton station. Those computed at the longest distance correspond to settlement versus abundance integrated over the 7-station grid. Filled symbols indicate statistically significant correlations with $\alpha=0.05$.

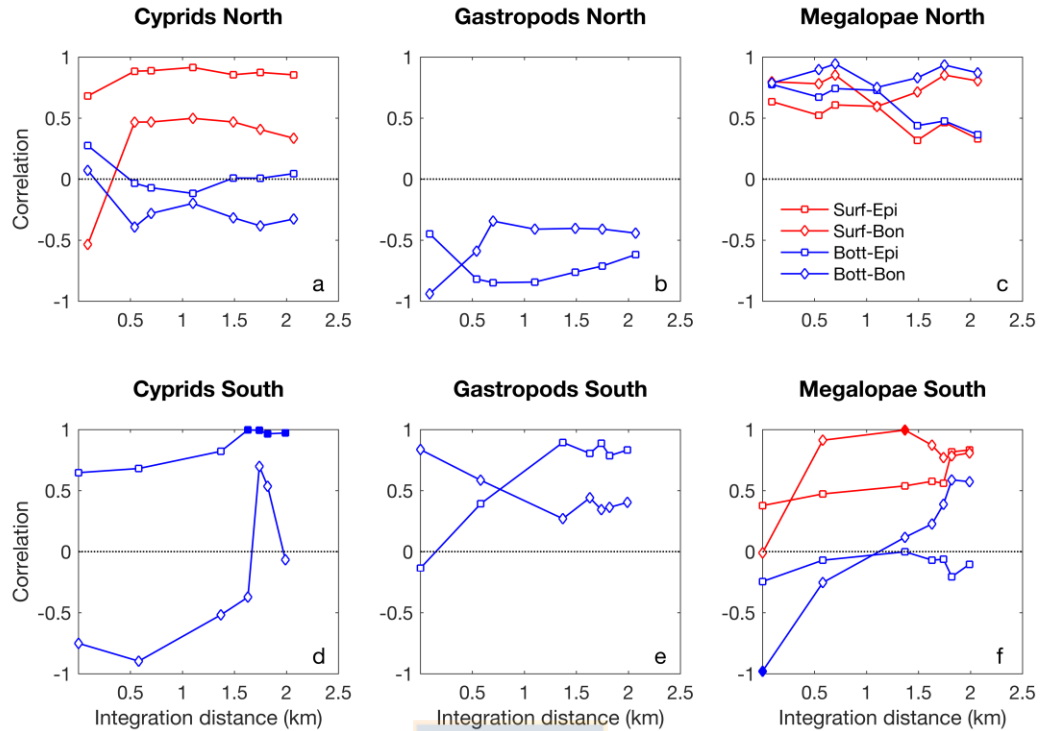


Figure 8

Correlations computed for near-surface (red) and near-bottom (blue) subtidal settlement versus larval abundance in the plankton integrated over a range of spatial scales. Symbols represent the two different types of plankton net utilized in this study. Correlations at the shortest distance on the x-axis correspond to correlations between settlement at a given collector and larval abundance at the nearest plankton station. Those computed at the longest distance correspond to settlement versus abundance integrated over the 7-station grid. Filled symbols indicate statistically significant correlations with $\alpha=0.05$.

Table 1

Pearson's correlation coefficients (and their corresponding p-values below) computed for larval settlement (log10-transformed data) versus cumulative wind stress along the cross-shore (u) and alongshore components (v). See Figure 1 for detail on the orientation of each wind axis.

	Cyprids		Gastropods		Megalopae		Bivalves	
	u	v	u	v	u	v	u	v
North								
Intertidal	-0.496 0.211	-0.152 0.719	0.225 0.592	0.287 0.491				
Subtidal Surface	-0.623 0.099	-0.238 0.570	-0.364 0.375	-0.323 0.435	0.357 0.386	-0.081 0.849	-0.327 0.429	0.312 0.452
Subtidal Bottom	0.339 0.411	-0.557 0.152	-0.004 0.993	-0.453 0.259	0.747 0.033	0.234 0.577	-0.859 0.006	-0.176 0.676
South								
Intertidal	0.269 0.520	-0.822 0.012	-0.202 0.631	-0.088 0.836				
Subtidal Surface	0.035 0.935	0.131 0.758			0.195 0.644	-0.163 0.700	-0.364 0.375	-0.323 0.435
Subtidal Bottom	-0.436 0.281	-0.243 0.562	0.169 0.690	0.357 0.386	0.082 0.848	0.176 0.678	-0.575 0.136	-0.179 0.671

Table 2

Pearson's correlation coefficients and their corresponding p-values for the spatial heterogeneity of planktonic abundance versus cumulative wind stress along its two main axes (see Figure 1). Spatial heterogeneity was assessed as the coefficient of variation of log-transformed abundances found on each sampling day (see Figures 5 and 6).

	Epineustonic net			Bongo net		
	Cyprids	Gastropods	Megalopae	Cyprids	Gastropods	Megalopae
Cross-shore wind	0.618 0.266	-0.557 0.329	-0.109 0.861	0.349 0.565	-0.663 0.223	-0.290 0.636
Alongshore wind	0.699 0.189	-0.665 0.220	-0.243 0.694	0.649 0.236	-0.920 0.027	-0.347 0.568

Table 3

Pearson's correlation coefficients (and their corresponding p-values below) computed for first-differenced time series of intertidal versus subtidal settlement. Only cyprids and gastropods were included in this analysis given absence of megalopae and the low counts of bivalves in the intertidal collectors (see Fig. 4).

	CYPRIDS				GASTROPODS			
	Subtidal North		Subtidal South		Subtidal North		Subtidal South	
	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Intertidal North	0.153	0.069	-0.167	0.487	-0.308	0.259	-	-0.287
	0.744	0.882	0.720	0.268	0.502	0.575		0.533
Intertidal South	-0.530	0.892	-0.383	0.431	0.442	-0.213	-	-0.082
	0.221	0.007	0.397	0.334	0.320	0.646		0.862

8. SUPPLEMENTARY FIGURE AND TABLE

Table S1

Pearson's correlation coefficients and their corresponding p-values for spatially-integrated abundance of planktonic larvae versus cumulative wind stress along its two main axes (see Figure 1).

	Epineustonic net			Bongo net		
	Cyprids	Gastropods	Megalopae	Cyprids	Gastropods	Megalopae
Cross-shore wind	0.082	-0.192	-0.364	-0.057	0.238	0.278
	0.895	0.757	0.547	0.927	0.700	0.650
Alongshore wind	-0.095	-0.541	-0.020	-0.048	0.578	0.608
	0.879	0.346	0.975	0.939	0.307	0.276

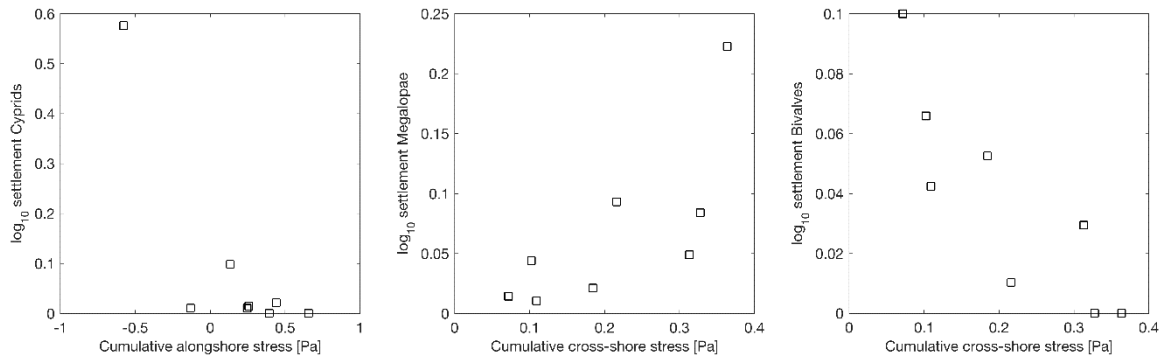


Figure S1

Relationship between settlement and cumulative wind stress for the taxa and sites/depths that produced significant correlations (see Table 1): (left) barnacle cyprids at the intertidal on the south of the bay, (center) megalopae, and (right) bivalves at the near-bottom subtidal on the north end the bay.



5. DISCUSIÓN

Si bien existen numerosos trabajos que documentan y analizan la variabilidad en el asentamiento intermareal en la costa de Chile y regiones similares (Vargas et al. 2004, Ladah et al. 2005, Lagos et al. 2005, Narváez et al. 2006, Porri et al. 2006, Jacinto & Cruz 2008, Tapia & Navarrete 2010, Bonicelli et al. 2014b), esta investigación está dentro de un grupo más reducido de trabajos en que se aborda simultáneamente el asentamiento larval en el intermareal y submareal, además de la presencia y abundancia de larvas en el plancton (ver Rilov et al. 2008, Dudas et al. 2009, Morgan et al. 2009).

En general, el asentamiento de larvas de invertebrados fue mayor en el submareal que en el intermareal. Es importante destacar que nuestros resultados sugieren que el asentamiento intermareal no es predictor del asentamiento en el submareal y que a su vez lo que arriba al submareal no necesariamente refleja lo que se encuentra en el plancton. Las posibles causas de este desacople han sido discutidas por diversos autores (e.g. Pineda 2000, Hoffmann et al. 2012) y entre ellas se encuentran factores tanto biológicos como físicos, tales como el tiempo de desarrollo de las larvas, comportamiento larval en el plancton, competencia de las larvas para asentarse al momento de arribar a la costa, y procesos de micro-escala debidos a la topografía local y su influencia sobre la hidrodinámica de un determinado sitio.

Los decápodos fueron el grupo dominante en el asentamiento submareal y en su mayoría se encontraron cerca de la superficie. Este patrón es consistente con investigaciones previas, que sugieren que estas larvas se encuentran en el neuston, es decir en los primeros centímetros de la columna de agua (Epifanio & Dittel 1982, Yannicelli et al. 2006). Dentro de los grupos dominantes en el plancton de los primeros 20 metros de la columna de agua, los gastrópodos estuvieron entre los más abundantes, y en su mayoría correspondieron a larvas del murícido *Concholepas concholepas*, con una abundancia promedio de ca. 2600 individuos 100 m^{-3} . Esta alta abundancia de larvas en el plancton costero no se reflejó en los conteos de larvas asentadas en los colectores tanto submareales como intermareales. Una explicación plausible para este desacople es que el estado de desarrollo o condición fisiológica de las larvas presentes en el plancton no hayan sido los adecuados. Pineda (2000) y Pineda et al. (2010) discuten la importancia de la competencia larval para el éxito del asentamiento, entendiendo la competencia como la doble condición de haber completado el desarrollo larval en el plancton

y encontrarse en una condición fisiológica adecuada para el proceso de asentamiento y posterior metamorfosis en el bentos. Alternativamente, es probable que aun cuando las larvas hayan estado en una buena condición para asentarse sobre los colectores intermareales, la frecuencia con que éstos fueron recuperados y reemplazados (diariamente) haya sido demasiado alta como para generar el biofilm y señales químicas necesarias para convertir a este sustrato artificial en una superficie suficientemente atractiva para el asentamiento. Determinar si la correlación entre asentamiento y abundancia larval aumenta cuando el asentamiento se monitorea con una menor frecuencia queda como una pregunta pendiente para abordar en futuras investigaciones.

Las larvas recolectadas en el intermareal fueron dos órdenes de magnitud menos abundantes que las recolectadas en el submareal, y correspondieron en su mayoría a larvas competentes de cirripedios, pese a que los colectores de tipo tuffy utilizados en este trabajo no son los que típicamente se utiliza para evaluar asentamiento de este tipo de organismos (ver por ejemplo Tapia & Navarrete 2010, Bonicelli et al. 2014b). Es conocido que el asentamiento larval de invertebrados intermareales se produce en pulsos más que en forma gradual. Dependiendo de las condiciones ambientales de cada temporada, pueden ocurrir uno o varios de estos pulsos de asentamiento, aunque la duración de dichos pulsos también depende de las condiciones ambientales. Es probable que las bajas tasas de asentamiento registradas en el intermareal sean producto de no haber capturado dichos pulsos de asentamiento durante el periodo de muestreo, que representó una fracción pequeña de la temporada de asentamiento de estos organismos (ver Lagos et al. 2007).

Por otro lado, la existencia o falta de correlación entre el asentamiento en colectores submareales y la abundancia de larvas en el plancton no fue consistente entre los grupos de invertebrados considerados en este estudio, o entre extremos de la bahía, dando cuenta del desacople que puede existir entre las larvas de invertebrados que se encuentran en el plancton y lo que arriba al submareal. Las correlaciones significativas detectadas sólo se observaron en el extremo sur de la bahía. El asentamiento submareal de larvas de cirripedios cerca del fondo en el extremo sur de la bahía se correlacionó positivamente con la abundancia integrada de larvas en el neuston, en un radio de integración de entre 1,6 y 2 kilómetros. El asentamiento submareal de larvas de decápodos cerca de la superficie y del fondo en el extremo sur de la BTN se correlacionó significativamente con la abundancia de sus larvas en la columna de agua a distintas escalas de integración espacial. Cerca del fondo, el asentamiento larval se

correlacionó con la abundancia larval en el plancton sólo a escala local, i.e. con la abundancia de larvas en la estación de muestreo más cercana a los colectores, mientras que en los colectores ubicados cerca de la superficie la correlación se observó en un radio de integración cercano a 1,5 kilómetros.

El bajo asentamiento de mitílidos observado en el intermareal, y que determinó la exclusión de este grupo de los análisis estadísticos, se puede atribuir a que el asentamiento de este grupo suele ocurrir preferentemente en verano (Narváez et al. 2006), y no en el periodo de primavera cubierto por este estudio. Es probable también que la trama de las redes de plancton utilizadas no haya sido lo suficientemente fina para capturar larvas planctónicas de mitílidos, cuyas larvas y post-larvas alcanzan tamaños de 120 y 250 μm respectivamente (Ramorino & Campos 1983). Por otro lado, un estudio reciente (Navarrete et al. 2015) reveló que las larvas competentes de al menos dos de los mitílidos más abundantes en el intermareal de Chile central, *Perumytilus purpuratus* y *Semimytilus algosus*, no se encuentran en el plancton cerca de la costa, sino que estarían concentradas en la interfaz agua-sedimento, donde su transporte hasta el hábitat intermareal estaría mediado por el oleaje. Esto podría explicar en parte la ausencia de larvas de mitílidos en los muestreos de plancton de la bahía, que sólo cubrieron el rango batimétrico de 0 a 20 metros, sin considerar el agua de fondo.

En relación al potencial efecto del estrés del viento sobre el asentamiento en la zona intermareal, se observó una correlación negativa entre el asentamiento de cirripedios en el extremo sur de la BTN y la componente v del estrés del viento, lo que sugiere que el viento dirigido hacia el sur de la bahía facilitaría la llegada de larvas de cirripedios al intermareal. Otros estudios también sugieren que el efecto directo del estrés del viento podría mediar el transporte de larvas de cirripedios al intermareal (Bertness et al. 1996, Bonicelli et al. 2014b).

Con respecto al efecto del viento sobre el asentamiento submareal, encontramos diferencias entre grupos taxonómicos tanto en el grado de correlación como en la componente del viento con que el asentamiento se correlacionó más fuertemente. Los resultados sugieren que, mientras el asentamiento de cirripedios responde al forzamiento del viento hacia el extremo sur de la bahía, el asentamiento de decápodos se ve favorecido cuando se intensifica el viento hacia la costa. El hecho que esta alta correlación se observó a escala diaria, y que la mayor densidad espectral observada para la componente perpendicular del viento corresponde a la frecuencia diurna, sugiere que la brisa marina podría ser un factor importante para el transporte

y asentamiento de larvas de decápodos en esta y otras áreas costeras. Trabajos previos en similares latitudes (e.g. Tapia et al. 2004) sugieren que la brisa marina puede mediar el transporte de partículas neustónicas, incluyendo larvas de invertebrados, hasta la línea de costa.

La ausencia de correlaciones significativas entre el asentamiento de algunos grupos y las variables físicas (viento y temperatura del mar) se puede deber a la restringida cobertura temporal de las observaciones y mediciones del presente trabajo, así como al bajo número de asentados de algunos tipos de larvas durante este periodo. Es probable también que no se haya considerado algunas variables físicas y ambientales de potencial importancia para la distribución de pequeña escala de las larvas, tales como corrientes, oleaje, oxígeno disuelto y concentración de clorofila-a en el agua. Estudios recientes han demostrado que existe una fuerte correlación entre el oleaje y el asentamiento de mitílidos (Navarrete et al. 2015), así como entre la turbulencia generada por el oleaje y el comportamiento natatorio de larvas de gastrópodos (Fuchs et al. 2018).

Al igual que en otras bahías de similar tamaño, como la bahía de Cartagena en Chile central (Bonicelli et al. 2014b), se encontraron marcadas diferencias de temperatura entre los extremos de la BTN. Considerando que los anclajes con termistores se instalaron a aproximadamente un kilómetro de distancia entre ellos, la diferencia de temperaturas entre los extremos norte y el sur de la bahía dan cuenta de un fuerte gradiente térmico. Según Bonicelli et al. (2014a), la brisa marina transporta agua cálida hacia el extremo norte de la bahía durante la tarde. Haber detectado que la isoterma de 14°C alcanza su mayor profundidad en horas de la tarde (4 PM), y que su profundidad aumente hacia el extremo norte de la BTN, indica una dinámica consistente entre ambas bahías. Esto también podría sugerir un patrón de transporte advectivo en el plancton superficial, que se vería reflejado en la diferencia entre el asentamiento de colectores superficiales de ambos extremos de la bahía. Si bien se encontró una relación entre el asentamiento de larvas de decápodos y la componente u del viento, esta relación se observó con las larvas asentadas cerca del fondo, no en la superficie. Es probable que lo acotado de la serie de observaciones realizadas haya dificultado encontrar relaciones significativas entre el asentamiento en superficie y el stress del viento, lo que no necesariamente quiere decir que dicha relación no exista.

En conclusión, encontramos una relación entre la abundancia de larvas en el plancton y el asentamiento submareal, pero no entre el asentamiento submareal e intermareal. El

asentamiento submareal se correlaciona con el viento, pero esta relación varía dependiendo del grupo taxonómico. Se hace necesario realizar observaciones durante periodos más prolongados y la inclusión de otras variables que no fueron consideradas en este estudio, pero sin disminuir la frecuencia de observación, para evaluar de una manera más conclusiva esta asociación entre patrones biológicos y forzamiento físico dentro de bahías.



6. CONCLUSIONES

En este trabajo se analizó la abundancia de larvas de invertebrados bentónicos intermareales en el plancton, el asentamiento submareal e intermareal de estas larvas en la bahía de Totoralillo Norte, la variabilidad diaria del estrés viento y de la estructura de la temperatura en la columna de agua, para examinar si existe un grado de acoplamiento entre estas variables. En base a nuestros resultados, podemos concluir que:

- El régimen de temperatura en la BTN presentó un marcado ciclo diurno relacionado significativamente con el estrés del viento en la costa.
- Existe un asentamiento heterogéneo tanto entre los extremos de la BTN como entre profundidades en el submareal.
- Si se busca utilizar el asentamiento submareal como *proxy* de suministro larval, la profundidad adecuada para monitorear el asentamiento dependerá del grupo taxonómico de interés. La elección del sitio de monitoreo debiese considerar las características geográficas de la costa y los forzantes físicos con mayor influencia sobre la advección en el eje perpendicular a la costa.

En relación a las hipótesis planteadas en este trabajo, la conclusión depende del taxón estudiado;

- El asentamiento intermareal se correlacionó positivamente con el asentamiento submareal, pero esto se observó sólo para cirripedios en el extremo sur de la bahía.
- El asentamiento submareal se correlacionó significativamente con la abundancia de larvas en el plancton, esto sólo se observó para las larvas de cirripedios y decápodos.
- La intensificación del viento favoreció el asentamiento de larvas de cirripedios y decápodos, aunque éstos respondieron a componentes distintas del viento.

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