UNIVERSIDAD CATOLICA DEL NORTE
CHILE

Facultad de Ciencias del Mar

Dinámica de poblaciones de *Macrocystis integrifolia* Bory (Laminariales, Phaeophyta) en el norte de chile

Juan Manuel Alonso Vega Reyes

Profesor Guía: Dr. Julio Vásquez C.

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Actividad de Titulación presentada
para optar al
Grado de Magíster en Ciencias del Mar

Coquimbo, 2005

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por

Juan Manuel Alonso Vega Reyes

Fecha:
Aprobado Comisión de Calificación:

Decano

Tesis entregada como un requerimiento para obtener el grado de Magíster en Ciencias del Mar, Facultad de Ciencias del Mar, Universidad Católica del Norte. Sede Coquimbo.

Coquimbo, 2005

Dedicada a

Ana, Anita, Rafael y Manuel

RESUMEN

El objetivo general de esta tesis fue el estudio de los efectos del evento El Niño y de la surgencia costera permanente en la dinámica de las poblaciones de *Macrocystis integrifolia* en el norte de Chile. Para cumplir con el objetivo general fue necesario desarrollar un enfoque mixto, usando distintas metodologías para caracterizar el ámbito de variación del sistema (norte de Chile), así como de la especie en estudio (*M. integrifolia*). Los resultados indican que a corto plazo (un año), *M. integrifolia* presentan un patrón de abundancia estable con una marcada estacionalidad reproductiva (invierno-primavera). Este patrón es modificado a largo plazo (8 años), por las anomalías térmicas causadas por el ciclo El Niño-Oscilación del Sur (ENOS) produciendo variabilidad interanual. Durante la fase cálida del ENOS o El Niño, y dependiendo de la intensidad y magnitud, ocurren procesos de extinción local de *M. integrifolia* correlacionados con la latitud. Sin embargo, áreas con surgencia permanente permiten la persistencia local de *M. integrifolia* durante El Niño, generando una diferenciación latitudinal del impacto a mesoescala, con zonas poco o no afectadas. Aunque disturbios de baja frecuencia y de escasa predictibilidad, como el incremento de la presión de herbivoría por el erizo negro *Tetrapygus niger*, pueden producir procesos de extinción local en condiciones normales o La Niña. Durante la fase fría del ENOS o La Niña, la variación de la temperatura superficial del mar causada por focos de surgencia permanente es la principal fuente de variación a mesoescala, modificando la producción y el crecimiento de las frondas en los esporofitos, pero no en la dinámica de las poblaciones de *M. integrifolia*, que presenta un patrón temporal común. Esto se traduce en cambios estacionales de la abundancia con reclutamientos asociados a la frecuencia y magnitud de la surgencia costera que ocurre a lo largo de toda la costa del norte de Chile con máximos durante primavera y verano, y controlados por factores abióticos (movimiento del agua, disponibilidad de sustrato, temperatura y nutrientes) y bióticos (predación y competencia) sitio-dependiente. Así, los factores abióticos y bióticos, la surgencia costera y el ciclo ENOS interactúan, regulando en múltiples escalas espacio-temporales la dinámica de las poblaciones de *Macrocystis integrifolia* en el norte de Chile. Esto sugiere que en el Pacífico sudamericano, los patrones de distribución y abundancia de *M. integrifolia* durante un evento El Niño es controlada por procesos que operan a escala geográfica que inciden en todas las escalas espaciales menores (efectos descendentes). Post-El Niño, en condiciones normales o La Niña, factores locales producen procesos de inhibición y facilitación que alteran la estructura geográfica poblacional con efectos que se propagan hacia escalas espaciales mayores (efectos ascendentes). Esto se traduce en distintas dinámicas y en un aumento de la heterogeneidad regional de las poblaciones, principalmente hacia latitudes bajas. Finalmente, esto genera diferencias entre las regiones norte y centro-sur del país en las estrategias de vida de *M. integrifolia* o con especies congenéricas (*M. pyrifera*) habitando más al sur (canales y fiordos).

ABSTRACT

The general aim of this thesis was the study of the effects of the El Niño event and of the permanent coastal upwelling in the population dynamics of *Macrocystis integrifolia* in northern Chile. To carry out the general objective of this study, it was necessary to develop a mixed view point, using different methodologies to characterize the environmental variation of the system (northern Chile), as well as of the kelp in study (*M. integrifolia*). The results indicate that at short-term (one year), *M. integrifolia* presents patterns of stable abundance with a marked and seasonal reproductive activity (winter-spring). This pattern is modified at long-term (8 years), due to thermal anomalies caused by El Niño-Southern Oscillation (ENSO) cycle producing interannual variability. During warm phase of this cycle or El Niño, depending of intensity and magnitude, occurred processes of local extinction of *M. integrifolia* correlated with the latitude. However, permanent upwelling areas allow local persistence of *M. integrifolia* during El Niño, generated a latitudinal differentiation of the impact to mesoscale, with areas less or not affected. Although, disturbances of low frequency and low-predictability, as the increment of herbivorous pressure for the black sea urchins *Tetrapygus niger*, can produce local extinction processes in normal or La Niña conditions. During the cold phase of ENSO cycle or La Niña, sea superficial temperature variation caused by permanent upwelling centers is the main variation source at mesoscale, modifying the growth of sporophytes, but not the population dynamics of *M. integrifolia* that present a common temporal pattern. This is translated in seasonal changes of the abundance with associated recruitment to the frequency and magnitude of seasonal coastal upwelling occurring along the coast of the north of Chile (with maximum during spring and summer), and controlled for abiotic (water movement, available substrate, temperature and nutrients) and biotic factors (predation and competition) site-dependence. In this way, abiotic and biotic factors, coastal upwelling, and ENSO cycle interact regulating in multiple spatio-temporal scales the population dynamics of *Macrocystis* in northern Chile. This suggests that in South American Pacific coast the distribution and abundance patterns of *M. integrifolia* during El Niño event are controlled by processes that operate at long-scale, which is reflected in all smaller space scale (descending effects). Post-El Niño, in normal or La Niña conditions, local factor produce inhibition or facilitation processes that alter the geographic structure of populations with effects that propagate on greater space scales (ascending effects). This is translated in distinct dynamics and increase of regional populations heterogeneity, principally toward low latitudes. Finally, this generates different life strategies of *M. integrifolia* among northern and southern populations located along of the coast of Chile or with con-generics species (*M. pyrifera*) habiting more at south (fiords and channels).

AGRADECIMIENTOS

Deseo empezar agradeciendo a los huiros, a los huirales y a los huireros del norte de Chile que fueron la fuente de inspiración para elaborar este "mamotreto". A continuación describo las distintas acepciones de la palabra HUIRO, debido al importante impacto económico, social y cultural que involucra escribirla o comentarla en cualquier situación contingente. (A) huiro es un cigarrillo artesanal que en vez de tabaco es elaborado a base del alcaloide denominado científicamente como *Cannabis sativa*, mejor conocida como marihuana (http://www.mainframe.cl/diccionario/diccionario.php?letra=h). (B) huiro, del quechua "wiru", es el tallo del maíz verde (o caña dulce del maíz). (C) huiro es el nombre común de varias algas marinas muy abundantes en las costas de Chile (http://buscon.rae.es/diccionario/drae.htm), y es el objetivo central de esta tesis. (D) Los Huiros, también, es el nombre de un poblado ubicado en el valle del Limarí (http://www.geocities.com/vallelimari/).

A continuación, deseo agradecer la colaboración desinteresada del equipo de "investigadores" y estudiantes del Laboratorio de Biodiversidad y Ecología Costera (LABECO), el cual ha evolucionado en el transcurso de este estudio. Inicialmente formado por el Dr. D. Véliz, Dr. L. M. Pardo, I. Herrera, C. Cerda y F. Véliz (1996-1999). Posteriormente conformado por J. Rivera, F. Díaz, E. Rojas, A. Masuero, P. Flores, A. L. Valdivia, B. Rubina, N. Godoy, S. Ramos, E. Brown, N. Piaget, K. Su, C. Ibacache, P. Bravo y C. Olivares. A los que actualmente se han agregado C. Ramírez, J. Barrios, J. Mitrovich, U. Rojas, H. Bastias, K. Ordenes, A. Letelier y M. Bravo. Todos ellos han ayudado ha concretar este trabajo colaborando en las actividades de buceo o de laboratorio con humor, voluntad y cariño.

Agradezco todas las correcciones y comentarios a los distintos manuscritos que componen esta tesis a: Dr. M. Graham, Dr. M. Edwards, Dr. S.

Navarrete, Dr. P. Camus, Dr. A. Buschmann, Dra. M. C. Hernández, Dr. E. Martínez, Dr. W. Stotz y otros Doctores anónimos. Un agradecimiento especial merece el Dr. M. Thiel, quien ayudó exhaustivamente en el mejoramiento de esta tesis. A los colegas y amigos del I-MAR, Puerto Montt. Agradezco al Dr. J. Vásquez, profesor guía, Director del LABECO y coordinador de los distintos proyectos de investigación que han sustentado la información utilizada en esta tesis. Agradezco las traducciones y comentarios de los manuscritos al Dr. L. Disalvo y a Sarah Allan por la revisión del ingles.

También deseo agradecer y hacer un reconocimiento muy especial a mi “colega” Nicole Piaget, quien ha iluminado el sendero de mi vida en el más amplio espectro de la felicidad. Juntos hemos encontrado el límite norte del rango de distribución geográfica de las distintas especies que conforman los huirales del Pacífico temperado de Sudamérica, los más influenciados por la interacción ENOS-Surgencia. En el verano 2005, el límite norte de *D. antártica* fue Lengua de Vaca (30º S), de *M. pyrifera* fue Pucusana (10º S), de *L. nigrescens* fue Arequipa (16º S) y de *L. trabeculata* y *M. integrifolia* fue Paracas (14º S). Por esto y un sin fin de otras cosas, muchas gracias Nicole.

También agradezco y dedico este trabajo a tres mujeres muy importantes en la motivación de mis estudios. A Lucy, la madre de mis hermosas hijas, a Catalina Paz Vega Varela (mi espíritu) y a Leonor de los Ángeles Vega Varela (mi alma), ambas son los regalos más grandes recibidos en mi vida.

La tesis y los manuscritos presentados en esta investigación han sido financiados por distintos proyectos del Fondo de Ciencia y Tecnología de Chile (FONDECYT), otorgados al Dr. J. Vásquez, identificados con las series Nº 5960001, 100044, 1010706 y por FONDAP Nº3 O&B, donde participe como investigador en formación.

INDICE

INTRODUCCIÓN GENERAL

Macrocystis integrifolia Bory, conocida en Chile como “huiro, canutillo o flotador” y “kelp” en Norteamérica, es un componente florístico que caracteriza los ambientes rocosos temperados protegidos y semi-expuestos al oleaje formando praderas desde el intermareal hasta los 30 m de profundidad (Alveal *et al.* 1973). El huiro presenta una distribución bipolar en el Océano Pacífico Oriental, desde Alaska (ca. 58º N) hasta California (ca. 25º N) en el Hemisferio Norte, y desde el norte del Perú (ca. 4º S) hasta Chile central (ca. 37º S) en el Hemisferio Sur (Druehl 1969, Ramírez & Santelices 1991). Sin embargo, los numerosos estudios poblacionales de *M. integrifolia* en el Pacífico Norteamericano (ver citas en North 1971, 1986, 1994, North *et al.* 1986, Steneck *et al.* 2002), contrastan significativamente con la ausencia de antecedentes similares en el Pacífico Sudamericano. *A priori*, el desbalance hemisférico en este tipo de estudios, por si solo, resalta la necesidad de realizar investigaciones que evalúen los parámetros poblacionales que sustentan los patrones de distribución y abundancia de *M. integrifolia*, y de los factores que los regulan.

A escala local (Fig.1), los patrones de distribución y abundancia de *Macrocystis* son el resultado del reclutamiento, productividad neta positiva y mortalidad (Steneck *et al.* 2002). Estos parámetros poblacionales, están regulados por: (a) factores abióticos como el movimiento del agua (o exposición al oleaje), el sustrato, la temperatura, los nutrientes y la luz (Santelices & Ojeda 1984, Tegner *et al*. 1997, Graham *et al.* 1997, Dayton *et al*. 1999); (b) factores bióticos extrínsecos como la competencia, la herbivoría y el epifitismo (Lawrence 1975, Santelices & Ojeda 1984, Dayton 1985, Vásquez & Buschmann 1997); (c) factores bióticos intrínsecos determinados por interacciones intraespecíficas que generan procesos de auto-raleo poblacional dependientes de la capacidad de carga del sistema (Reed & Foster 1984, Dayton *et al*. 1998).

A escala regional (Fig. 1), en ambos hemisferios, las poblaciones de *Macrocystis* ubicadas hacia latitudes bajas del Pacífico Americano son afectadas por el evento “El Niño, Oscilación del Sur” o ENOS (Glynn 1988, Halpin *et al.* 2004). ENOS, de origen ecuatorial, genera variabilidad interanual del clima oceanográfico alternando anomalías térmicas positivas (El Niño) y negativas (La Niña) de la temperatura superficial del mar cada 4,5 años en promedio, las que están correlacionadas con las variaciones interanuales de la presión atmosférica (Oscilación del Sur) (Fiedler 2002). Durante un evento El Niño, dependiendo de la magnitud e intensidad, la abundancia de algas Laminariales puede disminuir o pueden ocurrir procesos de extinción local correlacionados con la latitud (Soto 1985, Tomicic 1985, Glynn 1988, Godoy 2000, Llellish *et al.* 2001, Edwards 2004). Las poblaciones de *Macrocystis* y de otras Laminariales son restablecidas por recolonización durante un evento La Niña o en años “normales” (Tegner *et al*. 1997, Dayton *et al*. 1999, Ladah *et al*. 1999, Hernández-Carmona *et al*. 2001, Edward 2004), pero con una tasa de recolonización significativamente mayor en el Hemisferio Norte (Martínez *et al.* 2003). Sin embargo y aunque existen estudios descriptivos (ver Camus 1990), aún no se ha evaluado si el evento El Niño es una perturbación que modela el arreglo espacial y temporal de las poblaciones de *M. integrifolia* (Fig. 1), como ha sido sugerido para algas Laminariales intermareales del norte de Chile (Camus 1994, Martínez *et al.* 2003) y submareales de California (Tegner *et al*. 1997, Dayton *et al*. 1998, 1999, Edwards 2004).

A mesoescala (Fig. 1), se ha postulado que la persistencia de poblaciones de algas Laminariales durante y despúés de un evento El Niño en algunas localidades del norte de Chile se debe a la protección que genera la surgencia costera permanente que ocurre en áreas geográficas particulares (Ej. Penínsulas e islas costeras; ver Martínez 1999). En estas áreas, las masas de aguas subsuperficiales de baja temperatura y ricas en nutrientes suben a la superficie por transporte de Ekman durante todo el año (Halpin *et al.* 2004). Estos centros estables de surgencia se ubican en varios puntos a lo largo de la costa del norte de Chile (Strub *et al*. 1998), y su actividad persistió durante el evento El Niño 1997-1998 (Vásquez *et al*. 1998, Lagos *et al*. 2002, Takesue *et al*. 2004). Así, localidades cercanas a centros de surgencia podrían evitar las mortalidades masivas de *M. integrifolia* descritas durante eventos de gran magnitud como El Niño 1982-83 (Tomicic 1985, Soto 1985, Camus *et al*. 1994) y El Niño 1997-1998 (Godoy 2000, Llellish *et al*. 2001) (Fig. 1). Además, si las poblaciones de *M. integrifolia* establecidas en las cercanías de un centro de surgencia permanente en el norte de Chile persisten durante un evento El Niño, entonces debieran funcionar como áreas fuentes productoras de propágulos disponibles para recolonizar áreas sumideros donde el efecto catastrófico de esta perturbación ha generado procesos de extinción local.

En condiciones oceanográficas normales o La Niña, y a mesoescala (Fig. 1), la topografía de la costa del norte y centro de Chile producen un mosaico de áreas caracterizadas por gradientes de temperatura superficial del mar y disponibilidad de nutrientes (Lagos *et al*. 2002, Nielsen & Navarrete 2004). Esta condición oceanográfica costera del hábitat modulada por la presencia de centros de surgencia permanente, debiera modificar la dinámica de las poblaciones de *M. integrifolia* a mesoescala (Fig. 1). Sin embargo, no hay evidencia empírica que lo pruebe, usando por ejemplo experimentos naturales que consideren a los centros de surgencia permanente como un factor de variabilidad topográfica que regula la dinámica de poblacionales de *M. integrifolia* en el norte de Chile.

En este contexto, la presente tesis intenta contribuir al conocimiento de la dinámica de poblaciones de *M. integrifolia* en el norte de Chile teniendo dos focos principales: (a) el análisis de la variabilidad espacio-temporal de los patrones de distribución y abundancia de *M. integrifolia* a escala local, y (b) el estudio de las posibles relaciones entre los patrones de distribución y abundancia de *M. integrifolia* con procesos oceanográficos que actúan a mesoescala y a escala regional (Fig. 1). La investigación realizada privilegia el estudio en paralelo de distintas escalas espacio-temporales y el análisis simultaneo de procesos oceanográficos (ciclo ENOS y surgencia costera) que modulan la dinámica de poblaciones de *M. integrifolia* a lo largo de la costa del norte de Chile (Fig. 1). Por lo tanto, las explicaciones ofrecidas están centradas principalmente en procesos y patrones, en lugar de mecanismos, incurriendo necesariamente en el compromiso de priorizar los aspectos generales sobre los particulares. Para esto se plantearon los siguientes objetivos específicos:

1. Determinar, usando protocolos correlacionales, el efecto de factores abióticos (movimiento del agua, temperatura y nutrientes) en la dinámica de poblaciones de *Macrocystis integrifolia.*
2. Determinar, usando protocolos correlacionales, el efecto de factores bióticos (herbivoría) en la dinámica de poblaciones de *Macrocystis integrifolia*.
3. Analizar el efecto de la surgencia costera permanente en la dinámica de poblaciones de *Macrocystis integrifolia*.
4. Describir el efecto del evento El Niño 1997-98, en el arreglo espacial y la dinámica de las poblaciones de *Macrocystis integrifolia* en el gradiente latitudinal del norte de Chile.
5. Determinar el efecto del evento El Niño 1997-98 en la dinámica poblacional de *Macrocystis integrifolia* en una localidad con surgencia permanente.

La tesis se ha dividido en cuatro Capítulos, cada uno con la estructura de un artículo científico regular (Título, Resumen, Introducción, Métodos, Resultados y Discusión), siendo autoexplicativo en los contenidos y en su interpretación, y por estas razones esta introducción es una presentación general de estos. Los Capítulos no son necesariamente independientes, y en cada uno se indica a través de citas autoreferentes cuales de sus resultados, o en que forma, están vinculados entre sí. En el Capítulo 1 se examina el efecto de factores abióticos (movimiento del agua, temperatura y salinidad) sobre los patrones de producción y germinación de esporas, y crecimiento de esporofitos juveniles de *M. integrifolia* (objetivo 1) y *M. pyrifera*. Las comparaciones entre poblaciones de *Macrocystis* spp geográficamente separadas, proveen la base y el marco espacio-temporal para interpretar los resultados de los restantes Capítulos. En el Capítulo 2, se analiza el supuesto de que la persistencia de *M. integrifolia* (y de *Lessonia trabeculata*) durante y post El Niño 1997-1998 es causada por la protección generada por la surgencia costera permanente en un área geográfica particular (Península de Mejillones; 23º S), evaluando el efecto interactivo de procesos que actúan a mesoescala (surgencia) con otros que operan a escala geográfica (ENOS) (Objetivo 3 y 5). Conjuntamente, se analiza el efecto de un evento estocástico de baja frecuencia (herbivoría) en la persistencia de *M. integrifolia* (Objetivo 2). Los resultados del Capítulo 2, sirven de apoyo para la comprensión general de la dinámica temporal de las poblaciones de *M. integrifolia* y proveen la base conceptual para comparar y discutir los resultados de los siguientes Capítulos. En el Capítulo 3, se realiza una aproximación comparativa para determinar si la variación geográfica en la disponibilidad de nutrientes producida a mesoescala por los centros de surgencia permanente durante años normales modifica la dinámica de poblaciones de *M. integrifolia* (Objetivo 1 y 3), asumiendo que los sitios cercanos a centros de surgencia son más productivos y estables para la persistencia de los huirales. En el Capítulo 4, se analiza de manera integrada y sincrónica el efecto de los procesos oceanográficos dependientes de la escala (ENOS y surgencia) sobre la dinámica de las poblaciones de *M. integrifolia* en el gradiente latitudinal del norte de Chile (Objetivo 3 y 4). Los principales Resultados y Conclusiones obtenidos en los cuatro Capítulos se articulan en una Discusión General, evaluando de que manera y en que contexto pueden ser estos relevantes para el conocimiento de la dinámica poblacional de *M. integrifolia* en el gradiente de distribución latitudinal del Pacífico Sudamericano, sugiriendo nuevas direcciones de investigación y estudios claves para profundizar en aquellos aspectos débiles o más fuertes de esta tesis.

Figura 1. Esquema que muestra los factores y procesos que actúan a distintas escalas en el litoral del Norte de Chile, y los posibles efectos que producirían en la dinámica de poblaciones de *M. integrifolia*.

ESCALA	FACTORES Y PROCESOS	EFECTOS POBLACIONALES
Escala Regional (10^6 m)	**ENOS (El Niño y La Niña)** modifica el clima oceanográfico en el gradiente latitudinal del norte de Chile	(a) extinción local correlacionada con la latitud (El Niño) (b) favorece la tasa de recolonización (La Niña) (c) distintas dinámicas poblacionales en el gradiente latitudinal
Mesoescala (10^3- 10^5 m)	**Areas con surgencia permanente** (a) amortigua efectos de El Niño (b) genera gradientes en años normales	(a) Persitencia de las poblaciones durante El Niño (b) tasa diferencial de recolonización post El Niño (c) distintas dinámicas poblacionales en años normales
Escala Local (10^2- 10^3 m)	**- Factores abióticos** **- Factores bióticos intrínsecos** **- Factores bióticos extrínsecos**	(a) determinan la persistencia o extinción de la población (b) inhiben o facilitan el reclutamiento (c) regulan los parámetros poblacionales

CAPITULO 1

The effect of water movement, temperature and salinity on abundance and reproductive patterns *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile.

El efecto del movimiento del agua, la temperatura y la salinidad en los patrones reproductivos y de abundancia de *Macrocystis* spp. (Phaeophyta) a diferentes latitudes de Chile.

ALEJANDRO H. BUSCHMANN[1], JULIO A. VASQUEZ[2],
PAULINA OSORIO[1], ENRIQUE REYES[1], LUIS FILÚN[1],
MARIAM C. HERNÁNDEZ-GONZÁLEZ[1] & J. M. ALONSO VEGA[2]

[1]I~MAR Research Center, Universidad de Los Lagos, Casilla 577, Puerto Montt, Chile

[2]Facultad de Ciencias del Mar, Departamento de Biología Marina, Universidad Católica del Norte, Centro de Estudios Avanzados en Zonas Áridas (CEAZA). Casilla 117 Coquimbo, Chile

MARINE BIOLOGY (2004) 145: 849-862

ABSTRACT

This study describes the density variation and phenology of *Macrocystis integrifolia* and *Macrocystis pyrifera* populations from northern and southern Chile, respectively. Samples of both species were taken in wave-exposed and wave-protected areas. In addition, spore production, germination and early growth rate of sporophytes of each population was studied at monthly intervals under three temperature and salinity regimes. Results indicate that *M. integrifolia* from northern Chile present perennial plants with a mean density of three individuals per 0.25 m^2 throughout the year, and that it reproduces mainly during spring and winter. Although, *M. pyrifera* in exposed areas of southern Chile also have a perennial-type life strategy, they are able to reproduce all year round. In contrast, *M. pyrifera* populations in protected areas of southern Chile show a clear annual cycle, with high recruitment during late winter and fertile sporophytes in summer and autumn, although the populations become completely decimated thereafter. The effect of temperature and salinity on *M. integrifolia* shows that it is independent of water movement, but requires low temperatures and high salinities for the release of zoospores, germination and early sporophyte growth. This pattern differs from that of *M. pyrifera* in southern Chile, which has a broader tolerance range for salinity and temperature than does *M. integrifolia*. However, in southern Chile wave-protected populations showed higher spore release and germination at 15 and 18 ºC, whereas sporophyte growth responded better at the lowest temperature tested (8 ºC). In general, these results are contrary to those expected, since a seasonal reproduction pattern was observed in *M. integrifolia* inhabiting a less seasonal variable environment. In exposed sites of southern Chile, plants showed greater tolerance and continuous reproduction throughout the year, despite the greater environmental variability. Finally, population dynamics of protected kelps of southern Chile shows an annual pattern, which is contrary to the expected perennial strategy shown by exposed populations.

INTRODUCTION

Two species of *Macrocystis* (Lessoniaceae) have been identified along the Chilean coast (Hoffman and Santelices 1997). *M. integrifolia* is present along the Peruvian and northern Chilean coast (6º-32ºS), and inhabits bays at a depth of 0 to 15 m in wave protected and semi-protected areas. Periodically, these northern Chilean populations suffer the effects of El Niño-South Oscillation (ENSO) phenomena (Vásquez and Buschmann 1997, Vásquez *et al.* 1998). On the other hand, *M. pyrifera*, the most common species, can be found from 37ºS down to Patagonia (55ºS). This latter species is found in bays open to the Pacific Ocean, as well as in channels and fjords that are protected from strong wave action south of 41ºS (Dayton 1985). At lower latitudes, these populations are usually subjected to fewer and less-intensive seasonal variations in salinity, nutrients and temperature when compared to the southern region, where *M. pyrifera* is the dominant kelp and ENSO effects are normally less marked.

In general it has been indicated that *M. integrifolia* and *M. pyrifera* tolerate a broad range of temperatures, which can reach highs of 18-20ºC (North *et al.* 1986). Nevertheless, summer nutrient depletion, together with higher temperatures, is responsible for canopy die-off (*e.g.* North *et al.* 1986). Water motion certainly increases nutrient and carbon uptake (*e.g.* Wheeler 1980, 1982; Gerard 1982), but may cause the dislodgment of plants (Seymour *et al.* l989, Graham *et al.* 1997). This situation explains the general effect of El Niño: temperature increase, nutrient concentrations decline and winter storms increase (*e.g.* Gerard l984, Dayton and Tegner 1984, Harrold and Reed 1985). The effect of salinity has not been studied as closely as the above environmental parameters, but it has been suggested that kelp tolerate seawater dilution of almost one-third (North *et al.* 1986). In spite of the El Niño events in the north, we postulate that the stronger seasonal variation in southern Chile is correlated with a higher tolerance to environmental changes, such as salinity, due to the higher precipitation in south. Furthermore, effects of water movement on populations from northern Chile are not expect, but, in southern Chile, protected populations should be much more variable and show higher tolerance limits than exposed populations, because of the stronger environmental variability present in inland water habitats (Buschmann 1992).

This study shows the effect of water motion, temperature and salinity on the population dynamics of *Macrocystis* spp. in the southeastern Pacific coast. We describe annual variation in plant density in relation water motion, and assess the effect of temperature and salinity on sporulation, spore germination and early sporophytic growth in wave-exposed and -protected populations. The results are discussed in relation to latitudinal distribution, local upwelling, El Niño events, and the temperature and salinity variability present at the study sites along the Chilean coast.

MATERIALS AND METHODS

Study sites

This study was carried out in 12 locations, 6 in northern (~30ºS) and 6 in southern Chile (~41ºS) (Fig. 1). In each location, three exposed and three protected study sites were defined by using calcium carbonate blocks, as described by Doty (1971). Five blocks per site were installed along a depth gradient, for a period of 3 days, a procedure that was repeated on six occasions in different season. This methodology permitted us to identify study sites with different degrees of water movement by determining the dissolution rate of the carbonate blocks. Water temperature was determined daily (at hourly intervals) by using submerged digital thermographs (StowAway® Tidbit®), whereas salinity was measured at bi-weekly intervals on three samples per station with an Atago refractometer (± 0.5 ‰). Temperature and salinity were measured at different depths (1-10 m) to obtain an average value for each location.

In northern Chile, wave-exposed sites (ESN1, ESN2 and ESN3) are characterized by southern-facing areas with a sea bottom dominated by consolidated rocks from the intertidal zone up to a depth of 12 m. Patches of sand and boulders can be found between these rocky areas. At depths > 12 m, the sand and boulder areas outnumber the areas rocky substrate. Wave-protected sites (PSN1, PSN2 and PSN3) face towards the north and present a similar substratum structure as described for the exposed sites. *Macrocystis integrifolia* in these locations reaches a height of 5 m, with an average holdfast diameter of 30 cm and with up to 20 stipes and 50 sporophylls per plant. No published information on the population dynamics of *M. integrifolia* exists at present (see Vásquez and Buschmann 1997). Under the *M. integrifolia* canopy another kelp (*Lessonia*) is present. An understory assemblage of algae, composed principally by coralline crustose algae and turfs of Gelidiales and Ceramiales, can also be found. Other algae present in these areas are *Halopteris* spp., *Glossophora kunthii*, *Asparagopsis armata* and *Rhodymenia* sp. (Vásquez 1992). At depths > 10 m, *Lessonia* dominates over *Macrocystis*. The gastropod snail *Tegula atra*, the black sea urchin *Tetrapygus niger* and the fish species *Aplodactylus punctatus* are the main herbivorous species controlling kelp abundance (Vásquez 1993).

In southern Chile, the open coast is generally exposed (sites ESS1, ESS2 and ESS3), with a rocky sea bottom surrounded by boulder fields. Algal populations can be found in the shallow intertidal zone up to depths of 10-12 m (Buschmann 1992). *M. pyrifera* present at these locations can be 6 m long, with a holdfast diameter of 25 cm and whit only 3-4 stipes and 30 sporophylles per plant. Data related to the population dynamics of *M. pyrifera* in southern Chile indicate that it has a perennial-type of life history (Santelices and Ojeda 1984, Westermeier and Möller 1990). In addition to *M. pyrifera* stands, exposed sites in this area present an understory of flora dominated by *Ulva rigida*, but which also includes *Desmarestia*, *Sarcothalia crispata* and *Trematocarpus,* along with other less abundant red seaweed species. In the inner seas of southern Chile, wave-protected areas (PSS1, PSS2 and PSS3) can be found, with a conspicuous *Macrocystis* belt surrounding the coastline. The substratum is mostly granitic rock or boulder fields, and the kelp population can be found up to a depth of 12 m. The most common algal species are *U. rigida* and *S. crispata*. Two sessile mollusks are very abundant in this area, *Aulacomya ater* and *Crepidula fornicata fecunda.* In both exposed and protected sites of southern Chile, the black snail *Tegula atra* is the most abundant grazer in terms of number and biomass.

Population and laboratory experiments

Plants were counted at each study site at monthly intervals for a year from July 2000 to 2001, with the use of nine 0.25 m^2 random quadrats along transect, starting at 3-12 m. All plants (juveniles and adults) were counted in each quadrat. Following the counting of sporophytes, sporophylls were collected (*n*= 60 from at least 30 random plants), packed in plastic bags and transported in ice to the laboratory. When no fertile tissues or successful sporulation was observed, the period was described as non-reproductive. Otherwise, irrespective of whether the fertile sporophylls produced few or numerous spores, we qualified the period as a reproductive one. Every month, 45 randomly selected sporophylls from all the study areas of *M. integrifolia*, as well as from all study areas of *M. pyrifera* were brought to the laboratory. The sporophylls were gently brushed and rinsed with filtered (0.2 µm), sterile seawater and packed with filter paper and aluminum foil for 12 h at a temperature of 8°C. After this mild desiccation period, 1 cm^2 discs (one per sporophyll) were cut off each fertile sorus and placed in Petri dishes (5 cm diameter) with Provasoli culture medium (McLachlan 1973) to induce sporulation, germination and growth of new sporophytes. Five Petri dishes with tissues originating from different plants were considered for each of the following treatments: three temperatures (8ºC, 15ºC and 18°C) and three salinities (27‰, 31‰ and 34‰). The range of temperature and salinity chosen were in accordance with those found in the natural environment. Incubation was carried out in culture chambers under constant conditions, considering a neutral photoperiod (12 h light: 12 h dark) and a photon flux of 40 µmol m^{-2} s^{-1} provided by 40 Watt fluorescent tubes (Phillips). The photon flux rate was measured with a Li-Cor LI-189 photometer. The culture medium was changed on a weekly basis. The number of spores produced by each 1 cm^2 sorus disc was counted after 48 h of incubation, whereas the number of spores with a germination tube was determined after 144 h. Counting was carried out using an inverted Nikon microscope attached to a digital camera and an image analyzer (Image-Pro version 4.0). Three random areas of each dish were photographed, from which the total numbers of settled spores and the spores with the presence of germination tubes were counted. With this data we estimated the number of spores produced by a 1 cm^2 piece of sorus, and the germination percentage calculated as the number of spores with a germination tube divided by the total number of initially settled spores (x 100). After 30 days of incubation, the length of all the young sporophytes in each ocular field was determined following the same procedure as described above, to estimate the growth rate (mm $month^{-1}$) of the sporophytes under different temperature and salinity conditions.

After a year of repeated monthly experiments, the different data for protected and exposed northern and southern localities were pooled by season (winter, spring, summer and autumn). Mean and standard error were calculated for each case, and the data were analyzed by three-way ANOVA using SYSTAT 5.0, after verifying normality and homocedasticity of the data. The factors analyzed for every season were the temperature, salinity and location of plant collection (exposed or protected sites). If significant differences were detected for salinity and/or temperature, an *a posteriori* Tukey test was performed using SYSTAT 5.0.

RESULTS

Abiotic conditions

In both northern and southern Chile, calcium carbonate blocks permitted discrimination between protected and exposed areas. The northern area presents a significant ($p<0.01$) reduction in the dissolution rate when exposed sites are compared to protected sites (mean diffusion rate: 0.60 and 0.32 g h^{-1}, respectively). In the south, the dissolution rate was three to four times higher ($p<0.001$) in the exposed sites compared to the protected sites (mean diffusion rate: 0.68 and 0.17 g h^{-1}, respectively). Temperature and salinity variation during the year is presented in Fig. 2. Data show that in northern Chile there is almost no seasonal variation in salinity, with a mean value of 33 ‰, and that temperature varied between 13ºC and 18ºC (5ºC), with no differences between protected and exposed sites. On the other hand, in southern Chile salinity variation was greater than in northern Chile; salinity varied between 28‰ and 33‰ in exposed locations, whereas, in protected locations fluctuated between 22‰ and 31‰ (Fig. 2). Temperature in the exposed areas of the southern region varied from 8ºC to 16ºC (8ºC) and in the protected areas from 8ºC to 15ºC (7ºC).

Abundance and phenology

The plant density of *Macrocystis integrifolia* in all three study locations from northern Chile showed a very conservative annual variation (Fig. 3). In the exposed sites, the plant density varied between 2 to 4 plants per 0.25 m^2. Numbers were very similar in the protected sites, although one study site (PSN3) registered a density of over 5 plants per 0.25 m^2 in summer. Nevertheless, no significant differences were found between localities and season (Fig. 3).

The case of *M. pyrifera* in southern Chile is quite different (Fig. 3). In the exposed area, two of the most exposed sites (EES1 and ESS3) showed a similar pattern to that found in northern Chile, with almost no temporal variation in abundance and values varying between 2 and 4 plants per 0,25 m^2; in one exposed site (ESS2), a massive recruitment was detected in early spring (Fig. 3). However, the most striking difference was seen the protected area of southern Chile, where *M. pyrifera* populations showed an annual cycle, with recruitment starting during winter (July) and reaching densities of 15 or more plants per 0.25 m^2. Density at the protected sites in the south begins to decline during the spring and summer, but the largest specimens are found in early summer (Fig. 4). All the plants disappear in autumn, when it is possible to observe necrotized holdfasts. Regrowth of these holdfasts was never observed, even after several years (5) of observation.

The phenology of *M. integrifolia* indicates that, in both protected and exposed locations of northern Chile, this kelp contains sporophylls all year round (Fig. 4). However, during summer the number of spores produced is very low. On the other hand, *M. pyrifera* is reproductive all year round in exposed areas. The reproduction season of the protected populations in southern Chile is limited to summer and early autumn (Fig. 4). For this reason the protected population of *M. pyrifera* follows an annual cycle, in contrast to the other kelp populations studied.

Temperature and salinity experiments

In the north of Chile, the spores produced by a standardized area of sorus occur mainly in winter and spring, while the number of spores that can be obtained in summer seems minimal (<30 spores mm^{-2}), both in protected and exposed sites (Fig. 5). In autumn, these northern populations did not produce any spores. Statistical analysis indicates that the number of spores released by *M. integrifolia* was significantly (F=5.830; 2,792 df; $p<0.003$) greater in spring and winter at 8ºC than at the higher temperatures. Salinity had a significant effect on the spore release in winter (F=7.367; 2,792 df; $p<0.001$) and summer (F=4.901; 2,792 df; $P<0.008$), showing a higher success at 34‰ than at the two lower salinities studied (Fig. 5). Finally, spore production between the protected and exposed plants differed significantly in winter (F=6.789; 2,792 df; $p<0.009$), spring (F=17.908; 2,792 df; $p<0.001$) and summer

(F=4.245; 2,792 df; p<0.040), with a higher spore release observed in the exposed plants (Fig. 5). It is important to indicate that temperature interacted significantly with locality (exposed and protected sites) both in spring (F=7.671; 2,792 df; p<0.001) and in summer (F=4.248; 2,792 df; p<0.015), and that the effect of temperature was stronger for the exposed populations (Fig. 5).

Spore release by *M. pyrifera* in southern Chile presented a different pattern (Fig. 6). In this case, temperature only has a significant (F=33.57; 2,792 df; p<<0.001) effect in autumn, when spore release is higher at 15ºC than at 8ºC. Salinity only had a significant effect in autumn (F=4.757; 2,792 df; p<0.009), indicating that spore production was higher at 27‰ than at 34‰ (Fig. 6). However, in all four seasons significant (winter: F=400.76; 2,792 df; p<<0.001; spring: F=111.37; 2,792 df; p<<0.001; summer F=77.89; 2,792 df; p<<0.001; autumn F=16.454; 2,792 df; p<0.001) differences were found between the sporulation of protected and exposed sites, showing that in winter and autumn the spore production was higher in the exposed sites, but in summer and autumn the plants collected in protected areas had a higher spore production capacity (Fig. 6). Furthermore, in autumn the temperature interacted significantly (F=23.296; 2,792 df; p<<0.001) with locality, indicating that at 15ºC spore production was higher at 27 ‰ than at the two higher salinities tested in this study (Fig. 6). In summer, salinity interacted significantly (F=6.376; 2,792 df; p<0.002) with the collection locality, indicating that its effect was stronger for protected populations (Fig. 6). Another significant (F=3.086; 4,792 df; p<0.016) interaction was detected between temperature and salinity in summer, showing that spore release at low salinities and increased temperature enhances sporulation, whereas at higher salinities and higher temperatures sporulation is reduced (Fig. 6). Finally, a significant (F=4.143; 4,792 df; p<0.003) interaction was found in autumn, indicating that a temperature of 15ºC produced a stronger effect on sporulation for the protected kelps, especially at lower salinities.

Spore germination success determined for *M. integrifolia* indicated that, in the best situation, the germination percentage never exceeded 25%, whereas in autumn no response was observed in the few spore obtained (Fig. 7). In winter and summer temperature had a significant (winter: F=3.400; 2,792 df; p<0.034; summer: F=6.570; 2,792 df; p<0.001) effect on germination percentage, indicating that the success was higher at 15ºC than at 8ºC or 18ºC. In contrast, germination showed higher success in spring at 31‰ and in summer at 31‰ and 34‰ than at 27‰ (Fig. 7). A significant (F=22.241; 2,792 df; p<0.001) difference between exposed and protected locations was only found in spring, when the germination response was higher (Fig. 7). The effect of temperature in winter and spring also showed a significant (spring: F=7.363; 2,792 df; p<0.001; winter: F=4.310; 2,792 df; p<0.014) interaction with the location of the algal stands. Furthermore, salinity did not interact with locality, but interacted significantly (F=3.485; 2,792 df; p<0.008) with temperature in winter, and, finally, interaction of the three factors was also significant (winter: F=4.349; 4,792 df; p<0.002; spring: F=2.505; 4,792 df; p<0.041) in winter and spring (Fig. 7).

Germination success was much higher in southern Chile than in the north, as it reached values as high as 100% during several seasons and under different culture conditions (Fig. 8). Most importantly, only kelps collected in the protected areas of southern Chile provided viable spores in summer and autumn. Temperature had a significant (winter: F=22.07; 2,792 df; p<<0.001; summer: F=4.284; 2,792 df; p<0.014; autumn: F=19.47; 2,792 df; p<<0.001) effect on the germination percentage in winter, summer and autumn. In winter germination was more successful at 18ºC than at 8ºC or 15ºC; in the summer and autumn germination performance was better at 15ºC and 18ºC than at 8ºC (Fig. 8). Salinity only had a significant effect in winter (F=4.577; 2,792 df; p<0.011) and summer (F=15.043; 2,792 df; p<0.001). These data indicate that, in winter, germination performance was higher at 31‰ and 27‰, than at 34‰, but in summer, the improved performance only occurred at 31‰ (Fig. 8). Significant differences between exposed and protected locations were found in winter

(F=6903.8; 1,792 df; p<<0.001), spring (F=234.6; 1,792 df; p<<0.001) and also in summer (F=19.075; 1,792 df; p<0.001). In summer, a significant interaction indicated that at 18°C the exposed population had a higher germination percentage, while the protected sites had a better germination performance at 8°C (Fig. 8). Furthermore, a significant interaction between temperature and salinity was found during the winter (F=4.889; 4,792 df; p<0.001) and summer (F=3.734; 4,792 df; p<0.005), when the impact of increasing the temperature was more profound at higher salinities (Fig. 8).

After maturation of gametophytes, growth rate (length month^{-1}) of the sporophytic phase of *M. integrifolia* under culture conditions was determined (Fig. 9). Temperature only had a significant (F=3.892; 2,792 df; p<0.021) effect on the growth in summer, when the highest growth rate was found at 15°C. However, overall, the highest growth rate occurred in the plants collected in spring (Fig. 9). Salinity, on the other hand, significantly affected the growth rate in winter (F=4.169; 2,792 df; p<0.016), spring (F=4.653; 2,792 df; p<0.010) and summer (F=3.892; 2,792 df; p<0.021), indicating that better growth rates were found at 31‰ and 34‰ (Fig. 9). Significant (F=7.425; 1,792 df; p<0.007) differences between exposed and protected locations were only found during spring, when sporophytes produced in protected areas showed a higher growth rate than those from exposed plants. Furthermore, a significant interaction (F=4.403; 2,792 df; p<0.013) between locality and temperature was found in spring, as the effect of temperature had a synergic effect on the growth of protected populations of this kelp at 8ºC and 15ºC (Fig. 9).

Once again, the growth rate of *M. pyrifera* from southern Chile varied under the different studied factors (Fig. 10). The exposed population produced viable spores all year round, but sporophytes were mostly produced during winter and spring, and strongly reduced in autumn, whereas no growth rate was found for the sporophytes collected in the summer. On the other hand, the protected population produced sporophytes only in summer and autumn. Temperature significantly affected the growth rate of sporophytes in winter (F=3.623; 2,792 df; p<0.027), summer

(F=5.260; 2,792 df; p<0.005) and autumn (F=75.88; 2,792 df; p<<0.001), showing higher growth rates at 8º C and 15º C than at 18º C (Fig. 10). A significant interaction was found between the origin of the spores (exposed or protected) and temperature, indicating that in summer (F=3.339; 2,792 df; p<0.036) and particularly in autumn (F=72.26; 2,792 df; p<<0.001) the protected plants grew better at low temperatures, which was not the case for exposed kelps (Fig. 10). Salinity did not have a significant effect on the growth rate of *M. pyrifera* in any season.

DISCUSSION

The reproduction patterns of both *Macrocystis* species presented striking differences. The northern populations of *M. integrifolia* show a more intense reproductive period in winter and spring, which was independent of exposure. In contrast, continuous reproduction in *M. pyrifera* was observed in the southern populations located at exposed sites, while in protected sites the reproductive period was restricted to summer and early autumn. Exposed site patterns are similar to *M. pyrifera* in the northern hemisphere, which is continuously fertile (Reed *et al.* 1996), but contrast with *M. integrifolia*, which also show continuous recruitment throughout the year (Druehl and Wheeler 1986). Populations and species of southern Chile differ, not only in their reproductive cycle, but also in their abundance patterns. In northern Chile, *M. integrifolia* populations present a very stable value of 2-4 plants per 0.25 m^2, which is similar to that found in exposed locations of *M. pyrifera* in southern Chile. However, the protected kelp populations show a clear annual cycle (see also Buschmann 1992). In summary, we present three distinct patterns: (1) in northern Chile, a stable population abundance is observed, but with a clearly seasonal reproductive pattern (in winter); (2) in southern Chile, the exposed population shows stable population dynamics, with continuous reproduction; and (3) also in the south, we observed an annual population with a reproductive season restricted to summer (Fig. 4). Therefore, the adaptative capacity of the abundance and reproductive patterns shown by these kelps to different environmental conditions is a very important characteristic.

Seasonal fluctuations in the environment typically induce growth and reproduction in perennial organisms that live long enough to experience repeated seasonal changes. Furthermore, it is typical that plants living outside the tropics, i.e. in more fluctuating environments, do not reproduce all year round (*e.g.* Battey & Lyndon 1990). However, *M. pyrifera* is reproductive throughout the year in the northern hemisphere (*e.g.* Reed *et al.* 1996). Seasonal environmental changes provide external signals that trigger internal processes in plants. Only when habitat conditions are constant and benign, will the growth and reproductive patterns arise solely from the plant itself (Lyndon, 1992). Population patterns found in this study are not correlated with the fairly constant environmental conditions found in northern Chile, where the population is characterized by more seasonal reproductive dynamics than their southern counterpart in exposed areas. The explanation seems to be that, in the northern environment, *M. integrifolia* requires winter conditions (lower temperatures) to reproduce, even though they can grow all year round. In southern Chile, the appropriate reproduction conditions are present throughout the year, and, in this case, *M. pyrifera* has developed a reproductive strategy that enables plants to produce spores continuously. For this reason the populations in the north appear to have developed a different strategy: their populations are more perennial than those in southern Chile and their holdfast regeneration capacity is greater, as they are subjected to less intense winter storms than populations in southern Chile (Vásquez & Buschmann 1997). On the other hand, these results show that the exposed *M. pyrifera* reproductive strategy is to produce spores independent of water conditions, in contrast to the *M. integrifolia* populations in northern Chile that produce spores during a restricted time period that coincides with the sporophyte growth period.

Seaweed populations can be affected by the existence of upwelling regimes and ENSO effects (*e.g.* Dayton & Tegner 1984, Ormond & Banaimoon 1994). The three study locations in northern Chile show stable o discontinuous upwelling regimes (Vásquez *et al.* 1998). Thus, if *M. integrifolia* requires low temperatures in the spring (8º C) to enhance growth of the sporophytes (Fig. 9), we suggest that upwelling could be an important oceanographic requirement for the maintenance of these populations in northern Chile. Nevertheless, the different wave regimes do not alter the population density and reproduction patterns for unknown reasons. Furthermore, effects of El Niño events have been decimating populations of the kelp *Lessonia nigrescens* from Chile and other Laminariales in the northern hemisphere for decades (Dayton and Tegner 1984; Tegner and Dayton 1987; Castilla & Camus

1992; Camus 1992; Martínez *et al.* 2003). The link between these periodical events on the northern Chilean coast and the recovery of macroalgal populations requires close attention in the near future.

Salinity remains almost constant along southern California and Baja California, and has no apparent effects on kelp distribution except in the inner portions of estuaries (North *et al.* 1986). The same authors mention that, in water bodies in northern and central California, salinity may affect the population biology of giant kelp. Druelh (1979) observed that *M. integrifolia* beds from Vancouver Island are present in habitats where salinity varied between 23‰ and 30‰. In contrast, *M. integrifolia* in northern Chile shows a significantly better response at higher (>30‰) salinities. On the other hand, in the salinity-variable environments of southern Chile, *M. pyrifera* shows a tendency to perform better at 27‰ and 30‰. In some cases, the interaction with locality indicates that the better responses at lower salinities generally occur in protected annual kelp populations. This result suggests that giant kelp may have differentiated responses in relation to salinity, allowing this species to inhabits estuarine environments like those in southern Chile.

Reproductive plasticity may be an adaptive character if the cost of producing propagules is low, as seems to be the case for seaweeds (Pfister 1992). In this context, the strategy of *M. integrifolia* in northern Chile and *M. pyrifera* in developing annual population dynamic with adjustment of their reproductive output to the prevailing environmental conditions is particularly noteworthy. In this last case, we have kelp populations growing and producing sporophylls earlier and producing more spores per area fertile tissue than the perennial population. Nevertheless, the spore production and germination capabilities are very similar in exposed and protected *M. pyrifera* populations. However, the early growth responses of the sporophytes showed very different patterns. Data show that growth of the sporophytes is mainly restricted to winter and spring for the exposed populations and that the protected kelps grow mainly in autumn, at low water temperatures similar to those present in southern

Chile in winter. This evidence indicates that whenever the plants produce spores throughout the year they will become fertile, but will not produce viable sporophytes all year round. For this reason continuous production of new recruits cannot be extrapolated from continuous spore production. This result was only visible by repeating the experiments every month.

The main prerequisite for the annual *M. pyrifera* populations in southern Chile involves the coupling of spore production and the long survival period that is required. For seaweeds, the existence of seed banks has been indicated (Hoffmann and Santelices 1991, Santelices *et al.* 1995; Edwards 2003) and is invoked to explain the massive disappearance and subsequent recovery of decimated populations of *M. pyrifera* in the northern hemisphere (Ladah *et al.* 1999). In this case, we found that sporophyte growth is enhanced under low temperature conditions. This suggests that the plants produce propagules that are very successful in summer, but the sporophyte growth conditions are essential to survive the winter period. Light conditions have been demonstrated to be important in field for *M. pyrifera* (Graham 1996). For this reason we suggest that the low radiation and low temperatures present in southern Chile are responsible for the dormancy of microscopic stages of *M. pyrifera* during the winter period. Recently it has been demonstrated that limiting resources can delay recruitment of embryonic giant kelp sporophytes for at least 1 month (Kinlan *et al.* 2003). These results suggest that in variable environmental locations, such as those in southern Chile, dormant stages appear to be a requirement, but further studies need to be undertaken on these annual populations.

ACKNOWLEDGEMENTS

This paper was funded by FONDECYT (Chile) 1000044 and 1010706. The authors acknowledge the help, in the field and in the laboratory, of R. Espinoza, V. Muñoz, G. Aroca and C. Moreno. We also wish to recognize the advice and constructive criticism of D. Varela and R. Stead on various aspect of this manuscript and the English review of S. Angus. Paper Nº5 of I-MAR. This paper is part of Master of Science Thesis of JMAV, in the Master Program in Marine Sciences at the UCN.

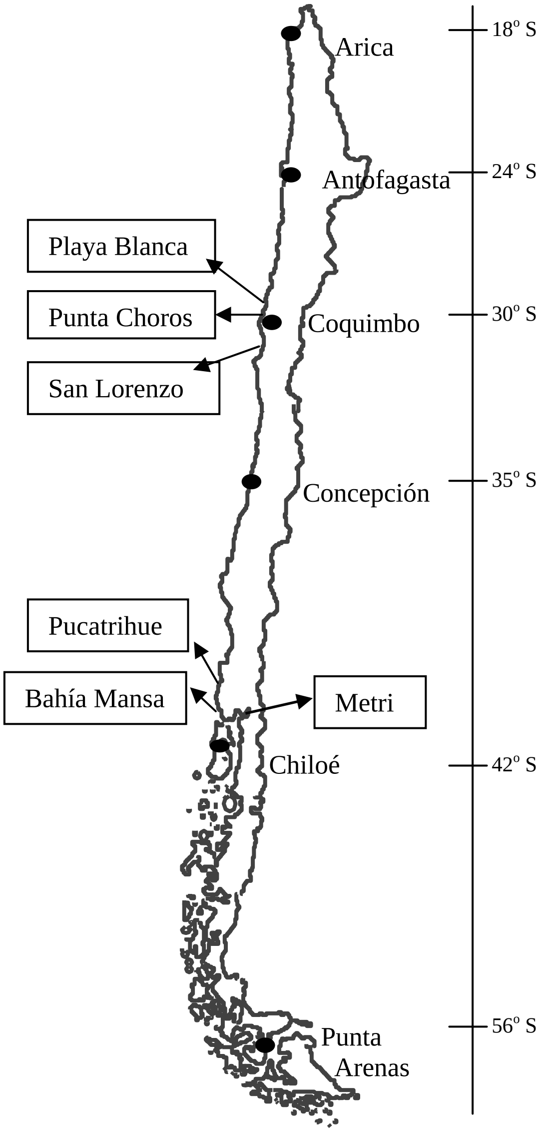


Figure 1. Map of the study areas of *Macrocystis integrifolia* in northern and *M. pyrifera* in southern Chile. Playa Blanca (ESN1 and PSN1) 28º11'S; 71º09'W; Punta Choros (ESN2 and PSN2) 29º14'S; 71º31'W; San Lorenzo (ESN3 and PSN3) 30º20'S; 71º49'W; Pucatrihue (ESS1) 40º33'S; 73º43'W; Bahía Mansa (ESS2 and ESS3) 40º34'S; 73º46'W and Metri (PSS1, PSS2 and PSS3) 41º36'S; 72º42'W.

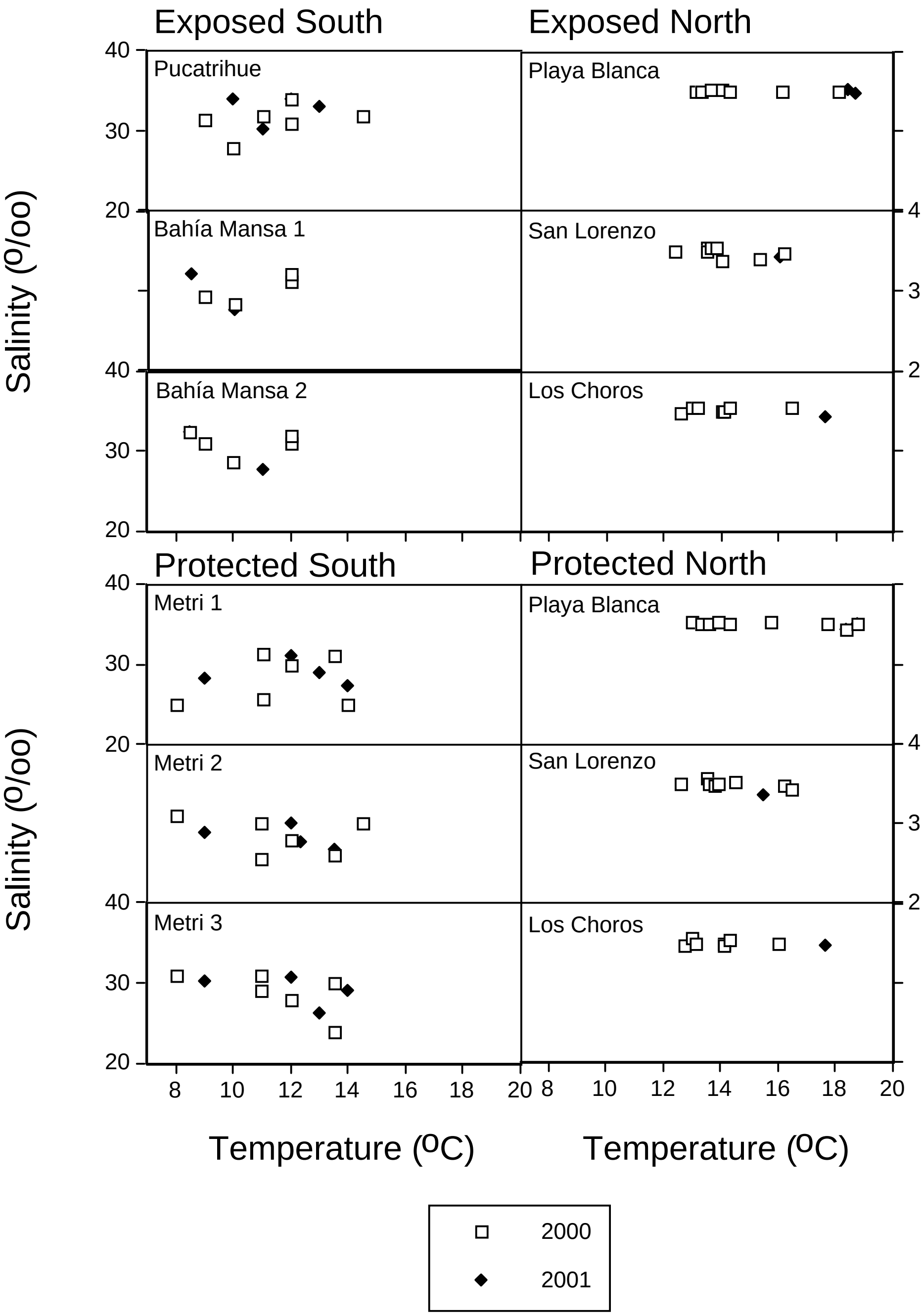


Figure 2. Salinity (‰) *versus* temperature (°C) variations over a 1-year period in protected and exposed *Macrocystis* spp. study locations (see **Figure 1** for abbreviations) in northern and southern Chile.

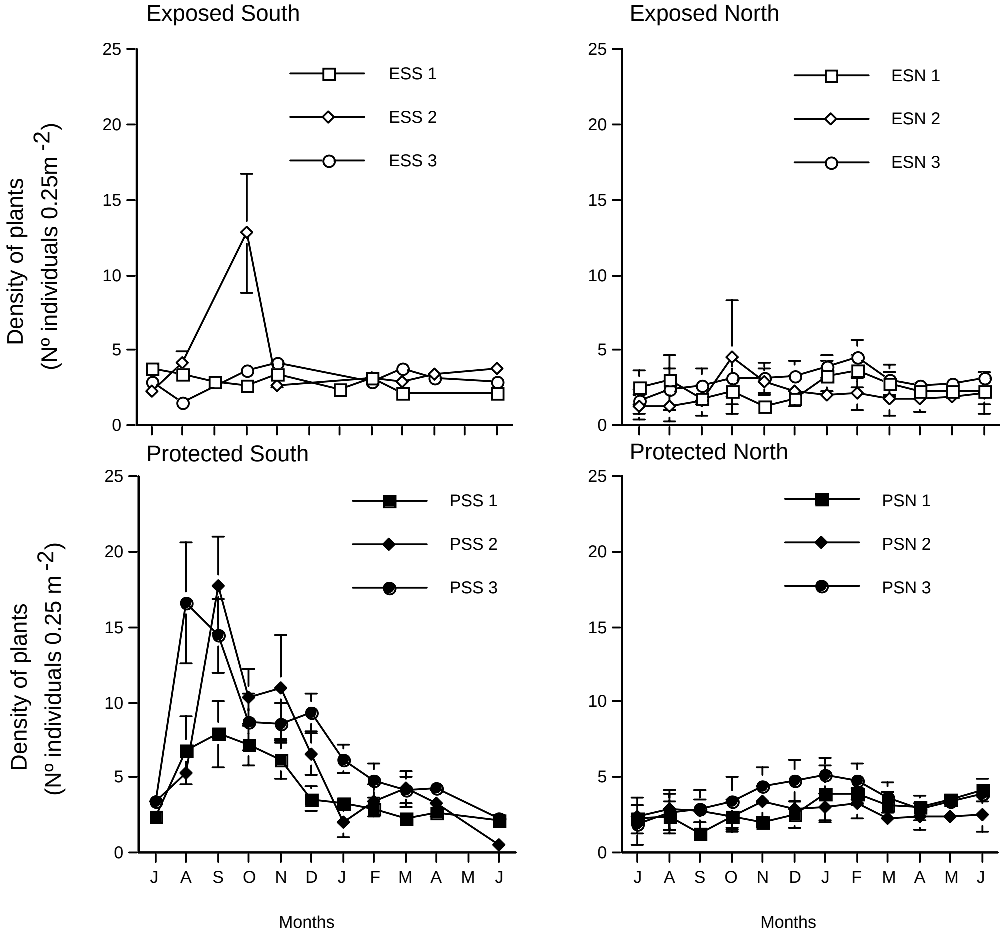
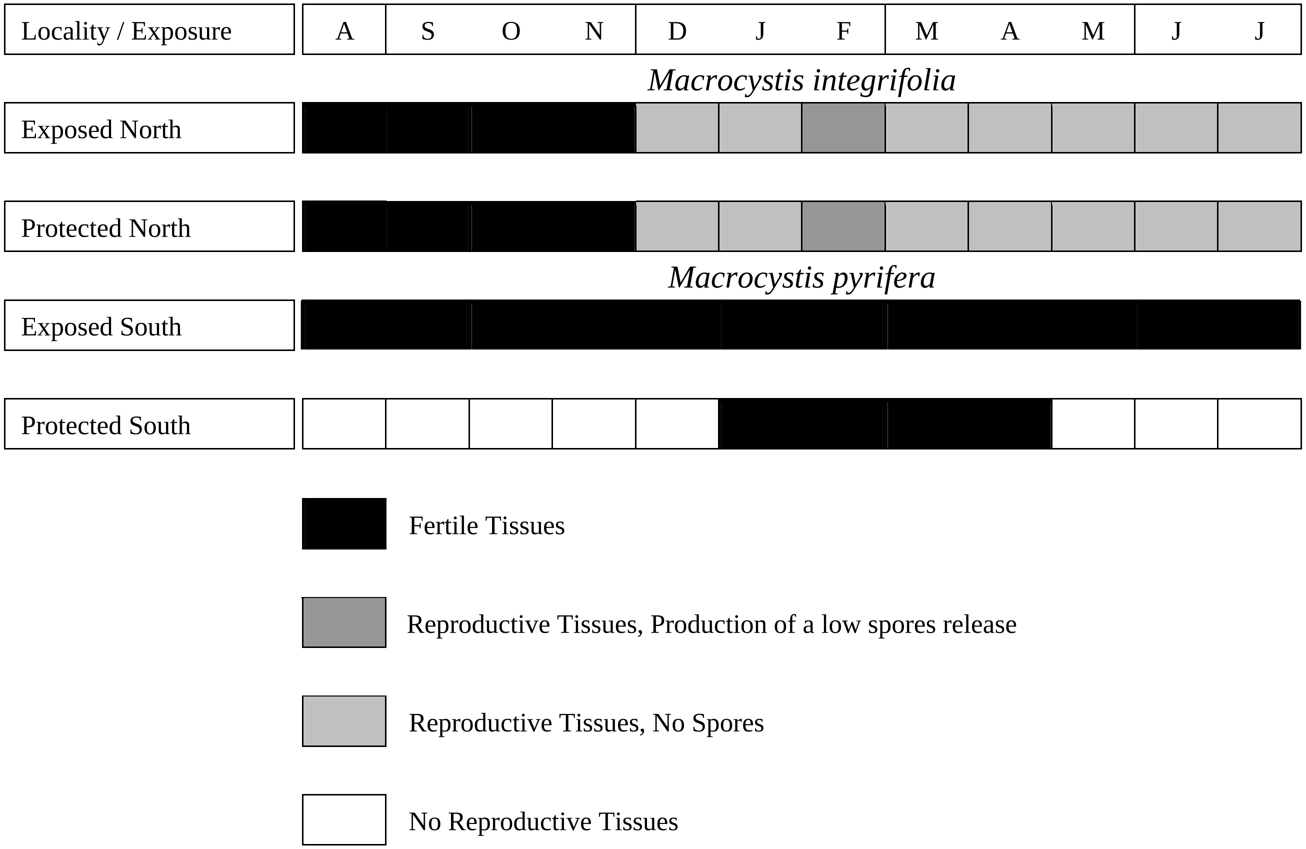


Figure 3. *Macrocystis* spp. Annual variations in plant density (number of individuals per 0.25 m^{-2}) of *Macrocystis integrifolia* in northern and *M. pyrifera* in southern Chile, also with respect to wave exposure (site abbreviations, see Fig. 1).



Locality / Exposure	A	S	O	N	D	J	F	M	A	M	J	J
Macrocystis integrifolia												
Exposed North	■	■	■	■	░	░	▓	░	░	░	░	░
Protected North	■	■	■	■	░	░	▓	░	░	░	░	░
Macrocystis pyrifera												
Exposed South	■	■	■	■	■	■	■	■	■	■	■	■
Protected South	□	□	□	□	□	■	■	■	■	□	□	□

■ Fertile Tissues

▓ Reproductive Tissues, Production of a low spores release

░ Reproductive Tissues, No Spores

□ No Reproductive Tissues

Figure 4. *Macrocystis* spp. Phenology of *M.integrifolia* in northern, and *M. pyrifera* in southern Chile, also with respect to water movement.

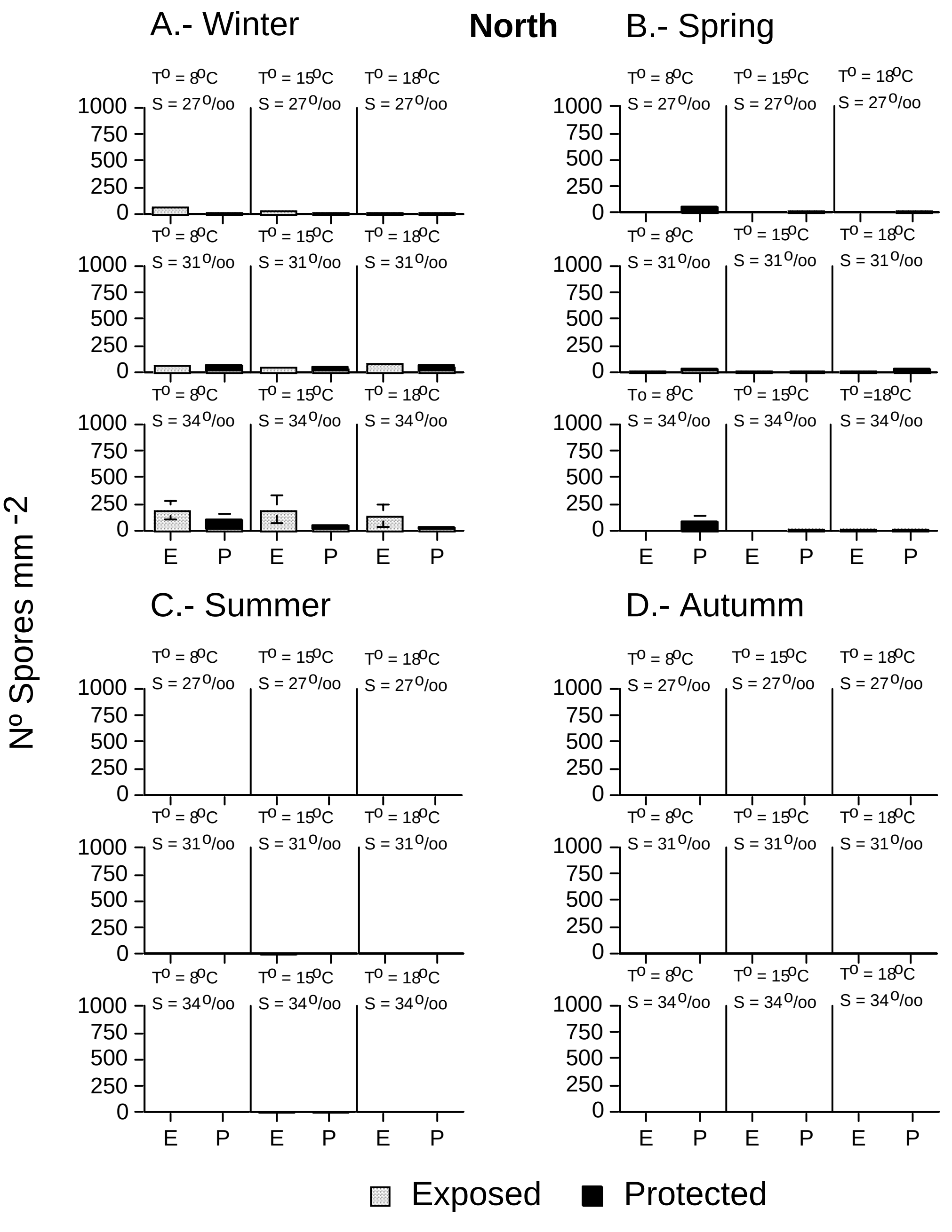


Figure 5A-D. *Macrocystis integrifolia*. Spore production (spores mm^{-2} of sorus tissue) of *M. integrifolia* in northern Chile under three temperature and three salinity conditions during: A winter, B spring, C summer and D autumn.

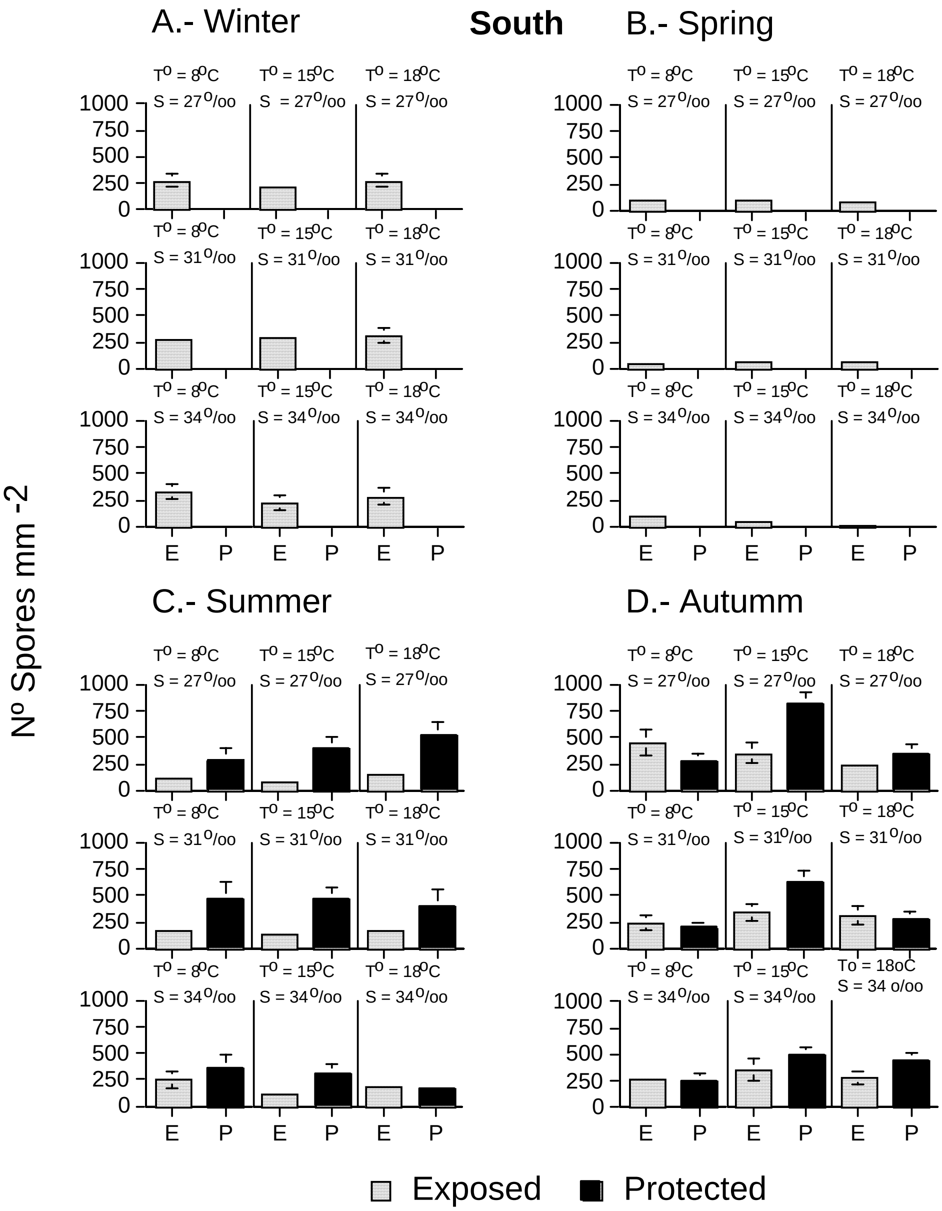


Figure 6A-D. *Macrocystis pyrifera*. Spore production (spores mm^{-2} of sorus tissue) of *M. pyrifera* in southern Chile under three temperature and three salinity conditions during: A winter, B spring, C summer and D autumn.

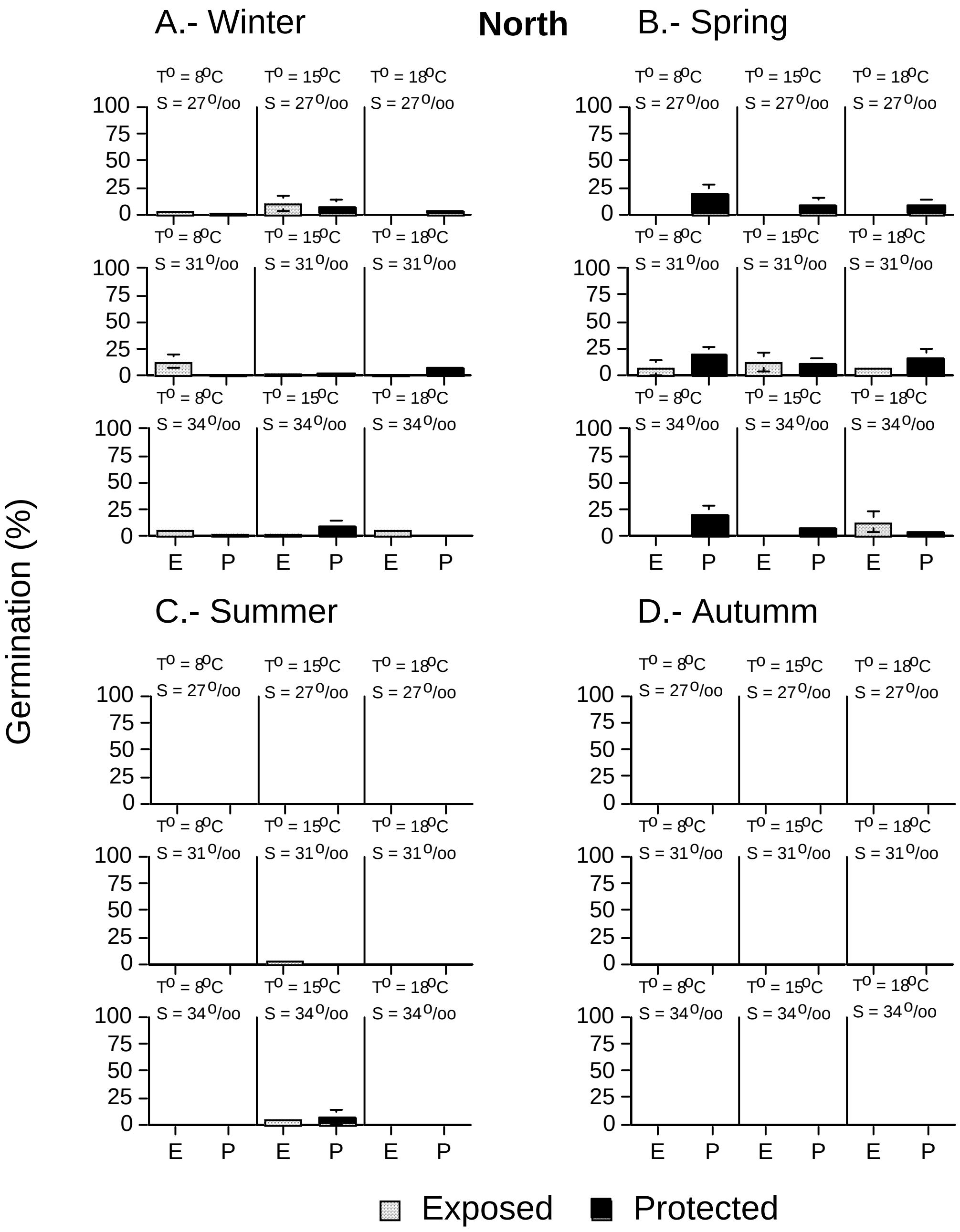


Figure 7A-D. *Macrocystis integrifolia.* Spore germination (%) of *M. integrifolia* in northern Chile under three temperature and three salinity conditions during: A winter, B spring, C summer and D autumn.

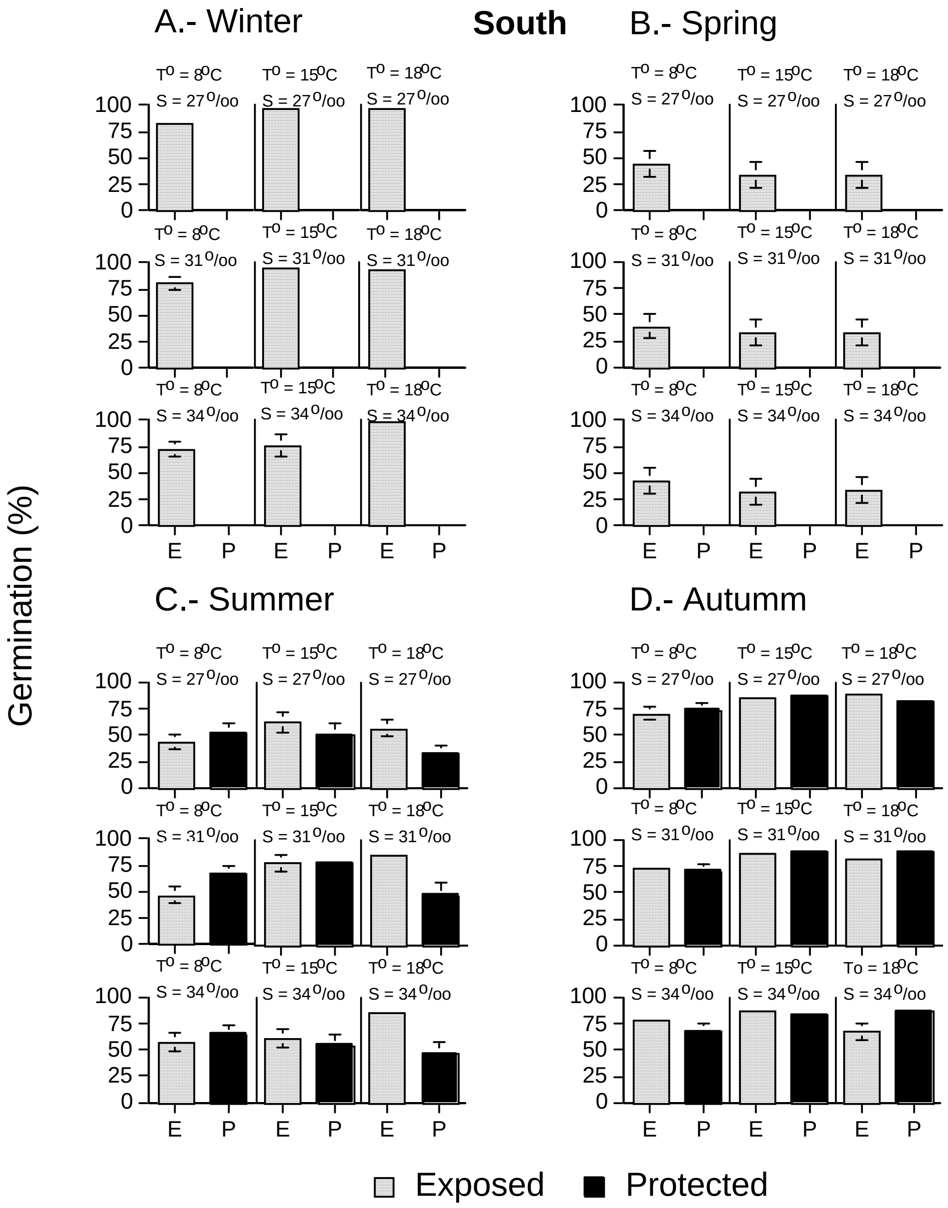


Figure 8A-D. *Macrocystis pyrifera*. Spore germination (%) of *M. pyrifera* in southern Chile under three temperature and three salinity conditions during: A winter, B spring, C summer and D autumn.

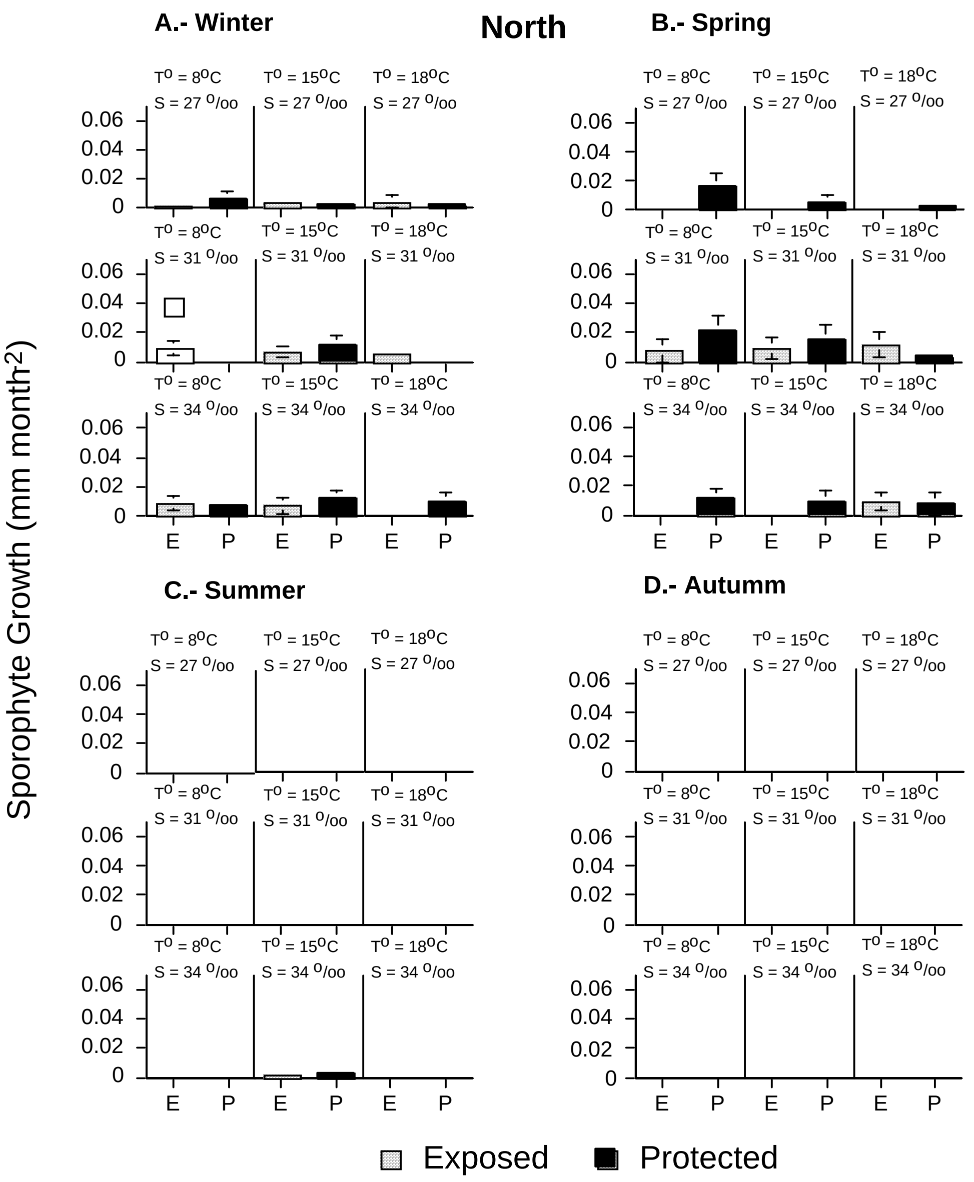


Figure 9A-D. *Macrocystis integrifolia.* Juvenile sporophyte growth (mm month^{-1}) of *M. integrifolia* in northern Chile under three temperature and three salinity conditions during: A winter, B spring, C summer and D autumn.

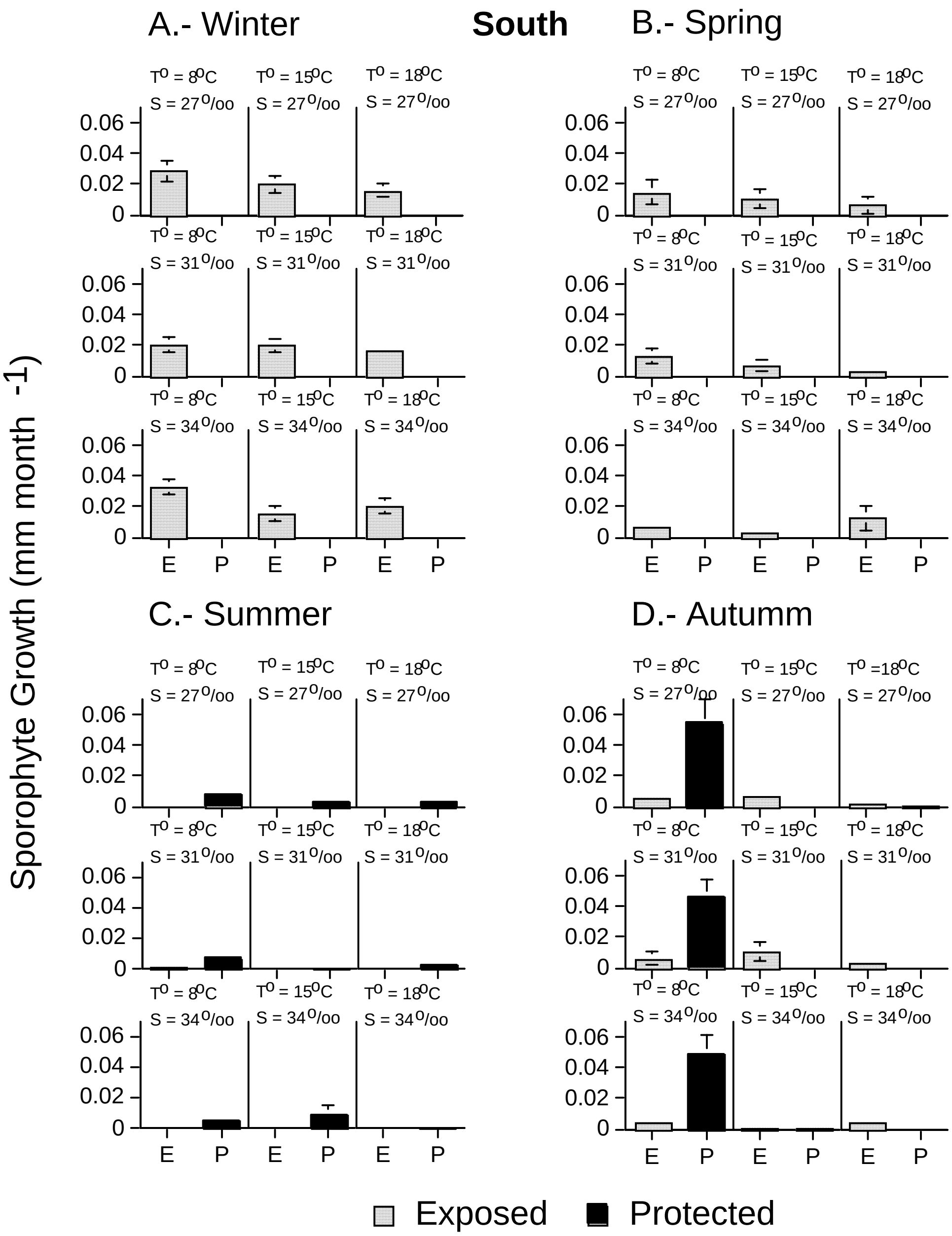


Figure 10A-D. *Macrocystis pyrifera.* Juvenile sporophyte growth (mm month^{-1}) of *M. pyrifera* in southern Chile under three temperature and three salinity conditions during: A winter, B spring, C summer and D autumn.

CAPITULO 2

Population biology of the subtidal kelps *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales, Phaeophyceae) in an upwelling ecosystem of northern Chile: interannual variability and El Niño 1997-98.

Biología poblacional de huirales submareales de *Macrocystis integrifolia* y *Lessonia trabeculata* (Laminariales, Phaeophyceae) en un ecosistema de surgencia del norte de Chile: variabilidad interanual y El Niño 1997-98.

J. M. ALONSO VEGA[1], JULIO A. VASQUEZ[1], ALEJANDRO H. BUSCHMANN[2]

[1]Facultad de Ciencias del Mar, Departamento de Biología Marina, Universidad Católica del Norte, Centro de Estudios Avanzados en Zonas Áridas (CEAZA). Casilla 117 Coquimbo, Chile

[2] I~MAR Research Center, Universidad de Los Lagos, Casilla 577, Puerto Montt, Chile

REVISTA CHILENA DE HISTORIA NATURAL (2005) 78: 33-50.

ABSTRACT

This paper describes the population biology of *Macrocystis integrifolia* and *Lessonia trabeculata* during and after the 1997-1998 El Niño in an area of permanent coastal upwelling in northern Chile. Spatial and temporal patterns of distribution were evaluated seasonally for adult and juvenile sporophytes of both species between 1996 and 2003. These two kelp form an assemblage distributed between 2 and 15 m depth, with disjunct patterns along a bathymetric gradient, including two morphs of *L. trabeculata*, the occurrence of which depends on the presence or absence of *M. integrifolia.* During the 1997-1998 El Niño the spatial-temporal patterns of abundance of the kelp assemblage were maintained by the continuity of coastal upwelling, which buffered and moderated superficial warming of the sea and depletion of nutrients. In this context, localities associated with coastal upwelling areas could function as "sources" of reproductive propagules after passage of El Niño, thus increasing kelp recolonization rates in "sink" localities, which suffered local kelp extinctions. Intensification of upwelling processes after the 1998-2000 La Niña increased nutrient inputs into subtidal habitats, favoring the productivity of the kelp assemblage. However, an abrupt change in the spatial-temporal patterns of abundance of the black sea urchin *Tetrapygus niger*, the most conspicuous benthic grazer in northern Chile, produced local extinctions of *M. integrifolia* and compression of the range of bathymetric distribution of *L. trabeculata*. Top-down (mortality of benthic carnivores during the 1997-1998 El Niño) and bottom-up effects (intensity and frequency of upwelling) in this subtidal coastal ecosystem appear to regulate the kelp-herbivore interactions in the study area. The main sources of reproductive propagules for the re-establishment of the assemblage kelp were fertile sporophytes which included isolated, low density patches of *M.integrifolia* located within the bed of *L. trabeculata*, although drifting kelp rafts and "seed banks" of microscopic dormant stages may provide supplementary recruitment. In the temperate SE Pacific, oceanographic events that act on different spatial-temporal scales plus low frequency biological processes (changes in grazer abundance), which act on local scales, produce inter-annual variability in the long-term dymanics of kelp populations. Furthermore, the interactive effects between centers of permanent upwelling and the oscillating temporal periodicity of oceanographic events that produce positive (El Niño) and negative (La Niña) thermal anomalies modify the spatial arrangement of subtidal kelp populations on a latitudinal gradient.

Key words: subtidal habitats, population and community ecology, extinction and re-colonization processes, kelp-herbivore interaction, 1997-1998 El Niño and 1998-2000 La Niña.

INTRODUCTION

The spatial-temporal patterns of kelp assemblages are generally determined by the diversity and population biology of the constituent species (Dayton *et al.* 1999). Seasonality of physical (eg. temperature, water movement, quantity and quality of light) and chemical (eg. nutrients) parameters are important in the regulation of reproductive and vegetative processes of specific components within kelp assemblages (Graham *et al.* 1997, Hernández-Carmona *et al.* 2001, Buschmann *et al.* 2004), and may covary in subtidal environments to produce synergistic interactions (Kain 1989). Conversely, biological processes such as inter- and intra-specific competition, pest and herbivory regulate kelp assemblage structure, modifying spatial and temporal patterns of species abundance (Dayton 1985, Vásquez & Buschmann 1997, Scheibling *et al.* 1999), and morphology (Vásquez 1991). Long-term studies in the Northern Hemisphere have shown that El Niño Southern Oscillation events (ENSO), which include alternation of a warm phase (El Niño) with a cold phase (La Niña), alter the structure and organization of subtidal kelp in temperate latitudes, modifying patterns of persistence, stability, succession, species diversity, and abundance (Dayton *et al.* 1992, 1999, Tegner *et al.* 1997). In the Southern Hemisphere, depending on the magnitude and intensity, El Niño can produce localized kelp extinctions (Camus 1994) and subsequent re-colonization that modify the spatial-temporal distribution and abundance of local populations (Camus *et al.* 1994, Martínez *et al.* 2003). Still, most studies of subtidal kelp population biology in the Southern Hemisphere are short-term (one year, see Vásquez 1993, Camus 1994, Buschmann *et al.* 2004, Tala *et al.* 2004), or are limited to high latitudes (≥ 40º S), where the influence of ENSO is minimal (Moreno & Sutherland 1982, Santelices & Ojeda 1984, Dayton 1985). As such, there are no long-term data concerning the effects of large-scale, low frequency events such as ENSO on kelp population biology. These oceanographic events are probably important in regulating interannual variability in the northern Chile biogeographic region (ca. 18-30ºS, see Camus 1990, Vásquez *et. al.* 1998).

The persistence of kelp populations on the northern Chilean coast during and after El Niño has been associated with coastal upwelling located at specific geographic areas (Mártinez 1999). One of the most important coastal upwelling centers of northern Chile is located near the Mejillones Peninsula (ca. 23ºS), which is seasonal, and related to the annual cycle of driving winds from the SW (Escribano *et al.* 2004). In this region, one of the main water masses being upwelled is that of Equatorial Subsuperficial Water (ESSW), characterized by low dissolved oxygen concentrations, low temperatures, and high concentration of nutrients (González *et al.* 1998). These water masses are transported shoreward by poleward flow in the first 200 m (Marin *et al.* 2001, Escribano *et al.* 2004). Interest in the Mejillones Peninsula sector has increased markedly in recent decades because some studies have reported that subsuperficial upwelling occurs in the area year round (Escribano 1998, Fonseca & Farias 1987). This promotes continuous, high primary and secondary production in the water column (Marin *et al.* 1993, Escribano & McLaren 1999, Fernández *et al.* 2002) as well as in the shoal litoral benthos (Vásquez *et al.* 1998; Camus & Andrade 1999), even during superficial warming generated by El Niño (Ulloa *et al.* 2001, Gonzalez *et al.* 2000, Vásquez & Vega 2004).

On the northern coast of Chile (ca. 23°S), the 1997-98 El Niño occurred as two pulses of positive thermal anomaly at the surface and sea level associated with strong poleward flows in the first 100 m (Takesue *et al.* 2004). The thermocline/oxycline and nutricline that normally rise to 40-60 m were depressed to 150-200 m depths between April and May 1997, and between Novembre 1997 and January 1998 (Ulloa *et al.* 2001). The 1997-1998 El Niño was immediately followed by La Niña conditions, characterized by a mild and moderate cooling of the water during 1998-1999, with cooling of greater intensity in 1999-2000 (Takesue *et al.* 2004). The 1998-2000 La Niña promoted the emergence of SW winds driving coastal upwelling, and intensifying the upsurge of subsuperficial water in the area of the Mejillones Peninsula (Lagos *et al.* 2002). The transition to a cold, nutrient-rich condition (La Niña) following a high-intensity warming event (El Niño) facilitates and increases the local recovery rates of kelp assemblages and their associated communities (Edwards 2004, Martínez *et al.* 2003). Within this context, a long term monitoring program of subtidal kelp at a site on the Mejillones Peninsula (beginning in 1996) permitted evaluation of the interactive effects of the ENSO cycle (1997-98 El Niño and 1998-2000 La Niña events) and effects of coastal upwelling on the population biology of South American subtidal kelps.

In Chile, between 18º and 32º S, two kelp species, *Macrocystis integrifolia* Bory and *Lessonia trabeculata* Villouta *et* Santelices, coexist in subtidal rocky environments, forming a broad subtidal assemblage from the intertidal to 15-20 m depths (Alveal *et al.* 1973, Vásquez *et al.* 2001). Both kelps have biphasic heteromorphic life cycles, with alternation of a microscopic gametophytic (n) generation, which is short lived, and a long-lived macrophytic perennial sporophytic generation (2n) (Buschmann *et al.* 2004, Tala *et al.* 2004). While there are some reports in the literature regarding the population biology of *L. trabeculata* (Villouta & Santelices 1984, Vásquez 1991, 1992, 1993, Tala *et al.* 2004), data are scarce on the population biology of *M. integrifolia* and the *M. integrifolia*-*L. trabeculata* assemblage. The available information is restricted only to evaluations of standing stock at some localities and observations on reproductive activity in controlled environments and in the field (Dieck 1993, Buschmann *et al.* 2004). In this context, the present study evaluated aspects of the population biology of the subtidal kelp assemblage formed by the canopy kelp *M. integrifolia* and the bottom kelp *L. trabeculata* in an area of intense upwelling in northern Chile. Specifically, we considered sporophyte distribution, abundance and reproductive phenology of both species. These data are the first to address the effects of the ENSO cycle (1997-1998 El Niño and 1998-2000 La Niña) on the South American subtidal kelp assemblage, and are contrasted with the effects of other El Niño events documented in both hemispheres.

MATERIALS AND METHODS

Study area

The density and reproductive phenology of *M. integrifolia* and *L. trabeculata* were evaluated on a seasonal basis between July 1996 and October 2003 at Caleta Constitución, on the Mejillones Peninsula (Fig. 1). This locality is within a bay, which is semi-protected from dominant SW winds and waves by the presence of Santa María I. The basal stratum of the subtidal kelp assemblage is composed of various foliose, turf, and crustose macroalgae. The macroalgae include crustose Corallinales, turfs of Gelidiales and/or Ceramiales, and often patches of *Halopteris spp*., *Glossophora kunthii* (C. Ag.) J. Ag., *Asparagopsis armata* Harley and *Rhodymenia spp*. and *Chondrus canaliculatus* (C. Ag.) Grev. (Vásquez *et al.* 2001). Detailed description of the study site and the marine ecosystem are give by Vásquez *et al.* (1998) and Vásquez & Vega (2004).

Oceanographic conditions

Mean daily *in situ* water temperature values were obtained using continuous-register thermographs (Onset Computer Corp., Bourne, Maine, USA) placed at three meter depth along the shoal boundary of the kelp assemblage. When *in situ* records of oceanographic variables were discontinued, large-scale climatic indexes were used, which permitted description of oceanographic conditions, and provided approximations of ecological processes that acted on smaller scales (Stenseth *et al.* 2003). Here, warm and cool phases of the ENSO were determined using monthly averages of the the Southern Oscillation Index (SOI) and the Multivariate El Niño Index (MEI) for the study period (1996-2003), from the Bureau of Metereology, Australia (www.bom.gov.au/climate/current/) and Climate Diagnostic Center of NOAA (www.cdc.noaa.gov/~kew/MEI/mei.html), respectively. Information on the temporal variability of upwelling events in the region (23-25ºS), was obtained from the monthly average index of upwelling (offshore Eckman transport, OET) between 1996 and 2001, obtained from the Pacific Environmental Laboratory (PFEL, www.pefg.noaa.gov/products/PFELindices.html). A detailed description of this calculation, and characteristics of the area of influence of the SOI, MEI and OET indexes have been presented by Navarrete *et al.* (2002).

Patterns of distribution and abundance of subtidal kelp assemblages

The spatial distribution of populations of *M. integrifolia* and *L. trabeculata* was evaluated seasonally (four times a year including summer, fall, winter, and spring) using four permanent transects laid perpendicular to the coast between the shoreline and 15 m depth, including the entire ranges of distribution of the kelp assemblage. The transects were 160 m in length and one meter in width, and were subdivided every 10 m to give 16 sampling units of 10 m^2. Juvenile and adult sporophytes were counted in each sampling unit. Juvenile sporophytes of *M. integrifolia* and *L. trabeculata* were plants with up to two lanceolate and laminar fronds without reproductive structures, and maximum holdfast diameter of ≤ 1cm. Sporophyte densities were expressed as the number of sporophytes per 10 m^2. Fertile sporophytes were recognized by the presence of sori on the sporophylls of *M. integrifolia*, or on the fronds of *L. trabeculata*.

The relative abundance and cover on different types of substrate in the study area were visually estimated in each sampling unit at the time of each seasonal sampling in order to estimate the abundance of substrate suitable for settlement of reproductive propagules. Substrate classifications included: (1) "barren ground" dominated by crustose calcareous coralline algae and two species of sea urchins (*Tetrapygus niger* Molina and *Loxechinus albus* Molina), (2) boulder fields, (3) consolidated rock, and (4) shell sand. The abundance of kelp species on the different substrates was also quantified.

Morphological variability of Lessonia trabeculata in the subtidal kelp assemblages

From 1996-1999, a total of 209 *M. integrifolia* and 203 *L. trabeculata* sporophytes were sampled haphazardly from each kelp bed. Also, 46 *L. trabeculata* sporophytes from below the canopy of *M. integrifolia* were randomly sampled, to contrast their morphologies with sporophytes collected from monospecific stands of *L. trabeculata*. Five morphological variables were determined after Vásquez (1991); these included the maximum diameter (cm) and weight (g) of holdfasts, the number of stipes, total plant length (cm) and total drained wet weight (kg) for each plant.

Kelp-herbivore interactions

The most conspicuous herbivorous grazer in the shallow rocky subtidal zone of the study site (and northern of Chile) is the sea urchin *Tetrapygus niger* (Vásquez & Buschmann 1997). Temporal changes in density of this species, related to the 1997-1998 El Niño and 1998-2000 La Niña, were determined by seasonal evaluation of 64 quadrats of 0.25 m^2 each, using steel frames haphazardly tossed among the perpendicular transects described above. The densities of sea urchins were expressed as the number of individuals per m^2. A correlation analysis between the average densities of the herbivores *T. niger* and *L. albus* (another sea urchin frequent in the area, but less abundant; Vásquez & Vega 2004) and the average densities of *M. integrifolia* and *L. trabeculata*, was carried out to evaluate the potential effect of herbivory on the spatio-temporal patterns and interannual variation in abundance of kelps.

Statistical Methods

A nested analysis of variance (ANOVA) using the year as the main variable and seasons of the year as nested factors was used to evaluate the hypothesis that ENSO generated interannual variability in patterns of abundance of *M. integrifolia* and *L. trabeculata*. For this, transects were considered as replicates, averaging the 10 m^2 quadrats within each transect. The nested analyses of variance (ANOVA) was done after visual determination of normality of the data and homocedasticity of variances by means of a Bartlett test (Sokal & Rohlf 1981), using SYSTAT 8.0® computational software for Windows; transformations (log abundance + 1) were applied when necessary to improve homoscedasticity (Sokal & Rohlf 1981). An *a posteriori* Tukey test (Sokal & Rohlf 1981) was used order to determine which groups differed from others. The year 2000 was excluded from the analyses of abundance of juveniles of *M. integrifolia* since no juveniles were found that year. The relationship between population variables and the substrate, and herbivore abundance (sea urchins) was examiend using Pearson correlation analyses (Sokal & Rohlf 1981).

A multivariate discriminate function analysis was applied to compare morphologies of the *L. trabeculata* sporophytes between inside and outside of the *M. integrifolia* canopy using SYSTAT 8.0. Discriminat analysis has been previously used to evaluate morphological variability between populations of *M. integrifolia* (Druehl 1978, Druehl & Kemp 1986).

RESULTS

Oceanographic conditions

The *in situ* sea temperature showed a seasonal pattern, with warm water between December and March (summer) and cool water between June and September (winter) (Fig.2A). During the study period between April 1997 and March 1998 the seawater was unusually warm, with maximum positive thermal anomalies fluctuating between +2 and +2.5°C. An exception occurred between August and November 1997 when upwelling events lowered the seawater temperatures, interrupting the anomalous warm period. Immediately afterward, beginning in April 1998, cooling of the water began with a weak, moderate, and strong La Niña event when the seawater anomaly ranged between -0.5 and -1.5°C until the end of 2000 (Fig.2A). The southern oscillation index (SOI, Fig. 2B) and the multivariate El Niño index (MEI, Fig. 2B) showed normal conditions in 1996 lasting until summer 1997. The El Niño event was clear between May 1997 and March 1998, coinciding with the thermal anomaly detected by the *in situ* temperature records (Fig. 2A). Following the nearly normal, weakly-cold period of 1998-2000, a new warmer period was observed between April 2002 and April 2003, which was of low to moderate intensity (Fig. 2B), casusing a positive thermal anomaly of 1ºC. Mean values for the upwelling index (OET) were always positive during the study period, showing the persistence over time of offshore Ekman transport conditions in the region (Fig. 2C). The upwelling index showed greater offshore transport between September and December (spring), and lower intensities between April and July (Fig. 2C). The highest upwelling activity occurred during the spring of 1996, decreasing significantly in May 1997 at the beginning of the 1997-1998 El Niño. Nevertheless, the Ekman transport remained active, constant, and intense between July 1997 and February 1998 (Fig, 2C) during the maximum thermal anomalies of the 1997-1998 El Niño (see also Ulloa *et al.* 2001, Navarrete *et al.* 2002).

Patterns of spatial distribution of subtidal kelp assemblages

Under “normal” oceanographic conditions (winter 1996 to summer 1997), the kelp assemblage formed by *M. integrifolia* and *L. trabeculata* at Caleta Constitución was distributed from 2 to 15 m depth, although the two kelp species demonstrated different bathymetric distributions. The maximum abundance of *M. integrifolia* occurred at onshore depths, between 5-8 m, while the maximum abundance of *L. trabeculata* occurred between 8 and 13 m (Fig.3A). Between 9 and 11 m depth, both kelp species reached similar abundances (Fig.3A). The percentage of consolidated rocky substratum per sampling unit was correlated significantly and positively with kelp abundance (Pearson r=0.74; p<0.001). There were no significant temporal modifications in the form of the substrate during the study period over the length of the bathymetric gradient studied. The density of *M. integrifolia* decreased in shoal bottoms onshore as the percentage of barren ground covered with crustose coralline algae increased (Fig.3B). In contrast, from 13 m depth to offshore, the frequency of shell sand increased, marking the deeper limit of kelp distribution due to a decrease in consolidated rocky bottom (Fig.3B). At depths greater than 15 m shell sand completely covered the bottom and neither kelp species was present.

Patterns of temporal distribution of subtidal kelp assemblages

The density of *M. integrifolia* adult sporophytes differed significantly ($F_{(6,21)}= 35.40$; p<0.001) between years in which measurements were made (Fig. 4A). The seasonal patterns of abundance of adult sporophytes differed significantly among years ($F_{(21,84)}= 8.57$; p<0.001), particularly during 1997-1998 (El Niño event) and 1999-2000 (La Niña event). Paradoxically the passage of 1997-1998 El Niño coincided with an increase in the abundance of adult sporophytes of *M. integrifolia*. Between fall 1999 and spring 2000 (Fig.4B) no *M. integrifolia* juveniles were observed in the sampling units (10 m^2), nor in the study area, where additional exploratory diving was carried out. Aside from this period, juvenile *M. integrifolia* were present throughout the year without a defined seasonal pattern (Fig.4B). Significant seasonal increases or decreases ($F_{(18,72)}= 5.63$; p<0.001) in the long term abundances of juveniles appeared to be determined by the intensity of upwelling events during the 1997-1998 El Niño, based on the significant decreases in adult sporophytes (1999) and characteristics of the re-establishment process of the *M.integrifolia* population (2001-2003).

Seasonal patterns in the abundance of adult *L. trabeculata* sporophytes differed significantly ($F_{(21,84)}= 88.18$; $p<0.001$) between years, but in contrast with *M. integrifolia*, the population maintained a mean annual abundance of about 3.9 ± 1.5 plants per 10 m^2 over the entire period of the study. The 1997-1998 El Niño negatively affected the abundance of *L. trabeculata* in spring 1997 and summer 1998, while the 1998-2000 La Niña increased the abundances (Fig. 4C). The abundance of juveniles *L. trabeculata* was significantly higher in spring ($F_{(21,84)}= 193.95$; $p<0.001$). In spite of the preceding, the re-establishment of adult sporophytes after the 1997-1998 El Niño and the mortality of these plants due to herbivore pressure (1999-2001) modified the seasonal pattern of abundance of juveniles between years (Fig. 4D).

Interannual variability of spatial patterns of subtidal kelp asemblages

The disjunct pattern of distribution of kelp over the bathymetric profile was persistent over the eight years of the study. Nevertheless, the spatial patterns of abundance of the adult and juvenile sporophytes of *M.integrifolia* over the bathymetric gradient differed for adult and juvenile sporophytes among years (Fig.5). The continuous incorporation of *M.integrifolia* juveniles to the system between 1996 and 1999 permitted the maintenance of spatial distribution patterns of the adult sporophytes. Although during the transition period between the El Niño and La Niña events (1998) an increase was detected in juveniles over the length of the bathymetric profile, the patterns of distribution and abundance of the adult sporophytes were not altered during the following year (1999). During 2000 a few shoal adult sporophytes (1-2 m depth) remained under the *L. trabeculata* canopy (> 10 m depth) in the study area; in contrast, no sporophyte juveniles were detected (Fig.5). Re-establishment of the subtidal kelp *M. integrifolia* occured by successful recruitment, demonstrated by the establishment of juveniles which surrounded the few surviving adult sporophytes, and generating a nucleus which expanded towards the extremes of the bathymetric gradient (2001, Fig.5). New recruitment of juvenile sporophytes in following years expanded the kelp (*eg*. 2002-2003), until a kelp forest was formed which was similar to that observed at the beginning of this study (Fig.3 y 5).

The patterns of abundance of the adult and juvenile sporophytes of *L. trabeculata* differed over the bathymetric gradient between years (Fig.6). The spatial pattern of abundance of *L. trabeculata* became modified during 2000 at the end of the 1998-2000 La Niña and not during the 1997-1998 El Niño (Fig. 6). Over the eight years of the study, the maximum abundances of adult sporophytes occured at the limits of depth of its distribution, with the juveniles occurring over the entire bathymetic distribution of this kelp (Fig.6).

Reproductive phenology of subtidal kelp assemblages

Adult sporophytes of *M. integrifolia* and *L. trabeculata* with reproductive structures (sporophylls and sori on the fronds, respectively) were present throughout the entire study period (Fig.7). During the 1997-1998 El Niño, the percentage of reproductive plants of both kelp species remained above 70%. During the 1999-2000 La Niña, all of the few sporophytes of *M. integrifolia* (average densities of 0.1 to 0.6 individuals per 10 m^2) were reproductive (Fig. 7A), while the percentage of fertile sporophytes of *L. trabeculata* remained above 75% (Fig.7B). During 2001-2002 the percentage of fertile soporophytes of *M. intergrifolia* was lower, as a consequence of the increases in infertile juvenile sporophytes as the population became re-established (Fig.7A). Between 2001 and 2003 the decrease in fertile *L. trabeculata* sporophytes by incorporation of juveniles was markedly seasonal (summer-fall 2001, and fall 2003), however, the frequency of reproductive plants was maintained over 50% (Fig.7B).

Herbivore-kelp interactions

The sea urchin *T. niger* was the most conspicuous herbivore at Caleta Constitución, coexisting with another, less abundant urchin, *L. albus*. The temporal patterns of abundance of *T. niger* showed three significant ($F_{(6,21)}$=18.032; p<0.001) maxima over the study period, which were different from each other (Fig.8). The sea urchins showed low levels of abundance between 1996 and 1999, including the 1997-1998 El Niño (Fig.8). During the 1998-2000 La Niña (fall 1999 -spring 2000) the mean density of black urchins increased three fold between 1996 and 1998 (Fig.8). During 2000 the black sea urchins formed herds over hard substrates at shoal depths from 8 to 10 m depth. This change in spatial-temporal patterns of abundance of *T. niger* coincided with the local extinction of the *M. integrifolia* population and the decrease in abundance of *L. trabeculata* at its depth limit. An inverse and significant correlation suggested that the density of juvenile and adult *M. integrifolia* sporophytes decreased with an increase in abundance of *T. niger* (Table 1). In contrast, non-significant correlations occurred between *T. niger* and *L. trabeculata* or between *L. albus* and both kelp species (Table 1). Beginning in 2001, the abundance of *T. niger* began to decrease until the end of 2003, giving values similar to those encountered between 1996 and 1999 (Fig.8).

Morphological variability of Lessonia trabeculata in subtidal kelp assemblages

We observed two different morphologies of *L. trabeculata* as previously described by Vásquez (1992) within the assemblage of subtidal kelp over the bathymetric gradient at Caleta Constitución. These included a "bushy" morph consisting of sporophytes with large numbers of small stipes, where the total weight of the plant was distributed among the many, highly flexible stipes. A second “arborescent” morph, was formed of sporophytes with few, long, thick stipes in which the weight of the plant was concentrated; these stipes showed little flexibility. Discriminate function analysis showed the number of stipes and the maximum diameter of the holdfast to be the main functions useful in discriminating between the two *Lessonia* morphs. *L. trabeculata* sporophytes with the bushy morph occurred mostly in stands dominated by *M. integrifolia* (Fig.9). Conversely, monospecific beds of *L. trabeculata* were made up of sporophytes with the arborescent morphology (Fig.9), particularly at the deeper limits of their distribution. The bathymetric distribution pattern of the bushy and arborescent morphs of *L. trabeculata* found within the kelp assemblage from 1996 to 1999 was re-established at the end of the study period (winter and spring 2003).

DISCUSSION

The structure of subtidal kelp assemblages on the exposed rocky shores of northern Chile is simple, and represented by monospecific stands of bottom kelp *L. trabeculata* (Villouta & Santelices 1984, Vásquez 1992, Tala *et al.* 2004). On semi-exposed and protected subtidal rocky shores, *M. integrifolia* forms the canopy that grows to the surface while the bottom kelp, *L. trabeculata,* forms the sub-canopy, although with disjunct distributions over the bathymetric gradient. This is in contrast to subtidal kelp assemblages found at equivalent latitudes in the Northern Hemisphere, where there is hierarchical organization through interspecific competition among the several components of kelp forests (Dayton *et al.* 1992, 1999, Tegner *et al.* 1997).

Spatial patterns of abundance in subtidal kelp assemblages

It has been proposed that the segregated patterns of bathymetric distribution in kelp assemblages are a reflection of species-specific morphological adaptations to wave exposure (Druehl & Kemp 1986, Santelices & Ojeda 1984, Utter & Denny 1996), species-specific physiological adaptations based on light and nutrient requirements for photosynthesis and/or growth (Druehl 1978, Gómez *et al.* 1997, Apprill & Lesser 2003), and on endogenous factors such as circadian or circannual rhythms that respond differentially to environmental changes (Schaffelke & Lünning 1994). Interspecific competition has also been suggested as a structural agent in kelp assemblages over bathymetric gradients (Reed & Foster 1984, Santelices & Ojeda 1984, Tegner *et al.* 1997). At Caleta Constitución, the higher rate of colonization and growth of *M. integrifolia* during 2002-2003 produced a negative effect on the recruitment and growth of *L. trabeculata* juveniles between 2 and 7 m depth. This appears to induce a modification of the morphology of the adult sporophytes of *L. trabeculata* under the *M. integrifolia* canopy. The potential effect of a *M. integrifolia* stand in reducing wave action and this, in turn, influencing *L. trabeculata* morphology instead of or in addition to competition must be explored. Hypotheses that explain the patterns of distribution of *M. integrifolia* and *L. trabeculata* over bathymetric gradients are not exclusive. Species-specific morphological and/or physiological adaptations, as well as interspecific competition may interact at different depth levels of the assemblage to produce a segregated pattern of distribution, generating different morphs of *L. trabeculata* over the range of bathymetric distribution. This hypothesis needs to be tested in the future by means of *in situ* experimental removal and competitive exclusion experiments, in order to evaluate recruitment and species-specific growth rates.

Temporal patterns of abundance in subtidal kelp assemblages

The abundances of *M. integrifolia* and *L. trabeculata* differed markedly between years during the study period. These annual differences are a reflection of modifications in seasonal patterns of both kelps. Temporal variations in the abundances of kelp in temperate environments of the Northern Hemisphere are correlated with thermal anomalies coupled to annual temperature oscillations. These co-vary inversely with the availability of nutrients (Dayton *et al.* 1992), generating different seasonal patterns of abundance (Dayton *et al.* 1999). Nevertheless, physical, (*eg.* storms and swells) and/or biological (*eg.* pests, herbivory) disturbances of low frequency and intensity produce breaks in spatial-temporal distributions (Tegner *et al.* 1997, Dayton *et al.* 1998), adding additional randomness to long-term patterns of abundance. Populations of *M. integrifolia* and *L. trabeculata* in northern Chile are formed by perennial and long-lived sporophytes, which maintain their levels of abundance during the year, with seasonal variability in growth and reproduction (Buschmann *et al.* 2004, Tala *et al.* 2004). This apparent temporal stability (annual variability) in the population dynamics of the South American kelp is, however, interrupted (interannual variability) by: 1) positive thermal anomalies during El Niño, which generate mortalities correlated with latitude (Tomicic 1985, Camus 1994, Godoy 2000), and (2) site-dependent recolonization events of varying intensity during cool and normal years (Camus 1994, Martínez *et al.* 2003). In this context, our results have shown that in the study area: (1) during the 1997-1998 El Niño the patterns of abundance of both kelp did not change significantly, (2) kelp productivity during the 1998-2000 La Niña event was reduced to minumum levels due to the extinction of *M. integrifolia* in shallow depths and decrease in abundance of *L. trabeculata*, and (3) the re-establishment of the kelp assemblage occurred post La Niña, during the mild, and poorly documented 2002-2003 El Niño event.

The temporal pattern of recruitment of sporophytes differed between the two kelps. While *M. integrifolia* showed recruitment throughout the year (as in other wave-protected environments; see Graham *et al.* 1997), *L. trabeculata* showed seasonal recruitment during the winter, producing greater abundance of juveniles during the spring. These differences in recruitment pattern (annual *vs* seasonal) imply differing reproductive strategies between the kelp species, which may in part explain the temporal dynamics of the assemblage and require clarification through application of experimental protocols in the future.

Spatial-temporal patterns of distribution in subtidal kelp assemblages

Spatial-temporal patterns of distribution and abundance of *M. integrifolia* and *L. trabeculata* did not become significantly modified during the 1997-1998 El Niño.This is in contrast with local extinction processes during this El Niño documented for other kelp-dominated areas in Peru and Chile (Fernandez *et al.* 1999, Godoy 2000, Lleellish *et al.* 2001) and California (Ladah *et al.* 1999, Edwards 2004). The persistence of spatial and temporal patterns in kelp assemblages during the 1997-98 El Niño in the study area may be explained by the frequency and intensity of coastal upwelling (González *et al.*1998, Vásquez *et al.* 1998, Lagos *et al.* 2002), which buffers and minimizes superficial heating of the sea and impoverishment of nutrients in littoral waters (Gonzalez *et al.* 1998, Takesue *et al.* 2004). Based on our results it can be suggested that the persistence of kelp populations in the above mentioned upwelling areas during the 1997-1998 El Niño might function as local "sources" which "export" propagules to other localities "sinks" without upwelling where mass mortalities have occurred (Camus 1994).

The recovery rate of kelp populations in localities in which extinction processes occurred as a result of the El Niño is favored when there is a rapid transition to cool periods or La Niña (Edwards, 1994). La Niña conditions reinforce coastal upwelling processes, generating conditions favorable for the growth and development of juvenile kelp sporophytes (Tegner & Dayton 1987, Dayton *et al.* 1998). During the period of the present study, La Niña (1998-2000) conditions occurred almost immediately after passage of the 1997-1998 El Niño. However, the spatial-temporal pattern of distribution de *M. integrifolia* and *L. trabeculata* became modified in the study area during the 1998-2000 La Niña due to significant changes in the patterns of distribution and abundance of the sea urchin *T.niger* during 1999-2000.

Kelp-herbivore interactions

An increase in grazing pressure was documented as simultaneously occurring with warming of coastal surface waters at low latitudes (10-23ºS) of both Hemispheres during the 1997-1998 El Niño (Halpin *et al.* 2004). In this context, positive thermal anomalies and bathymetric migrations of grazers produce a sinergistic effect, causing local extinctions of *Macrocystis spp.* (Godoy 2000, Llellish *et al.* 2001), and decreases in the bathymetric range of *L. trabeculata* (Fernández *et al.* 1999, Vásquez & Vega 2004). In contrast, the present study showed an absence of local extinctions during the 1997-98 El Niño. A combination of "top-down" and "bottom-up" effects appear to regulate these ecosystemic changes, including (**1**) the 1997-98 El Niño significantly decreased the density of starfish between 2 and 10 m depths, the bathymetric range with the highest density of *M.integrifolia* (Vásquez & Vega 2004). These benthic organisms form the most important guild of carnivores on the SE Pacific coastline (Vásquez & Buschmann 1997). (**2**) Warming of surface waters in the study area, moderated by upwelling events during 1997-98, induced many sea urchin spawnings which produced successful recruitment during the 1999-2000 La Niña (Vásquez & Vega 2004), (**3**) the dephase in local extinction of kelp populations two years after the 1997-98 El Niño occurred atypically during the 1999-2000 La Niña.

The mass mortality of *M. integrifolia* in the study area thus seems to be a consequence of the relation of predator-prey abundances. Top-down and bottom-up regulation generated by the El Niño in communities dominated by *Macrocystis pyrifera* in California have recently been reviewed by Halpin *et al* (2004).

The survival of a few fertile sporophytes after local extinctions of *M. integrifolia* in 2000 appears to have been the main source of reproductive propagules for the re-establishment of the subtidal assemblage at Caleta Constitución. Drifting rafts of kelp, and “seed banks” of microscopic dormant stages may be considered as complementary strategies for the re-establishment of assemblages of kelp (Dayton *et al.* 1992, Ladah *et al.* 1999, Buschmann *et al.* 2004, Edwards 2004).

Centers of upwelling may act to modify the littoral biota, but in contrast with El Niño events, they act on a local scale. Permanent upwelling has an upwardly cascading or "bottom-up" regulation of the communities on coastal ecosystems (Vásquez *et al.* 1998, Camus & Andrade 1999, Nielsen & Navarrete 2004). The permanent subsidy of nutrient-rich waters and low temperature has been considered an important factor in the increase in biodiversity and productivity of coastal zones where it occurs (Bosman *et al.* 1987, Ormond & Banaimoon 1994, Nielsen & Navarrete 2004). Our study suggests, as well, that areas with permanent upwelling decrease the effects of upper-layer warming generated by high-intensity El Niño events, permitting the persistence of kelp populations. Here, the correspondence between intensity and frequency of coastal upwelling during El Niño events may explain variability among effects produced in coastal communities by this oceanographic event. In the present study area, the 1982-1983 El Niño caused mass mortalities of intertidal and subtidal kelp (Tomicic 1985), with a recovery time of over 10 years (Martínez *et al.* 2003). In contrast, superficial warming during the 1997-1998 El Niño did not modify the spatial and temporal patterns of the coastal kelp assemblages at Caleta Constitución.

Infrequent and hard-to-predict disturbances, such as the significant increase in herbivores during the 1998-2000 La Niña event, further add randomness to the spatial-temporal patterns of the distribution and abundance of organisms inhabiting communities dominated by kelp. Other poorly predictable biological disturbances that document changes in patterns of abundance and distribution of kelp species include pests (Graham *et al.* 1997), and mass mortalities of benthic grazers (Dayton *et al.* 1998), as well as mortalities of high-level predators (Estes *et al.* 1998). Although coastal upwelling processes and large-scale oceanographic events such as El Niño and La Niña produce local variability, their effects have been studied and documented separately both on a temporal and spatial basis. Our results suggest the need for maintaining long-term studies, which allow integration of physical and biological processes on a local scale (*eg.* upwelling, predator-prey interactions, plant-plant interactions, pests, mass mortalities), with low frequency, large-scale climatic event (El Niño-La Niña).

ACKNOWLEDGEMENTS

The authors are thankful for the collaboration received from D.Veliz, L.M.Pardo, C.Cerda, F.Veliz, J.Rivera, N.Godoy, E.Rojas, C.Ibacache, J. Barrios, P.Bravo and N.Piaget during the demanding days of diving research. Also the authors thank S. Navarrete, M. Graham, M. Edwards and one anonymous reviewer for helpful comments on the manuscript. This work was supported by FONDECYT-SECTORIAL 5960001, FONDAP 0&BM N°3, FONDECYT 1000044-1010706. This research is part of Masters of Science Thesis of the first author, in the Masters Program in Marine Sciences at the UCN.

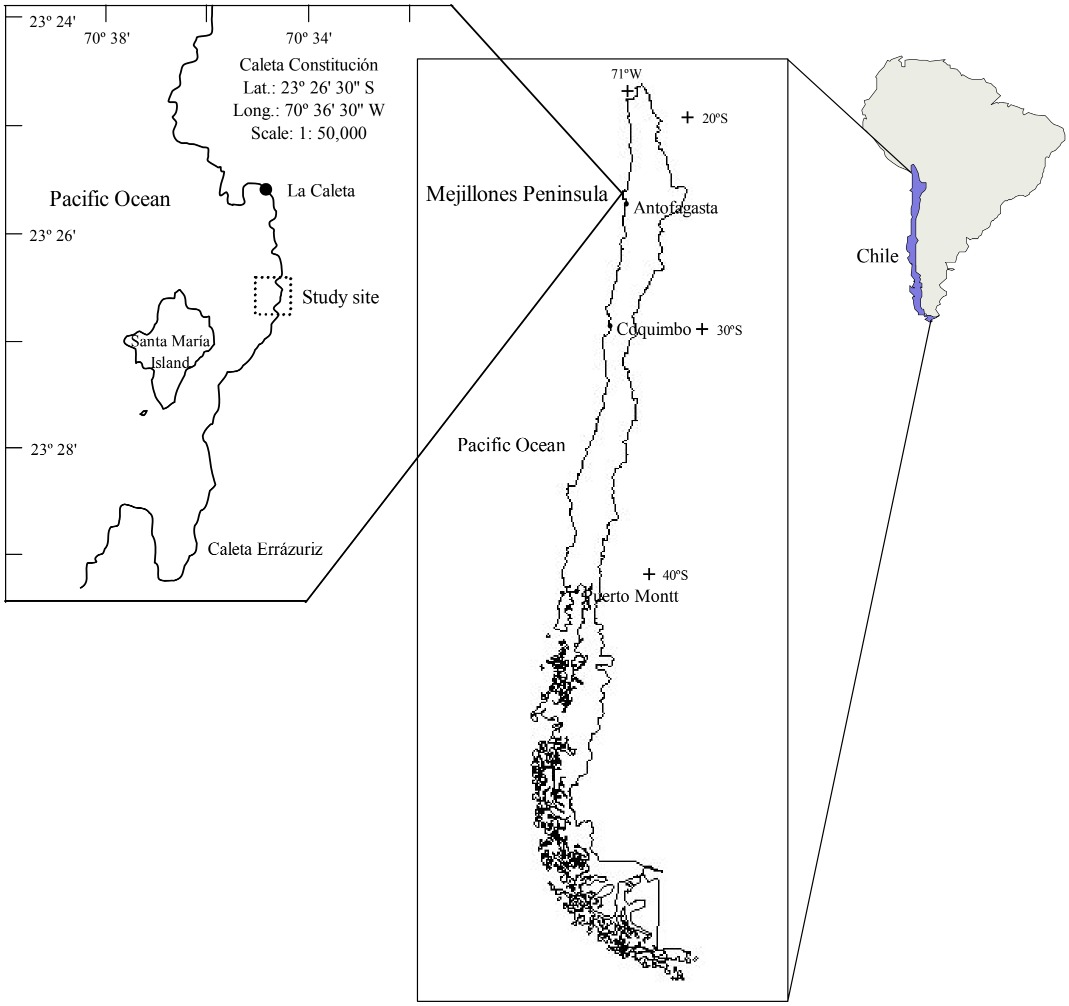


Figure 1. Geographic location of the study area.

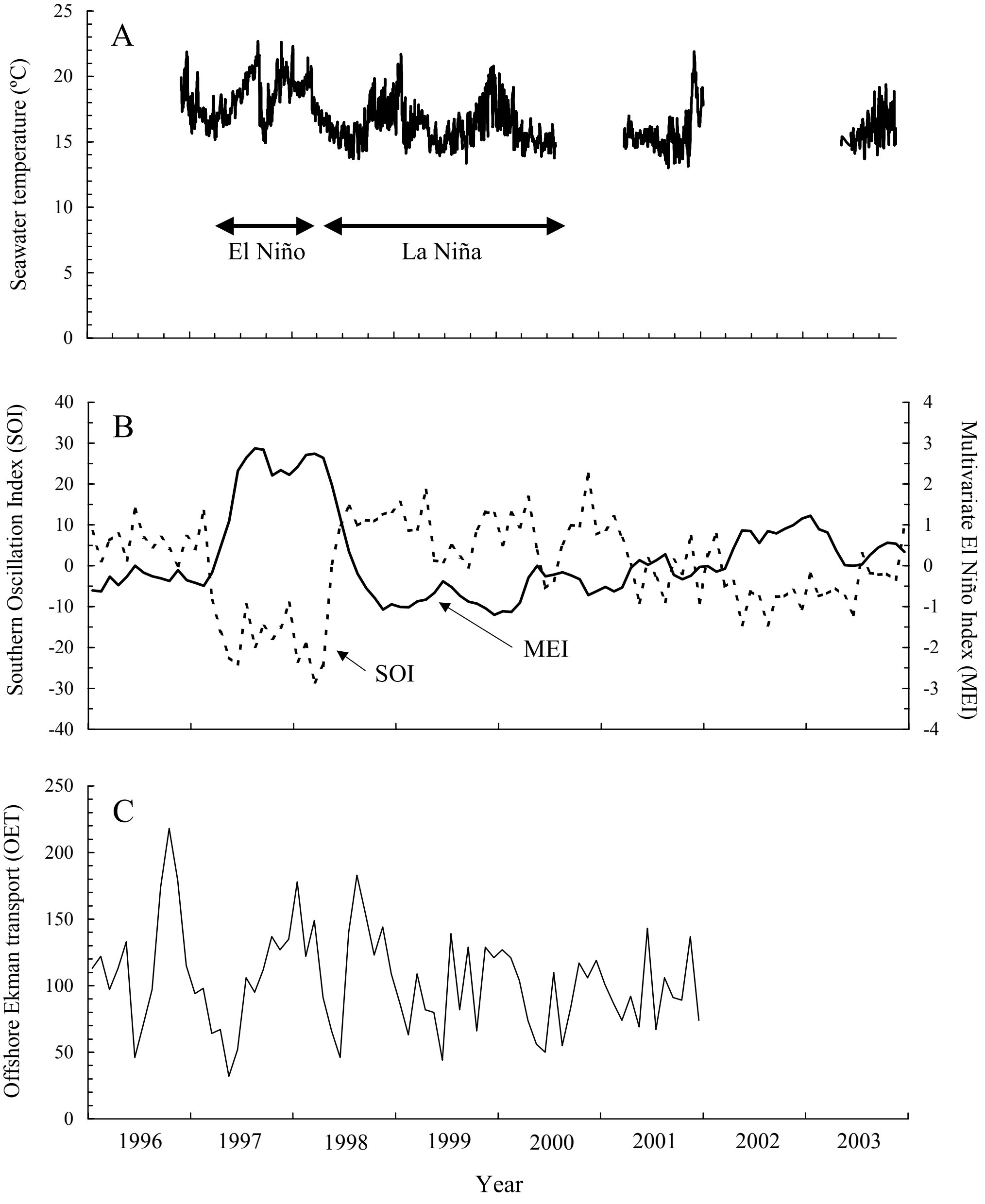


Figure 2. Seawater temperature to 3 m depth into of kelp assemblage (A), Multivariate El Niño (MEI) and Southern Oscillation (SOI) indexes (B), and upwelling index (Eckman transport, OET) (C) during the study period.

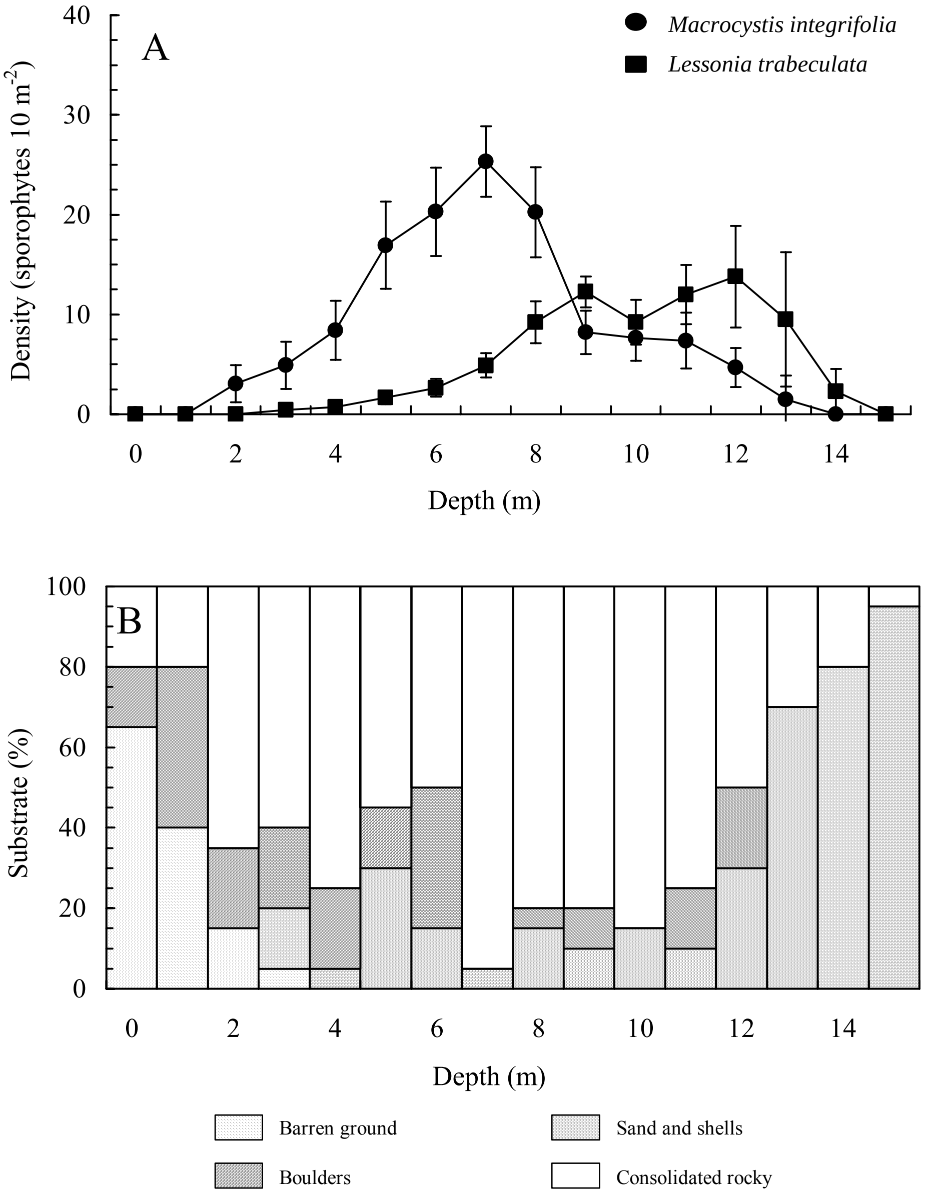


Figure 3. Spatial patterns of abundance of adult sporophytes of *Macrocystis integrifolia* and *Lessonia trabeculata* (A) and relative frequency of different substrates across the bathymetric profile in the study area (B) in no El Niño condictions between 1996-1997. Data are means ± SD.

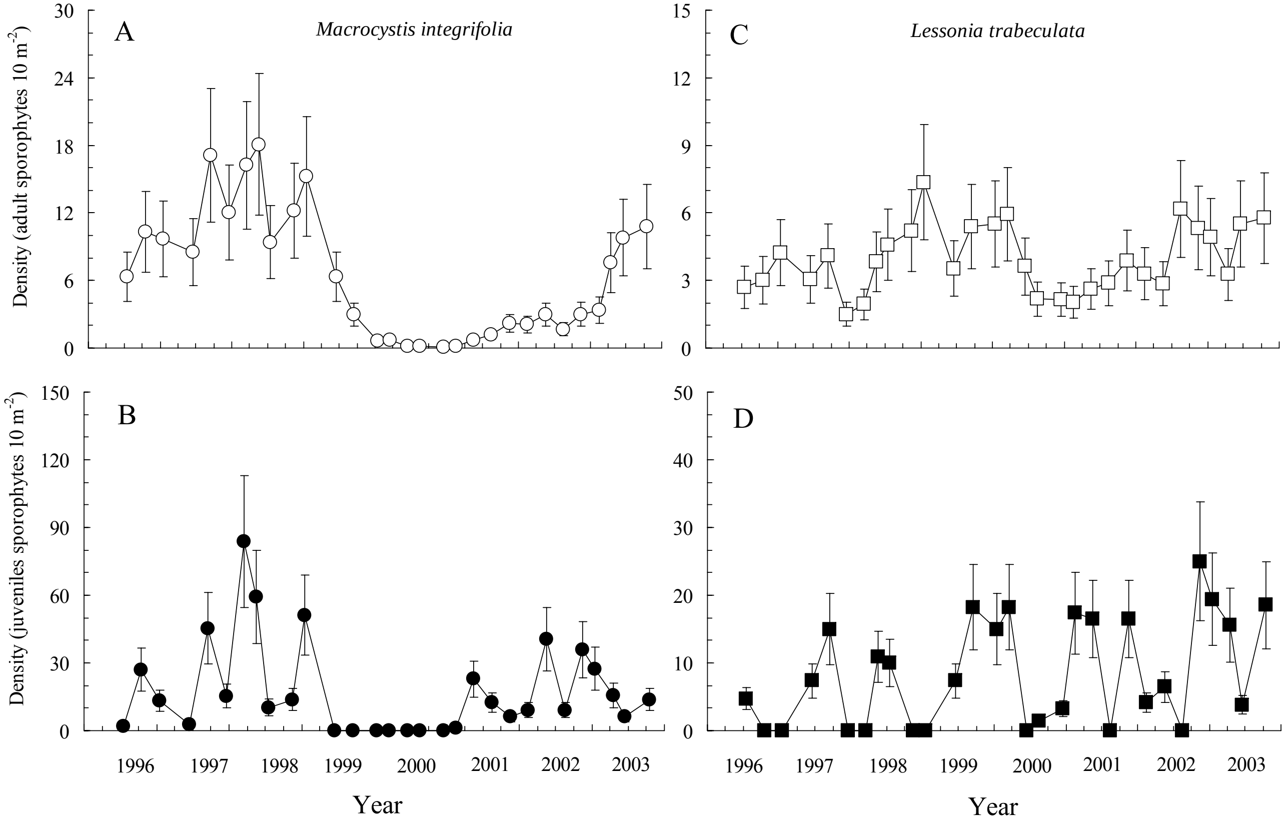


Figure 4. Temporal patterns in the abundance of adult (A) and juvenil (B) of sporophytes of *Macrocystis integrifolia* and adult (C) and juvenil (D) of sporophytes of *Lessonia trabeculata.* Date are means ± 2EE.Fig.

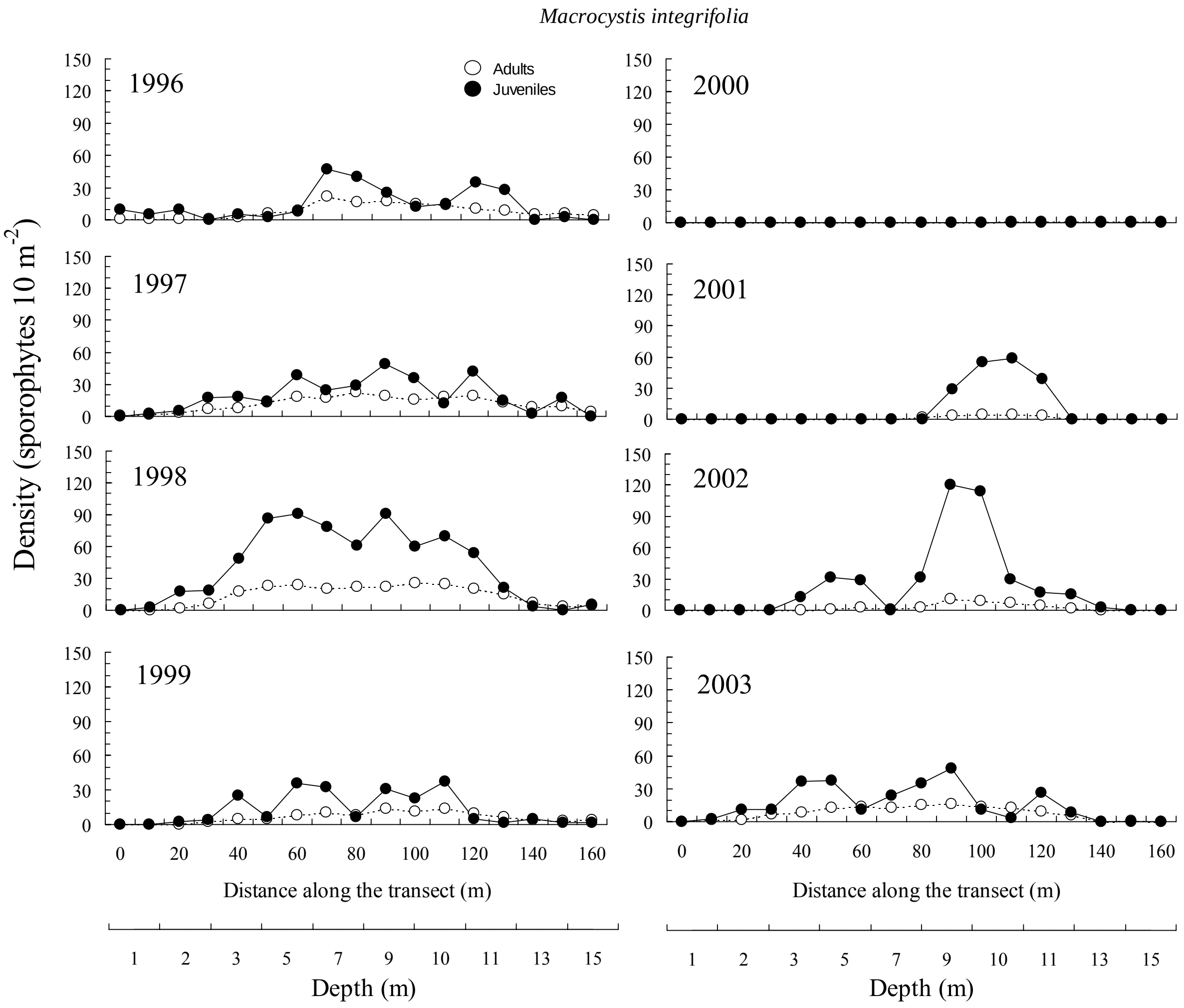


Figure 5. Interannual variability patterns in the average abundance of adult and juveniles sporophytes of *Macrocystis integrifolia* along bathimetric profile.

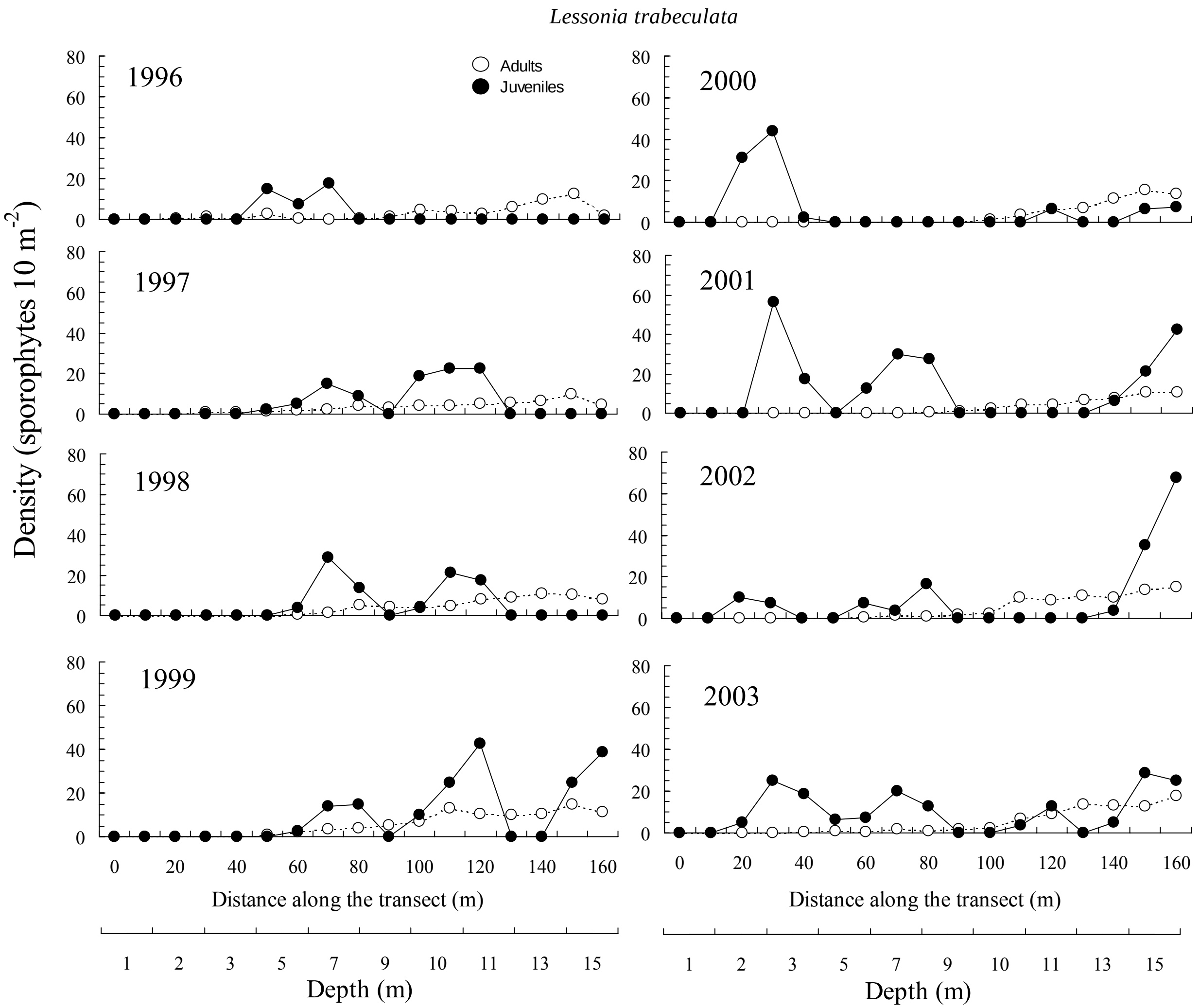


Figure 6. Interannual variability patterns in the average abundance of adult and juveniles sporophytes of *Lessonia trabeculata* along bathimetric profile.

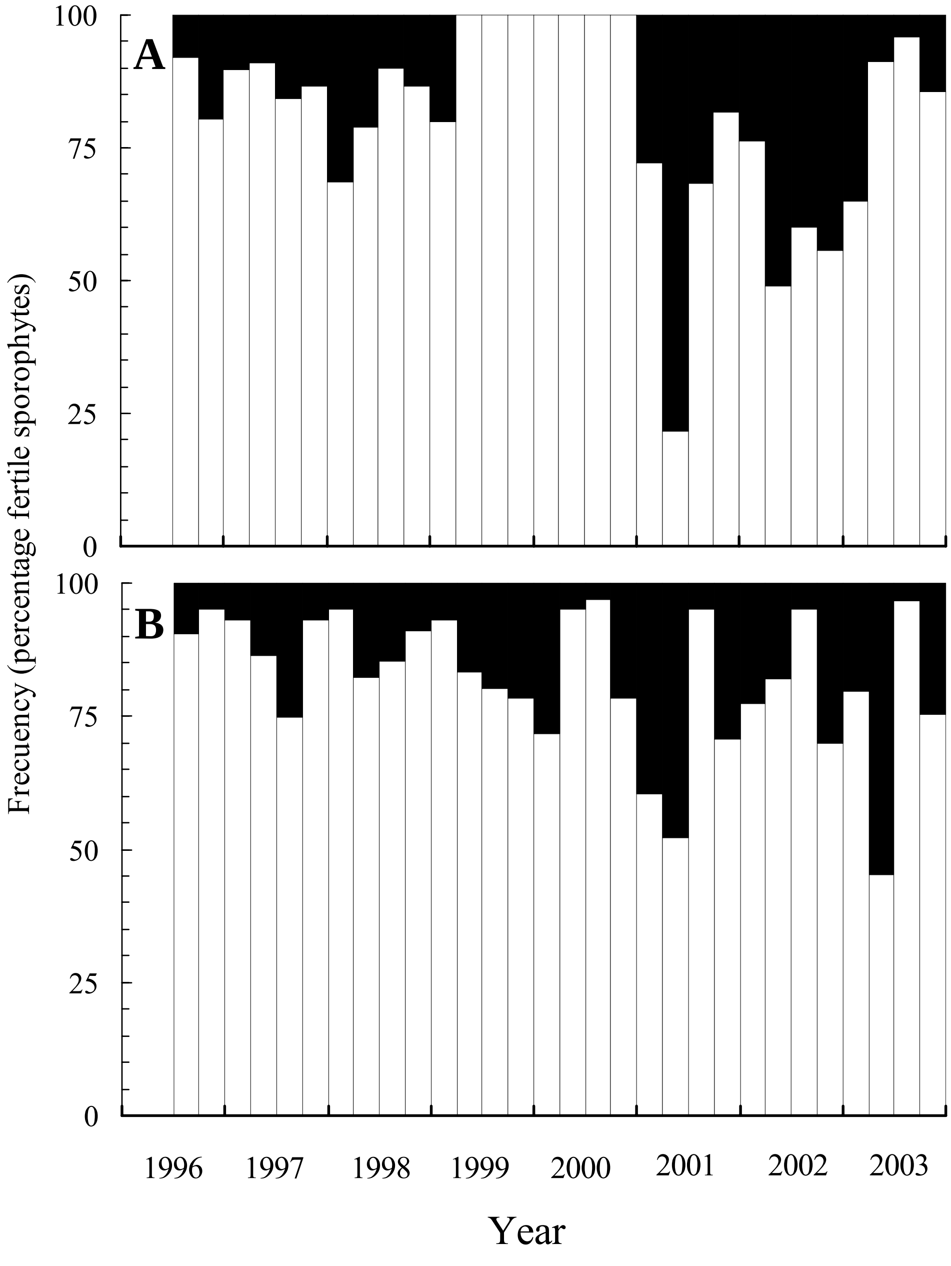


Figure 7. Reproductive frecuencies of sporophytes of *Macrocystis integrifolia* (A) and *Lessonia trabeculata* (B) during study period. White bars indicate fertile sporophytes and black bars indicate infertile sporophytes.

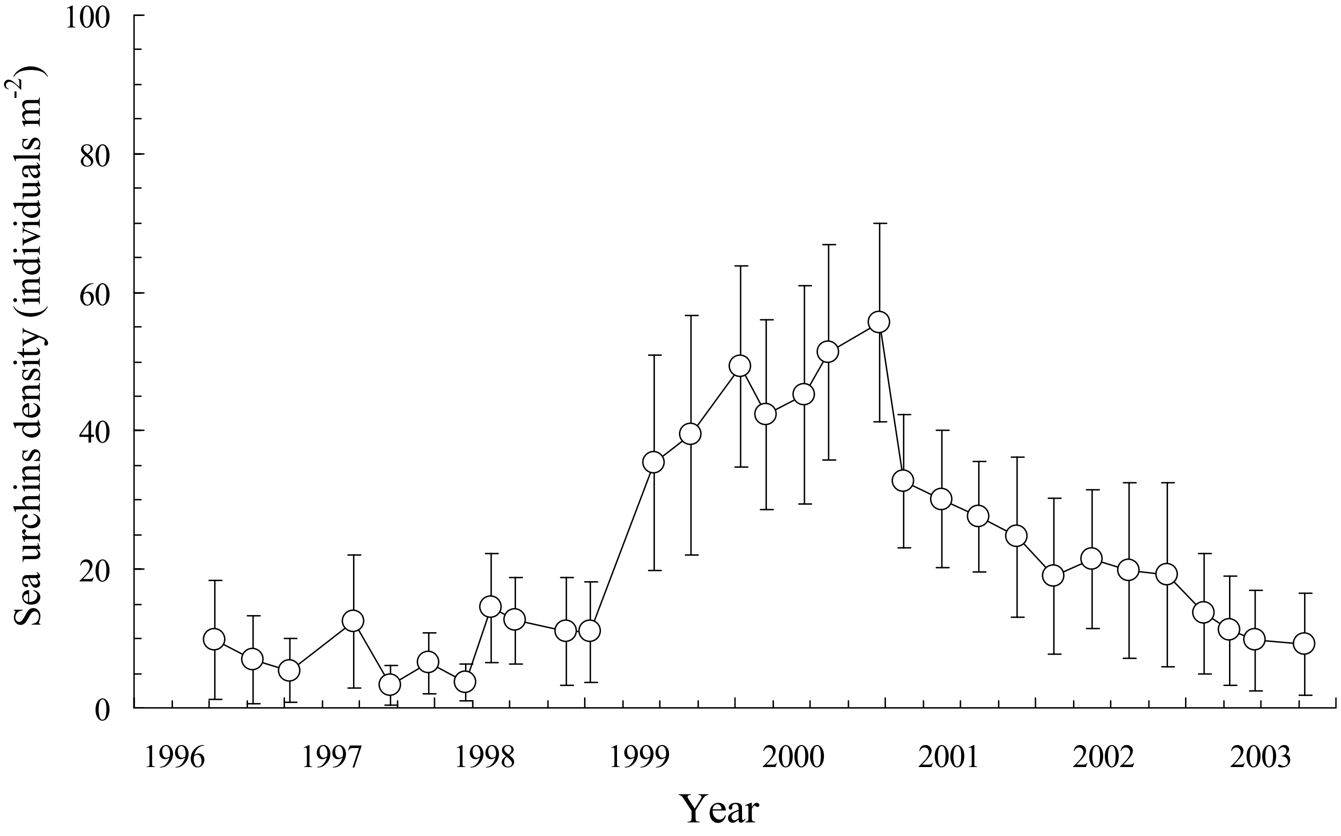


Figure 8. Temporal patterns in the abundance of *Tetrapygus niger*. Data are means ± 2EE.

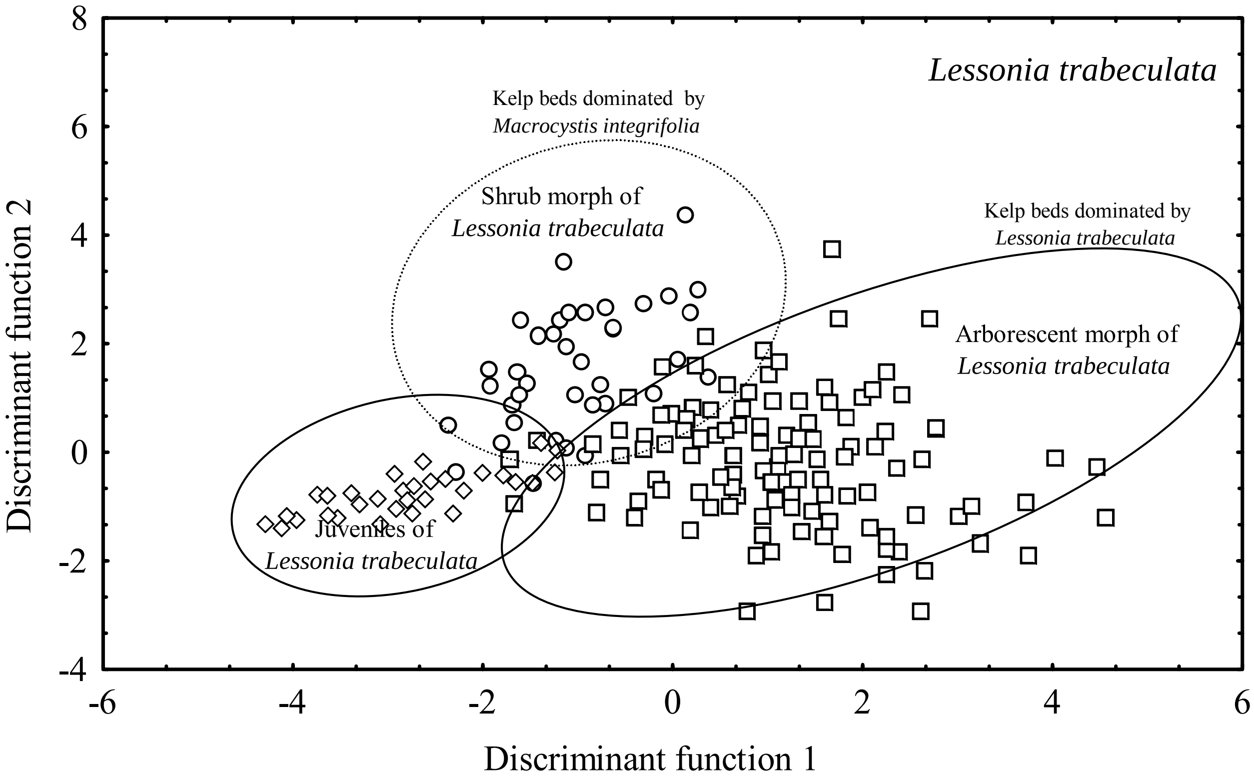


Figure 9. Analysis of discriminate functions using five morphological parameters to differentiate juvenile and adult plants of *Lessonia trabeculata* in presence/absence of *Macrocystis integrifolia*.

Table 1. Pearson correlation coefficient (probability in parenthesis) between sea urchins and kelp abundance. Significant association at alpha = 0.05.

	Tetrapygus niger	*Loxechinus albus*
Macrocystis integrifolia		
Adults	-0.67	-0.17
	(0.0001)	(0.3631)
Juveniles	-0.51	0.06
	(0.0036)	(0.7374)
Lessonia trabeculata		
Adults	-0.22	0.30
	(0.2343)	(0.1075)
Juveniles	-0.36	0.25
	(0.0507)	(0.1868)

CAPITULO 3

Local and mesoscale population dynamics of *Macrocystis integrifolia* (Laminariales, Phaeophyta) in northern Chile: effects of wave exposure and nearness to upwelling centers

Dinámica de poblaciones de *Macrocystis integrifolia* (Laminariales, Phaeophyta) a mesoescala y escala local en el norte de Chile: efecto de la exposición al oleaje y de la cercanía a centros de surgencia

J. M. ALONSO VEGA[1], JULIO A. VASQUEZ[1]

[1]Facultad de Ciencias del Mar, Departamento de Biología Marina, Universidad Católica del Norte, Centro de Estudios Avanzados en Zonas Áridas (CEAZA). Casilla 117 Coquimbo, Chile

ABSTRACT

The present study evaluates the effect of permanent coastal upwelling on the population dynamics of *Macrocystis integrifolia* in northern Chile. Protected and exposed sites located near and away from permanent upwelling centers were selected at three locations between 28º and 30º S. Abundance and survival of juveniles and adults, reproductive phenology, and frond growth were monitored monthly at each site between 2000 and 2002. These observations were accompanied by simultaneous measurements of seawater temperature, nutrient concentrations, and salinity. The temporal variability of abiotic parameters were modulated by normal or La Niña conditions (2000-2001), which changed to a weak El Niño condition in spring 2002. In northern Chile, *Macrocystis integrifolia* sporophytes were reproductive throughout the entire year, producing continuous, low-density recruitment. Occasional episodic and synchronic high-density recruitments were also observed. Juveniles of *M. integrifolia* showed high mortality during the first months, but when the survivors reached reproductive maturity the annual mortality decreased considerably, with an average longevity of two years. In this way one-year-old sporophytes could be considered perennial with a life expectancy of up to 3-4 years. The different population parameters of *M. integrifolia* presented greater temporal than spatial variability. The frond production and growth of *M. integrifolia* was significantly greater and temporally more extensive at sites distant from permanent upwelling centers, and directly associated with the seasonality of abiotic factors (nutrient availability, light and seawater temperature). There appeared to be indirect, although not yet definitive evidence of the effect of distance of a kelp bed from permanent upwelling centers. The positive thermal anomalies produced by the El Niño Southern Oscillation in spring 2002, although gradual, modify temporal abundance and distribution patterns of kelp beds, and together with large-scale seasonal upwelling processes introduce a further level of complexity to *M. integrifolia* population dynamics in northern Chile. Finally, under normal or La Niña conditions the variability of *M. integrifolia* populations is reduced to a restricted dynamic including perennial sporophytes with high life expectancy, and with a high rate of replacement throughout the year.

Keywords: *Macrocystis integrifolia,* kelp, population dynamics, upwelling, ENSO, nutrients, SE. Pacific, Chile coast.

INTRODUCTION

Macrocystis integrifolia (Bory) has a bipolar distribution along the eastern rim of the Pacific Ocean. In the NE Pacific, this kelp occurs from Alaska (ca. 57º N) to central California (ca. 35º N), and in the SE Pacific from Peru (ca. 6º S) to central Chile (ca. 37º S) (Druehl 1969, Ramirez & Santelices 1991). The persistence of kelp beds toward lower latitudes of the SE Pacific is associated with negative thermal anomalies in sea surface temperature generated by the Humboldt Current, and by coastal upwelling, during the spring and summer, due to sub-superficial cold water which is nutrient-enriched and poor in oxygen (Steneck *et al.* 2002). In this system, at periods roughly approximating 4.5 years, higher positive thermal anomalies caused by the El Niño-Southern Oscillation (ENSO) interrupt upwelling processes and modify the oceanic climate between 6° S and 30° S (Camus 1990). The large-scale ENSO events produce local mass mortalities of *M. integrifolia* as a function of latitude (Tomicic 1985, Glynn 1988, Vega *et al.* 2005), correlated with nutrient deficits, surface warming, and increases in coastal swells (Takesue *et al.* 2004). In northern Chile, permanent upwelling areas buffered the effect of the 1997-1998 El Niño on littoral benthic communities (Vásquez *et al.* 2005), favouring local persistence of kelp species (Martínez *et al.* 2003, Vega *et al.* 2005).

Under normal, and/or La Niña events, topographic variability in the intensity and/or frequency of upwelling events is the main source of mesoscale variation ($\approx 10^2$ km) in sea surface temperature (SST) and nutrient concentration along the length of the temperate coast of the SE Pacific (Nielsen & Navarrete 2004). The SST co-varies inversely with nutrient availability and the distance from upwelling centers (Nielsen & Navarrete 2004). This produces different patterns of chlorophyll concentration, abundance of consumers, macroalgal growth rates and kelp coverage at the meso-scale (Vásquez *et al.* 1998, Camus & Andrade 1999, Broitman *et al.* 2001, Wieters *et al.* 2003, Martínez *et al.* 2003, Nielsen & Navarrete 2004). Here, it has been suggested that coastal upwelling is an important requirement for the persistence of *M.*

integrifolia populations in northern Chile (Buschmann *et al.* 2004). In the Northern Hemisphere along much of the California coast, periods of low nutrient availability are related to high summer SST (Hernández-Carmona *et al.* 2000, 2001). This is in contrast with other areas along this coast (*e.g.* points and peninsulas) where permanent upwelling processes reduce summer surface warming and increase nutrient availability (Steneck *et al.* 2002). Upwelling decreases the annual variability of SST, and produces a continuous nutrient flow to coastal systems, buffering or neutralizing the effects of "summer syndrome" described for kelp beds located in areas away from permanent upwelling centers (North 1986). The "summer syndrome" presents when fronds of *Macrocystis* deteriorate due to an increase in SST and there is a decrease in nutrients to below critical levels required to maintain photosynthetic capacity (Gerard 1982, 1984), causing an increase in the respiration rate (Gagne *et al.* 1982). As a result, the degradation rate of the fronds is greater than their growth, producing decomposition and death of adult sporophytes. Thus, in the NE Pacific, topographic variability in the frequency and intensity of upwelling appear to be an oceanographic modulating factor on abundance, growth, and reproduction patterns of *Macrocystis*, which under "normal" oceanographic conditions generate different population dynamics at the mesoscale.

As in all kelp species, *M. integrifolia* in northern Chile persists in a balance between favourable and unfavourable ecological processes. The development of kelp begins with fertilization of the microscopic female gametophyte, and establishment of the zygote on the substrate, which with time develops into a juvenile sporophyte or "recruit" (Reed & Foster 1984). The persistence of a kelp bed depends on seasonal or continuous recruitment processes, which recover the abundance of perennial adult sporophytes that may be lost through decomposition or detachment (Dayton *et al.* 1984, 1992). Recovery of an adult population by recruitment is dependent on availability of reproductive propagules and environmental conditions at the time of settlement (Graham 2002, Kinlan *et al.* 2003), such as nutrient availability and light (Reed & Foster 1984, Graham *et al.* 1997, Dayton *et al.* 1999). Disturbances on different spatial-temporal scales, which minimize the coverage of kelp beds due to detachment of fronds and sporophytes (*e.g.* water movement; Vásquez 1992, Graham *et al.* 1997), or which produce local extinctions (*e.g.* ENSO; Camus 1990) promote recruitment. Nevertheless, survival and growth of recruits depends on the continuity of the nutrient supply (Tegner *et al.* 1997, Hernández-Carmona *et al.* 2000, 2001, Kinlan *et al.* 2003). The temporal dynamic of *M. integrifolia* in northern Chile depends on synergistic effects of nutrient availability, seawater temperature, and light (Buschmann *et al.* 2004). When some of these factors reach critical levels, the sporophytes undergo physiological stress, which together with disease and herbivory modify the patterns of distribution and abundance, and in extreme cases produce local extinctions of *M. integrifolia* beds (Vásquez & Buschmann 1997, Vega *et al.* 2005).

We hypothesised that nutrient availability, regulated by permanent coastal upwelling, determined the *M. integrifolia* population dynamics by modifying survival and growth of juvenile and adult sporophytes. Thus, *M. integrifolia* population dynamics at sites near or at permanent upwelling centers would be characterized by continuous, low-density recruitment produced by the persistence of perennial adult sporophytes. In contrast, kelp population dynamics at sites distant from upwelling centers, or with seasonal upwelling, should experience seasonal recruitment, which permits annual renovation of the adult sporophyte population otherwise subjected to deterioration and detachment due to the "summer syndrome". If areas near to permanent upwelling centers are more productive and stable for macroalgal development (Nielsen & Navarrete 2002), we would predict greater growth of sporophytes of *M. integrifolia* in kelp beds located in the vicinity of these centers. If however, as in northern Chile, the abundance patterns of kelp are significantly modified during ENSO events due to physiological stress (Vega *et al.* 2005), the preceding prediction would only be valid for kelp bed dynamics during normal periods, or during La Niña conditions. Finally, we predicted that these dynamics would be dependent on the distance of kelp beds from the permanent upwelling centers.

MATERIALS AND METHODS

Study area

The northern coast of Chile is exposed to prevailing winds from the SW (Rutlland & Montecinos 2002), which produces exposed habitats on the SW coasts of small peninsulas (Playa Blanca and San Lorenzo) and coastal islands (Isla Damas) where wave forces and bottom currents are intense. In contrast, the NE habitats of small peninsulas and coastal islands are protected from the effects of prevailing winds. Occasional winter storms and swells produced by northerly winds produce high exposure to waves along the entire Chilean continental coastline (Strub *et al.* 1998). Figure 1 shows the locations of the study sites in the present research. The subtidal substrate at all study sites was composed of consolidated rock platforms interrupted by channels perpendicular to the coastline, from the intertidal to depths of 10-12 m. Some scattered boulders were present, interspersed with patches of shelly sand, heterogeneously distributed across the bathymetric gradient. From depths of 12 to 20 m the presence of consolidated rock surface diminishes, and is replaced by shelly sand cover with some boulder-strewn areas. Table 1 gives bathymetric range of distribution of *M. integrifolia* beds at the study sites. This kelp forms the principal living substrate at all the sites, with a canopy of fronds reaching the surface. A second stratum of bushy sporophytes of *Lessonia trabeculata* (Vega *et al.* 2005) may or may not be present. A third, or basal stratum in these assemblages is variable in composition and structure (Vásquez *et al.* 2001a). The kelp assemblages in northern Chile are a high biodiversity focus (Godoy 2000, Vásquez *et al.* 2001b), where the gastropods *Tegula* spp and *Prisogaster niger*, the decapod crustaceans *Taliepus* spp and the sea urchins *Tetrapygus niger* and *Loxechinus albus* are important benthic regulators of local abundance of *M. integrifolia* (Vásquez & Buschmann 1997, Vásquez *et al.* 2001b).

Observations and measurements for the present study were carried out in the Humboldt Current upwelling ecosystem, which has oceanographic characteristics broadly similar to those of other upwelling systems, particularly the California Current (Strub *et al.* 1998; Halpin *et al.* 2004, Takesue *et al.* 2004). Kelp beds were found in both wave-exposed and protected sites at three locations in northern Chile, between 27°S and 31°S (Fig. 1), which experience comparatively different intensities of upwelling (Table 1). Table 1 also shows the distance of each locality from a permanent upwelling center. Two sampling sites were established at each location (Table 1), based on wave exposure, salinity, and temperature (see Buschmann *et al.* 2004), and nutrients. Monthly evaluations at each study site, from May 2000 to December 2002, included adult and juvenile sporophyte abundance, production and growth rate of fronds, and the reproductive phenology of *M. integrifolia*.

Oceanographic conditions

The degree of water movement in exposed and protected sampling sites at each study site was characterized using the method of dissolution of calcium sulphate cubes (Doty 1971). Five 5 x 3 x 3 cm cubes were positioned at each site across the depth gradient for a period of three days, and then recovered, rinsed in fresh water, dried and weighed to determine their comparative weight loss. This procedure was repeated on six occasions during different seasons of the year (see Buschmann *et al.* (2004), providing a relative evaluation of the degree of movement of water at each study site. Temperature was determined daily at one hour intervals using StowAway® TidbiT®, continuous-register thermographs installed at 3 m depths. The levels of nitrates, nitrites, and phosphates were determined on water recovered from central sectors of *M. integrifolia* kelp beds, taking samples at depths of one, 2-4, and 4-8 m depths, plus three samples from near the bottom. One-litre, chemically clean plastic bottles were used to collect samples by diving. Nutrient analysis was carried out using photometric assay kits (Merck) for seawater using a Spectroquant® NOVA 60 spectrophotometer. Three additional samples were obtained at each study site in glass bottles, and analysed for salinity using an Autolab®, model 601 MKIII salinometer. Data on temperature, nutrients, and salinity were averaged on a monthly basis for each sampling site.

Population dynamics

The patterns of *M. integrifolia* abundance were evaluated using a randomly stratified sampling design. Three transects of about 100 m in length were established at each study site, perpendicular to coastline, over the entire extension of each kelp bed. Each transect was subdivided into four equal segments. Three steel-frame quadrats measuring 50 x 50 cm were thrown haphazardly from a boat onto the central portion of each of four transect segments, to give a total of 12 sampling units of 0.25 m^2 for each sampling site. The juvenile and adult sporophyte abundances under each quadrat was determined by divers using SCUBA. Juvenile sporophytes were defined as those having one lanceolate frond, without reproductive structures, and with a maximum holdfast diameter between one and four cm. The frond densities per sporophyte were determined in adult plants, as was their reproductive phenology, which was determined by the presence of fertile sporophylls in the basal portions of fronds. The density of juvenile and adult sporophytes were expressed per m^2 of rocky substrate, while the reproductive phenology was expressed as a percentage of sporophyll abundance as a function of the number of stipes per unit of substrate (North 1971).

Growth

The standard growth rate (G) of *M. integrifolia* was estimated at each study site from July 2000 to January 2002 using the method described by North (1971). The monthly increases in lengths of 12 fronds of at least 1.0 ± 0.1 m in length were determined at each sampling site, on individually selected and marked sporophytes. Each frond was individually tagged with a double monofilament nylon line, one end of which was attached to the base of the plant and the other affixed to a plastic tube 2 cm in length and 0.25 in diameter as described by Sharp & Tremplay (1985). The fronds or sporophytes that were lost from monthly measurements were replaced by substitute sporophytes to maintain a constant sample number throughout the experiment.

Survival

Temporal survival of adult sporophytes at each of the sampling sites was determined by haphazardly marking 30 sporophytes which had holdfasts with basal diameters larger than 15-25 cm, following the methodology proposed by Sharp and Tremplay (1985). Juvenile survival was evaluated using five permanent, haphazardly distributed 0.25 m^2 quadrats, which were observed during an entire year at each site between August 2001 and December 2002.

Data analysis

A three-way analysis of variance (ANOVA) employing the three variables of locality, site, and time, was used to test the hypothesis that permanent upwelling modified the population dynamics of *M. integrifolia* on a mesoscale. A similar statistical analysis was used to evaluate the hypothesis that the permanent upwelling modified the environmental conditions of sites inhabited by *M. integrifolia*. To detect differences due to water movement between the study sites in relation to location and time, a three way ANOVA was used with the main variables being site (exposed or protected), location (Playa Blanca, Isla Damas, San Lorenzo), and season (fall, winter, spring, summer). In all cases the data was analysed considering the fixed variables to be the location (with and without upwelling), the site (protected and exposed), and the time (months, or season of the year), following visual confirmation of normality of the data and homocedasticity of the variances using the Bartlett test (Sokal & Rohlf, 1981). Computational software employed was SYSTAT 8.0 (Systat Software Inc.). When the data lacked homocedasticity, they were transformed by log (x+1) or root (x+1) methods. Differences between groups were tested using the *a posteriori* Tukey test (Sokal & Rohlf, 1981). We also applied Pearson correlations between population parameters and environmental variables (Sokal & Rohlf 1981).

RESULTS

Wave exposure

Dissolution of the calcium sulphate blocks was a convenient method for the relative distiction between protected and exposed sites. No differences between localities with and without permanent upwelling were detected, but the dissolution rates at the protected sites were significantly lower ($F_{(1,168)}=322.66$; $p<0.001$) than at the exposed sites (Fig. 2). Seasonal changes in dissolution rates among localities ($F_{(6,168)}=16.76$; $p<0.001$) and between sites ($F_{(3,168)}=97.63$; $p<0.001$) can be related to high swells and storms during fall/winter, when these events increase in frequency and magnitude (Strub *et al.* 1998, Halpin *et al.* 2004).

Oceanographic conditions

The average monthly water temperature demonstrated a common seasonal pattern for all the study sites with a maximum of 17.2 to 19.1ºC in the summer and a minimum of 12.5 to 13.8ºC in the winter (Fig.3). The sea surface temperature showed a significant correlation ($r^2=0.97$; $p<0.001$) between exposed and protected sites per locality. The annual thermal oscillation in seawater at the Isla Damas and San Lorenzo localities (near permanent upwelling centers as noted above) was between 1-2°C lower in comparison with the two Playa Blanca sites.

The nitrate availability differed significantly between protected and exposed sites at each location ($F_{(1,810)}=19.30$; $p<0.001$), and over the study period ($F_{(26,810)}=71.41$; $p<0.001$). The ANOVA did not, however, discriminate between locations with and without permanent upwelling. The nitrate concentration at protected sites was significantly greater than at exposed sites (Tukey test; $p<0.001$) at all locations. The monthly nitrate availability differed significantly, depending on site ($F_{(26,810)}=3.50$; $p<0.001$) and location ($F_{(52,810)}=7.69$; $p<0.001$), with average values ranging between 1.0 and 2.5 mg/L during 2000, in contrast with a marked seasonality observed during 2001-2002 (Fig. 4). During 2001-2002, nitrate concentration was minimal (≈0.5 mg/L) from April to August, and reached a maximum (≈ 1.5-2.5 mg/L) in summer (Fig. 4). In contrast, nitrite availability was only significantly different over time ($F_{(26,810)}$= 171.84; p<0.001). The nitrites demonstrated annual, rather than seasonal tendencies, with low concentrations (<0.04 mg/L) between 2000 and mid-2001; from this period onward nitrites showed maximum average values of 0.05 to 0.06 mg/L in spring 2001 and 2002 (Fig. 4), with haphazard, significant monthly differences, depending on site ($F_{(26,810)}$=3.50; p<0.001) or location ($F_{(52,810)}$=7.69; p<0.001). The phosphates maintained average values near 0.1 mg/L during the study period, with haphazard, significant increases ($F_{(52,810)}$=5.88; p<0.001) depending on location and site study (Fig. 4). Seawater salinity at all sites showed low variability, ranging between 34.323‰ and 34.928‰. Low or non-significant correlation was obtained among study localities between annual seawater temperature variation and its nutrient concentration (Playa Blanca r^2: 0.1095; p < 0.028; Isla Damas r^2: 0.0036; p < 0.6706; San Lorenzo r^2: 0.1095; p < 0.0019 for nitrates + nitrites).

Population dynamics

Recruitment processes of *M. integrifolia* into kelp beds located near upwelling centers showed no differences when compared with those located in areas away from upwelling centers. Significant differences among locations ($F_{(2,1782)}$=39.98; p<0.001), were due to a greater abundance of juveniles in kelp beds at Isla Damas, when compared with those of San Lorenzo and Playa Blanca (Tukey test; p<0,05) which are located near to, or distant from permanent upwelling centers, respectively. The juvenile density in kelp beds in protected sites was significantly higher than in exposed sites ($F_{(1,1782)}$= 14,60; p<0,001), giving a consistent pattern for the three locations. The temporal variation in juvenile density of *M. integrifolia* differed significantly among locations ($F_{(52,1782)}$=2,96; p<0,001) and between sites exposed to and protected from waves ($F_{(26,1782)}$=2,91; p<0,001). The kelp beds contained juvenile sporophytes during all months of the year, independent of their distance from permanent upwelling centers, suggesting continuous, low-density recruitment (Fig. 5). We also recorded some massive, synchronic recruitment at all the locations, as was observed between September and November 2001, although with significant differences (Tukey test, $P<0.05$) among months for each site (Fig.5). Other significant monthly increments in the juvenile abundances were site-dependent. At Isla Damas, the juvenile abundances increased gradually from August 2000 until reaching an average maximum in January-February 2001, and a secondary increase in October 2000. This was in contrast with Playa Blanca, where the juvenile abundances increased significantly in January 2001, and San Lorenzo in October 2000. High juvenile densities were only observed at exposed sites at these two locations. During spring 2002, however, sites at locations near upwelling centers (Isla Damas and San Lorenzo) showed a higher density of juveniles when compared with Playa Blanca (without permanent upwelling, Fig. 5). The absence of significant correlations between nutrient concentrations and juvenile abundances suggested that recruitment patterns of *M. integrifolia* were not directly regulated by temporal variability in nutrient availability (nitrate + nitrite).

The adult sporophyte densities of *M. integrifolia* differed significantly between locations ($F_{(2.1782)}=65.38$; $p<0.001$), independent of distance from permanent upwelling centers. The kelp beds at protected sites, however, showed a significantly ($F_{(1,1782)}=87.33$; $p<0.001$) greater abundance of adult sporophytes when compared to exposed sites (Tukey test $p < 0.001$). The temporal variation in adult sporophyte abundances was dependent on location ($F_{(52,1782)}=4.74$; $p<0.001$) and wave exposure ($F_{(26,1782)}=1.98$; $p<0.0024$), with a high variability in monthly averages during the study period (Fig. 6). The absence of a significant inverse correlation between adult and juvenile sporophyte abundance suggested that the replacement of the adult fraction of the populations through recruitment was a continuous process over time for all of the kelp beds studied.

The frond density per sporophyte differed significantly among locations near to and distant from permanent upwelling ($F_{(2,1782)}=10.75$; $p<0.0001$). In kelp beds located in areas distant from upwelling centers (Playa Blanca), sporophytes had a greater frond density compared with kelp beds in locations near at upwelling centers (Tukey test, $p<0.05$). The sites protected from water movement had greater frond densities per sporophyte than exposed sites ($F_{(1,1782)}=9.91$; $p<0.0017$), although these differences were location dependent ($F_{(2,1782)}=15.18$; $p<0.0001$). The temporal variability in frond density per sporophyte differed significantly at each location ($F_{(52,1782)}=3.41$; $p<0.0001$) and at each site ($F_{(26,1782)}=1.38$; $p<0.0975$), which suggested that decreases in the number of adult individuals of *M. integrifolia* were recovered by gradual incorporation of successful recruits. This was observed at all sampling sites and in particular at the exposed site at San Lorenzo during October 2000 (Fig. 7). During spring 2001 and summer 2002 there was a significant increase (Tukey test, $p<0.05$) in densities of adult sporophytes following a period of high juvenile abundance. When sporophyte density was high (>15 sporophyte adults per m^2), density dependent processes appeared to regulate recruitment, and although significant increases in juveniles were detected, incorporation to the adult fraction of the population by these recruits was probably not very effective. This appeared to be the case at sites at Playa Blanca during spring 2001 and summer 2002 (Fig. 6). Significant monthly decreases in adult sporophytes occurred in fall and winter as a consequence of winter swells, which favour the detachment of fronds and plants. Other site-dependent mortality factors, not experimentally evaluated but visually observed in kelp beds monitored, were the effects of drag produced by drifting plants which became entangled with the canopy of sporophytes, as well as the effects of abrasion produced by movements of sand beds from the intertidal to the subtidal zone which caused the erosion of holdfasts. Monthly increments in the density of fronds per sporophyte in the summer (Tukey test; $p< 0.001$) were associated with the production of new fronds from the holdfast. Although the initiation and extension of the season of high productivity of fronds from *M. integrifolia* holdfasts was dependent on location and site, this occurred in spring and summer, with high interannual variability (Fig. 7).

Macrocystis integrifolia populations presented fertile sporophylls during the entire annual cycle, with significant differences ($F_{(34,1836)}$=4.368; p<0.0001) between locations, although not between exposed or protected sites (Fig. 8). The Playa Blanca kelp beds, distant from upwelling centers, showed a significantly larger production of fertile fronds than kelp beds located in areas near at permanent upwelling centers ($F_{(2,1836)}$=31.45; p<0.0001), with monthly variations in fronds bearing fertile sporophylls of 30 to 50% during the study period. In locations near upwelling centers (Isla Damas and San Lorenzo), the fertile fronds had a seasonal pattern of abundance with maximum (≈50-60%) in spring and summer, and minimum (≈20-30%) in winter (Fig. 8).

Growth

In areas away of permanent upwelling centers, the fronds of *M. integrifolia* sporophytes showed standard growth rates (G) significantly higher ($F_{(2,1218)}$=368.27; p<0.0001) than sporophytes from kelp beds near permanent upwelling (Table 2). Furthermore, sporophyte fronds from protected sites showed significantly more growth ($F_{(1,1218)}$=28.15; p<0.0001) than those of the exposed sites (Table 2). Exposure to the waves did not, however, modify the pattern observed among localities. The tendency detected in the standard growth rate (G) was similar to that observed in the frond elongation rate "E" (%). Here, the sporophytes of Playa Blanca (distant from permanent upwelling centers) had an E significantly greater ($F_{(2,1122)}$=210.48; p<0.0001) than sites located near permanent upwelling centers, with significant differences ($F_{(1,1122)}$=20.93; p<0.0001) between protected and exposed sites. Temporally, the fronds showed a marked seasonality in their elongation rate (Fig. 9), with significant monthly changes which were location dependent ($F_{(32,1122)}$=52.90; p<0.0001) and site-dependent ($F_{(16,1122)}$=4.23; p<0.0001).

Survival

The juvenile sporophytes underwent high mortality (≈80-90%) during the first four months (Fig. 10), independent of the distance from permanent upwelling centers. At

Playa Blanca, the location without permanent upwelling, the cohort of juveniles recruited in August 2001 showed the least survival. In January 2001 the sporophytes did not survive at the exposed site, and there was only a 2% survival at the protected site, represented by one adult (38 cm diameter holdfast, with 31 fronds and some reproductive sporophylls), which remained in place until the end of the study. In contrast, survival of juveniles recruited in September 2001 at locations near permanent upwelling was near 5%, at both exposed and protected sites (Fig. 10). At Isla Damas the initial recruit densities in September 2001 were 8.2±3.3 per 0.25 m^2 at the exposed site and 5.0±2.3 per 0.25 m^2 at the protected site. In September 2002, the adult sporophyte densities at Isla Damas was 0.4±0.5 per 0.25 m^2 (two individuals) for the exposed site, and 0.2±0.4 per 0.25 m^2 (one individual) at the protected site, with holdfasts measuring 28 to 33 cm in diameter and having 13 to18 fronds with reproductive sporophylls. This represented a survival of 6.7% at the exposed site and 4.2% at the protected site (Fig. 10). At San Lorenzo, the initial recruit density was greater than at Isla Damas (12.4±3.0 recruits per 0.25 m^2 at exposed site and 11.2±3.2 recruits per 0.25 m^2 at protected site). At the end of the study, however, the adult sporophyte density was 0.8±0.8 per 0.25 m^2 (4 individuals) at the exposed site, and 0.4±0.5 per 0.25 m^2 (2 individuals) at the protected site (18-26 cm diameter holdfasts, 10-15 fronds, with some reproductive sporophylls). Survival at the exposed site was 6.5% and 3.6% at the protected site (Fig. 10). The probability that recruits would reach reproductive maturity appeared to be similar at locations with permanent upwelling and without upwelling.

The adult sporophytes of *M. integrifolia* showed greater annual survival than the juvenile sporophytes. At all study sites, the adult sporophytes tagged in August 2000 (n=30 per site) underwent 50-60% mortality during the first year of recording (to August 2001), and near 80-90% by August 2002. Combining the survival of adults and juveniles, it is expected that the sporophytes, which reach reproductive maturity during the first year and show a mean longevity of two years, may reach a projected life span of three to four years.

DISCUSSION

In a temporal perspective, our results suggest that large-scale coastal upwelling is an important oceanographic process for the persistence of *M. integrifolia* populations in the study area. In the temperate SE Pacific, upwelling processes are directly and positively correlated with frequency and intensity of prevailing SW winds, producing seasonal variability with maximum nutrient availability in spring/summer (Rutlland & Montecinos 2002). This seasonality is particularly relevant with regard to the nitrate concentration, which is a nutrient that has an important effect in the annual recovery of kelp abundances at temperate latitudes (Buschmann *et al*. 2004, Edwards 2004). Nutrient availability co-varies with the temporal tendencies of light and SST (Edding *et al.* 1990, Vásquez & Vega 2001). These interactions regulate the temporal patterns of abundance, growth and fertility of *M. integrifolia* beds located in the present study region (28-31ºS). In contrast, spatial organization factors related to coastal topography, such as permanent upwelling centers (mesoscale) or wave exposure (local scale), were less effective in the regulation of *M. integrifolia* population dynamics.

Permanent upwelling centers and population dynamics *M. integrifolia*

The coastal variability in nutrient distribution and SST generated by nearness to permanent upwelling centers did not appear to be a modulating factor in abundance and reproductive patterns of *M. integrifolia*. Independent of the closeness to upwelling centers, *M. integrifolia* populations were formed of perennial sporophytes, which were fertile during the entire annual cycle, with continuous and low juvenile abundance throughout the year. Subtidal populations of *M. integrifolia* at higher latitudes have shown similar reproductive patterns, although they present differences in their abundance patterns (Druehl & Wheeler 1986). In contrast to our results, abundance and fertility patterns of *Macrocystis* sporophytes at lower latitudes of the NE Pacific (25-30ºN) depended mainly on local nutrient availability associated with nearness to upwelling centers (Hernández-Carmona *et al.* 2000, 2001).

Contrary to our prediction, frond production and growth rates in *M. integrifolia* sporophytes were greater at sites distant from upwelling centers. Ecotypic traits of kelp populations associated with local characteristics inherent to the habitat could explain these differences (Martínez 1999, Graham *et al. in litteris*). This appears to constitute indirect evidence of effects of distance from upwelling centers on kelp dynamics. *Macrocystis* inhabiting areas without upwelling couple their maximum frond production and growth to periods with higher nutrient availability, low SST and optimal light conditions (Tegner *et al.* 1997, Hernandez-Carmona *et al.* 2000, 2001). At our Playa Blanca sites these conditions occur from September to March, correlating with the period of the greatest frond production and growth. In areas near upwelling centers (*e.g.* San Lorenzo and Isla Damas sites) sporophytes undergo slower, continuous frond production and growth because nutrient availability is not a critical factor at any time of the year (see also Dayton *et al.* 1992, 1999).

Wave exposure and population dynamics of *M. integrifolia*

Exposure to wave action is an important factor in the modulation of the local variability in abundance patterns of subtidal *Macrocystis* beds (North 1994). In general, we observed a decrease in sporophyte abundance with increase in bottom currents and waves, which has also been reported from the Californian coast (Dayton *et al.* 1984, Graham *et al.* 1997). Our results showed that some population parameters of *M. integrifolia* responded differentially to increases in water movement. Significantly greater sporophyte abundance, as well as frond production and growth rates, have been described for kelp beds located at protected sites in association with nutrient availability and habitat stability (Graham *et al.* 1997, Hurd 2000). Significantly greater frond production and growth rates of *M. integrifolia* were observed in our study at the protected sites, in contrast with results reported for other kelp beds (Wheeler & Druehl 1986). This could be because in our study the differences in the exposure gradient between protected and exposed sites were not as extreme as those reported at higher latitudes (Hurd *et al.* 1996). On a local scale, differences in frond growth rates of *M. integrifolia* between sites can be associated with the frond capacity for nutrient capture, which is dependent on water movement and nutrient availability (Hurd *et al.* 1996, 2000). In this context, nutrient availability was always significantly greater in protected sites at all of the localities monitored in our study area.

Temporal variability in population dynamics of *M. integrifolia*

Macrocystis integrifolia was fertile all year round in our study area, producing continuous, low-density recruitment. This recruitment pattern is typical of kelp populations inhabiting protected environments, where temporal stability in sporophyte abundance reduces substrate availability for settlement (Graham *et al.* 1997). As stated above, high-density recruitment episodes occasionally occurred in all the kelp beds monitored. High-density recruitment is characteristic of exposed environments where abundance of adult sporophytes is temporally more variable, producing "colonization pulses" (Reed & Foster 1984). In northern Chile, SST and irradiance covary seasonally (Edding *et al.* 1990, Vásquez & Vega 2001), and may influence the patterns of annual recruitment, while nutrient availability does not appear to be limiting (Buschmann *et al.* 2004). In *Macrocystis* beds, covariance between low temperature (16ºC) and low irradiance (0,4 E $m^{-2}d^{-1}$) generates “recruitment windows” (Deysher & Dean 1986), which together with nutrient availability stimulate colonization pulses (Graham *et al.* 1997). The synchronic recruitment of kelp juveniles in spring at all sites can be related to large-scale seasonal upwelling (Vásquez *et al.* 1998), which may be considered as a generator of recruitment windows. The weak ENSO conditions registered in spring 2002 (Vega *et al.* 2005) produced a recruitment window at all our study sites due to an increase in available substrate and was reflected by the abundance of juveniles. Short-term disturbances (*e.g.* frond harvest, herbivory, storms, substrate availability, etc.) may decrease adult densities producing "colonization pulses", differentially stimulating the recruitment of *M. integrifolia* among sites (North 1994, Santelices & Ojeda 1984). However, episodic settlement does not always lead to successful kelp recruitment (Deysher & Dean 1986). Interactions between physical and biological factors may limit the growth rate and increase mortality among the kelp recruits (Dean & Jacobson 1984, Dayton 1985, Graham 2002, Kinlan *et al.* 2003, Vega *et al.* 2005). For example, high irradiance levels reduced or inhibited recruitment of *M. integrifolia* juveniles on shallow bottoms in summer conditions (Graham 1996). Other factors acting at the local-scale such as the mechanical action of con-specifics or other kelp species (*L. trabeculata*), grazing pressure by sea urchins and gastropods, and sedimentation (residence, transport and rate) should be taken into account when attempting to explain failures in recruitment or mortality of juveniles within kelp beds (Devinny & Volse 1978, Vásquez 1992, Vásquez & Buschmann 1997). Although the degree of importance of each of these factors is site-specific (Vega *et al.* 2005), it is probable that interactions among these different factors can explain the low survival of the *M. integrifolia* cohort, which occurred in September 2001.

The age-dependent mortality of the sporophyte is also important in the determination of temporal patterns of kelp abundance. *Macrocystis integrifolia* juveniles showed high mortality during the first months of life, but when the survivors reached reproductive maturity, the annual mortality decreased considerably and they attained an average longevity of two years. As a consequence, one-year-old sporophytes can be considered perennial, with a life expectancy of up to 3-4 years. This result is similar to life expectancies of *Macrocystis* described for some sites on the coasts of California and southern Chile (Santelices & Ojeda 1984, Dayton *et al.* 1984, Graham *et al.* 1997), but is in contrast with other sites where life expectancies vary from several months to 2 years (North 1971, Druehl & Wheeler 1986; Westermeier & Möller 1990). In northern Chile, the main agents that cause seasonal variability in mortalities of adult sporophytes in *M integrifolia* beds are large swells and winter storms (Buschmann *et al.* 2004, Vega *et al.* 2005). This factor increases significantly during ENSO events (Tegner *et al.* 1997, Vega *et al.* 2005). The weak 2002 ENSO conditions could have increased the mortality rate of sporophytes, explaining the interannual variability in the patterns of kelp abundance. Other phenomena commonly observed in *M. integrifolia* populations, and frequently reported for *M. pyrifera,* is the drag effect caused by fronds and floating plants which become entangled in the canopy of attached plants, contributing to their detachment (Dayton *et al.* 1984, 1992).

The seasonality observed in frond production and growth rate suggests that natural processes of pruning and frond regeneration should be considered as critical components in the annual renovation and productivity of *M. integrifolia* beds. Natural pruning occurs during the entire year, with a higher rate in fall and winter, acting mainly on older fronds and sporophytes. The production of new fronds in *M. integrifolia* occurs at the end of winter and beginning of spring. This process may extend, in certain localities, until summer, depending on nutrient availability, quality and quantity of light, and SST, all of which affect photosynthetic activity (North 1984). Seasonality of abiotic factors in temperate latitudes regulates the photosynthetic capacity of kelp (Gagne *et al.* 1982, Gerard 1984). In addition, vegetative growth and frond regeneration of perennial sporophytes may be another explanation for the persistence of *M. integrifolia*, which may be more important at times than recovery of abundances by means of sexual reproduction (Graham 1996). Nevertheless, in some kelp beds, frond regeneration does not appear to be sufficient to replace the biomass lost during winter storms (Druehl 1978, Wheeler & Druehl 1986). Seasonal tendencies in frond production and growth rates of *M. integrifolia* in this study coincide with those described for populations of *Macrocystis* in the Northern Hemisphere at similar latitudes (ca. 30°N) (North 1971, 1994, Hernández-Carmona 1996), but differs from those described for populations at higher latitudes (> 40°; North 1971, 1994, Lobban 1978, Westermeier & Möller 1990). The capacity for frond production and elongation and growth of sporophytes can be limited by loss of the apical meristems due to herbivory, wave stress, sedimentation stress, and microbial decomposition (Westermeier & Möller 1990, North 1994, Buschmann *et al.* 2004). In our study area, seasonality observed in frond production in *M. integrifolia* was principally due to the loss of apical tissue and low photosynthetic rates in the fronds during fall and winter, and not by differences in frond production and growth rate associated with life strategies as occurs in *M. pyrifera* in southern Chile (Westermeier & Möller 1990, Buschmann *et al.* 2004).

In conclusion, the *M. integrifolia* beds between 28º and 30º S show similar temporal patterns, where large-scale seasonal upwelling appears to be an important factor in determining patterns of distribution and abundance of their populations, independent of nearness to local upwelling centers. *M. integrifolia* populations are characterized by having perennial sporophytes, which are fertile during the entire annual cycle and which continuously produce juveniles. This contrasts with descriptions for California where water movement significantly modifies the population dynamics of *Macrocystis* on a local scale (Graham *et al.* 1997), or where the vicinity of upwelling centers appears to regulate the persistence of sporophytes affected by the "summer syndrome" (Steneck *et al.* 2002). The fertility, frond production and growth rate patterns of *M. integrifolia* are slightly greater and temporally more extensive in kelp beds distant from permanent upwelling centers. This tendency, though, is weak, and is possibly caused by complex interactions of various factors (nutrient supply, wave exposure, grazing pressure). Finally, positive thermal anomalies produced by the weak 2002 ENSO event, modified temporal patterns in abundance and distribution of *M. integrifolia* on a local scale, generating synchronic mesoscale responses which produced a decrease in adult sporophyte abundance, facilitating a massive recruitment of new juveniles. This produced a greater level of complexity in the population dynamics of *M. integrifolia* in northern Chile. We recommend future research be done in order to evaluate the interactive effects of these factors on local, and mesoscales, based on their critical importance to the population dynamics of *M. integrifolia.*

ACKNOWLEDGEMENTS

This research was financed by (FONDECYT Nº100044-1010706) granted to JAV and is part of JMAV Master of Marine Sciences in UCN Program. The authors are grateful for expert help in the field and laboratory rendered by F. Diaz, J. Rivera, E. Rojas, A. L. Valdivia, B. Rubina, S. Ramos, N. Piaget and C. Olivares (LABECO team). We also wish to recognize the advice and constructive criticism of M. Thiel on various aspect of this manuscript.

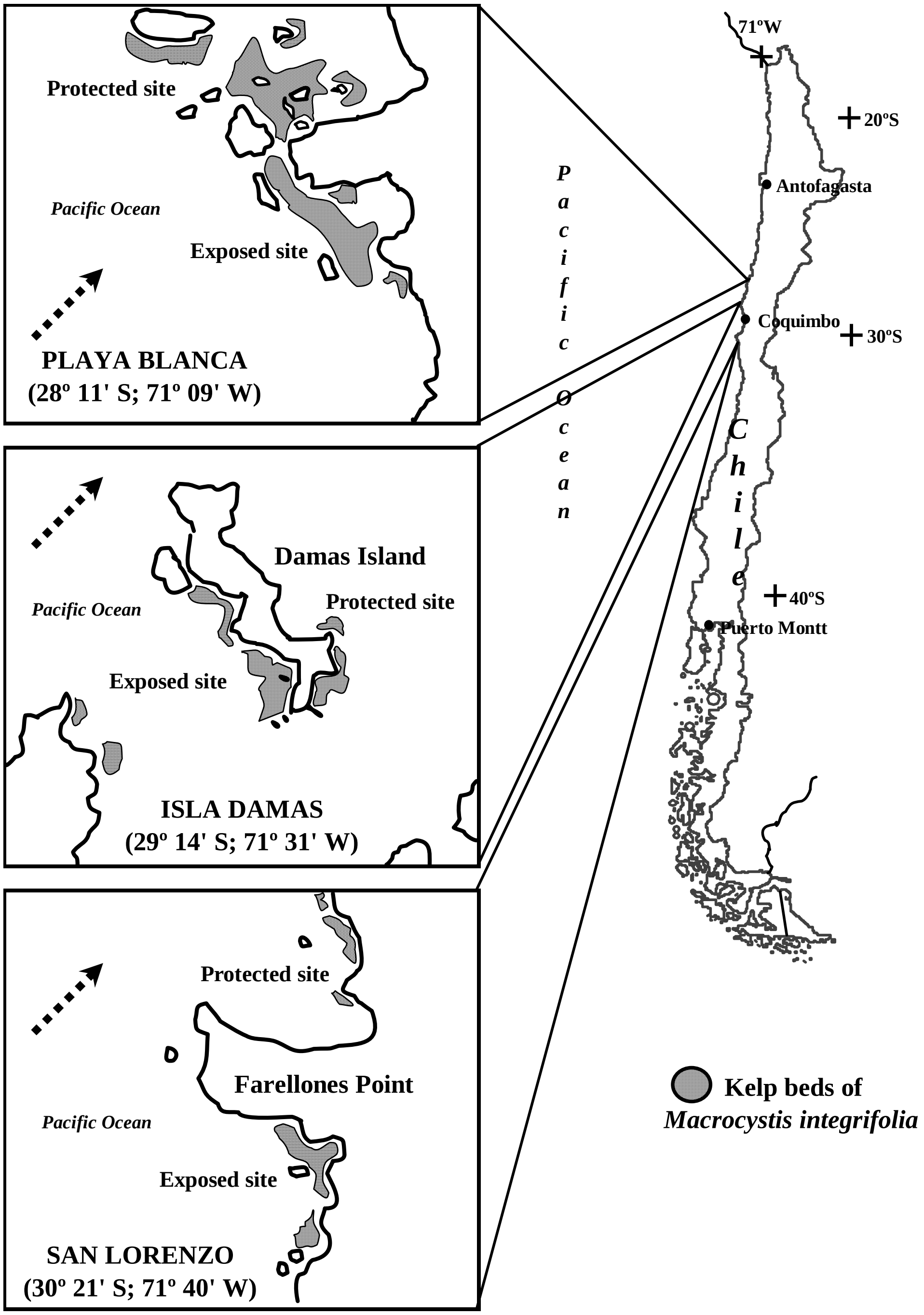


Figure 1. Geographic location of the study area, showing exposed and protected sites in locations with seasonal upwelling (Playa Blanca) and those with permanent upwelling (Isla Damas and San Lorenzo). In the figure, arrows indicate dominant South-Western winds, and shaded areas represent kelp beds.

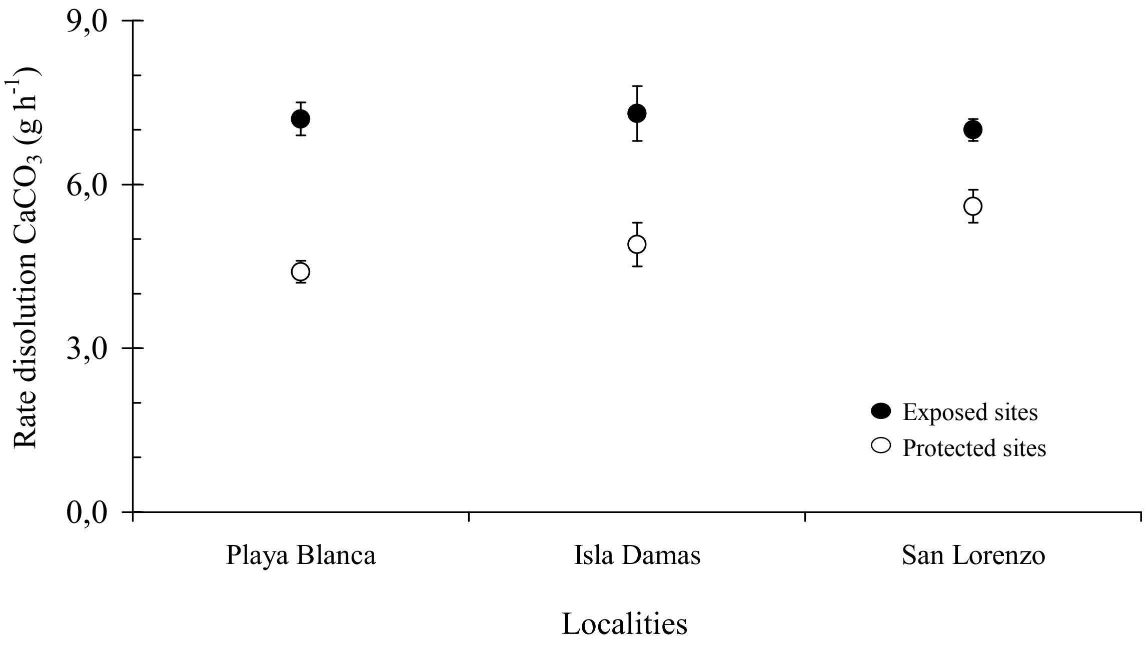


Figure 2. Sampling sites in relation to water movement at each study location. Mean ± SD.

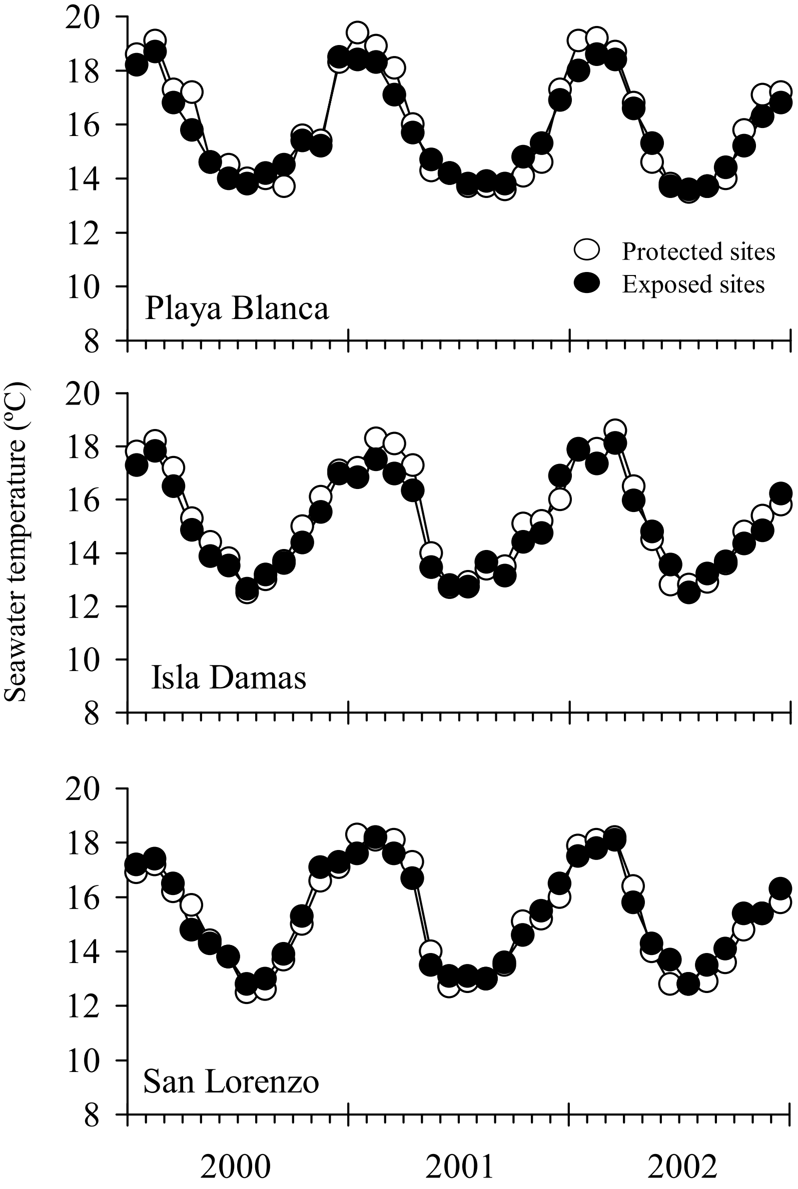


Figure 3. Monthly averages of the seawater temperature (SST) registered in 2000-2002 at each sampling site.

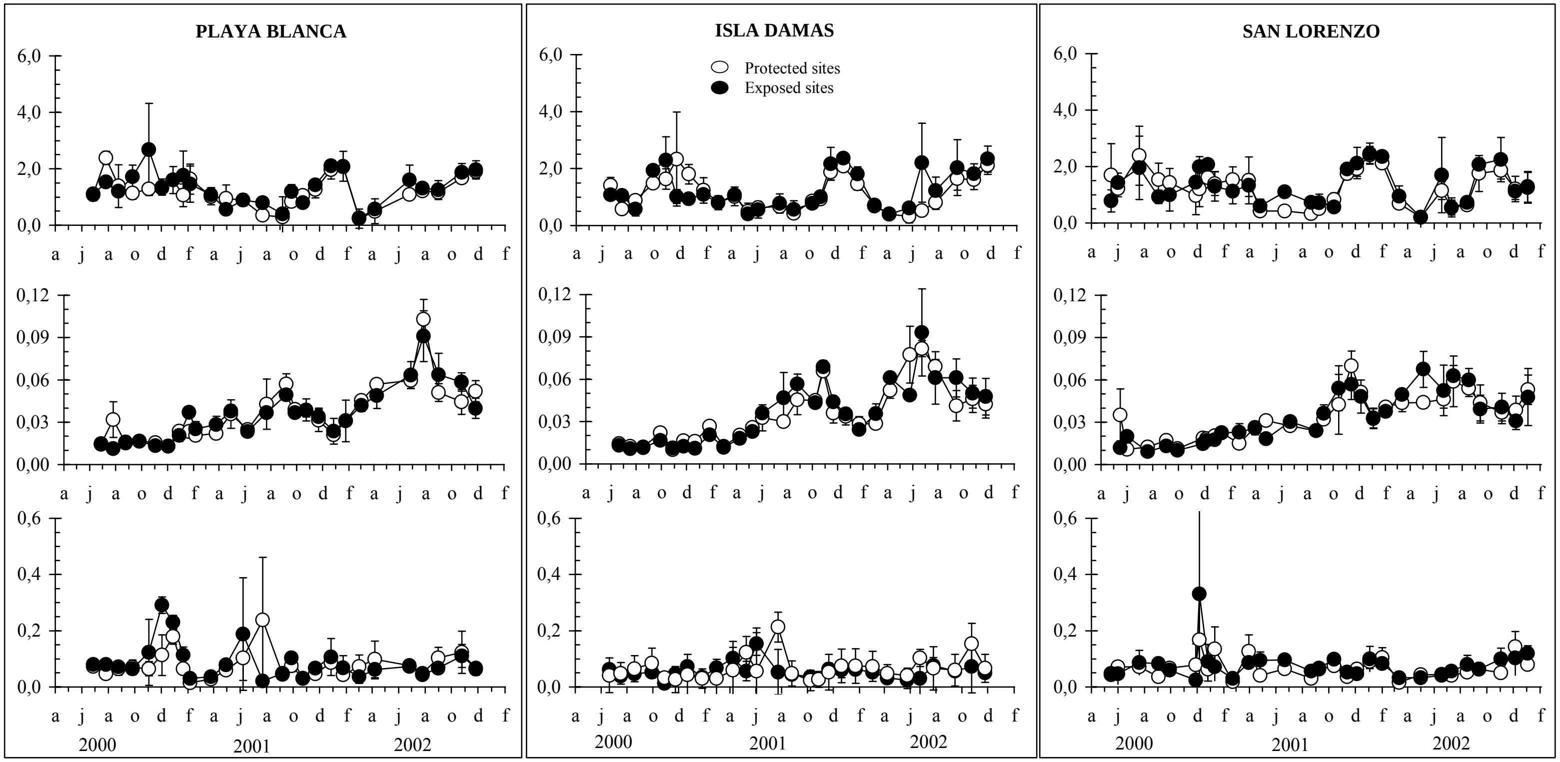


Figure 4. Temporal variations in the concentration of nutrients (nitrates, nitrites and phosphates) at each sampling site. Mean ± SD.

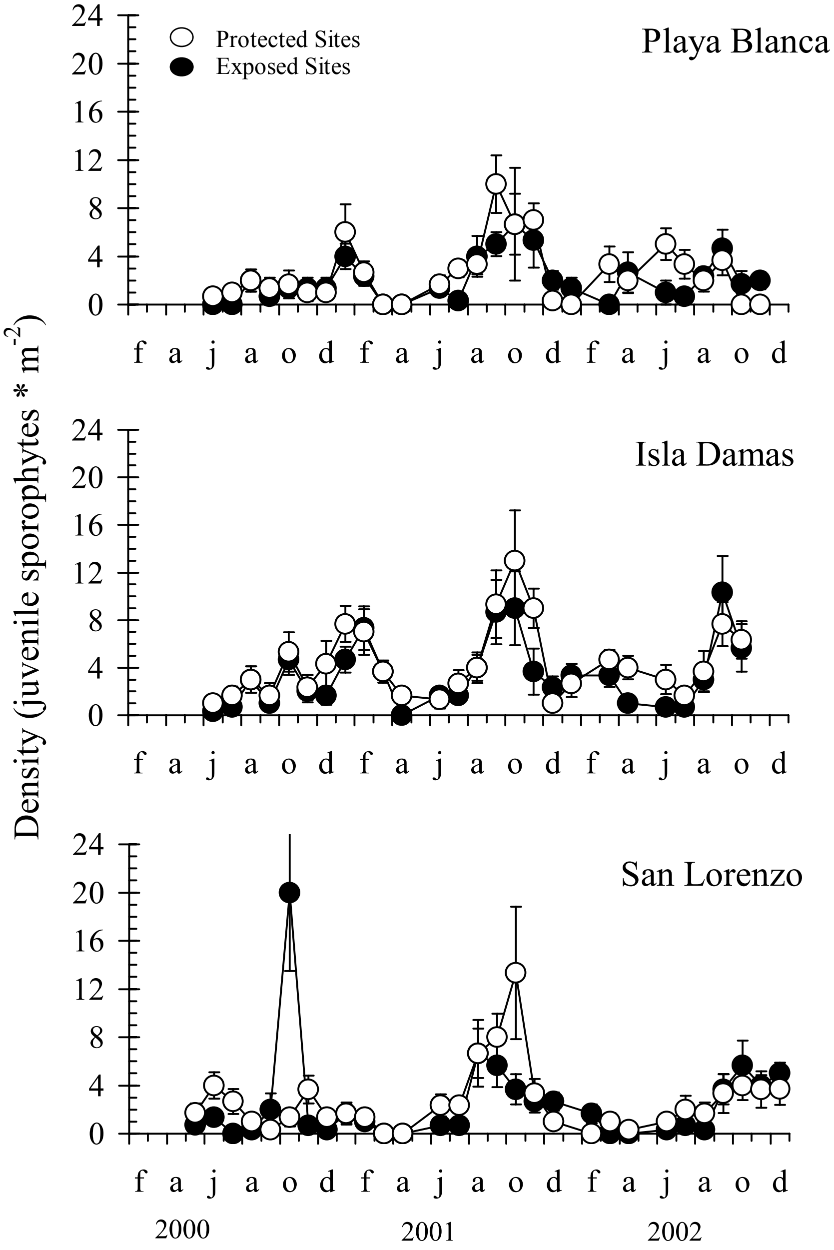


Figure 5. Temporal patterns of abundance of *Macrocystis integrifolia* juvenile sporophytes by sampling site. Mean ± SD.

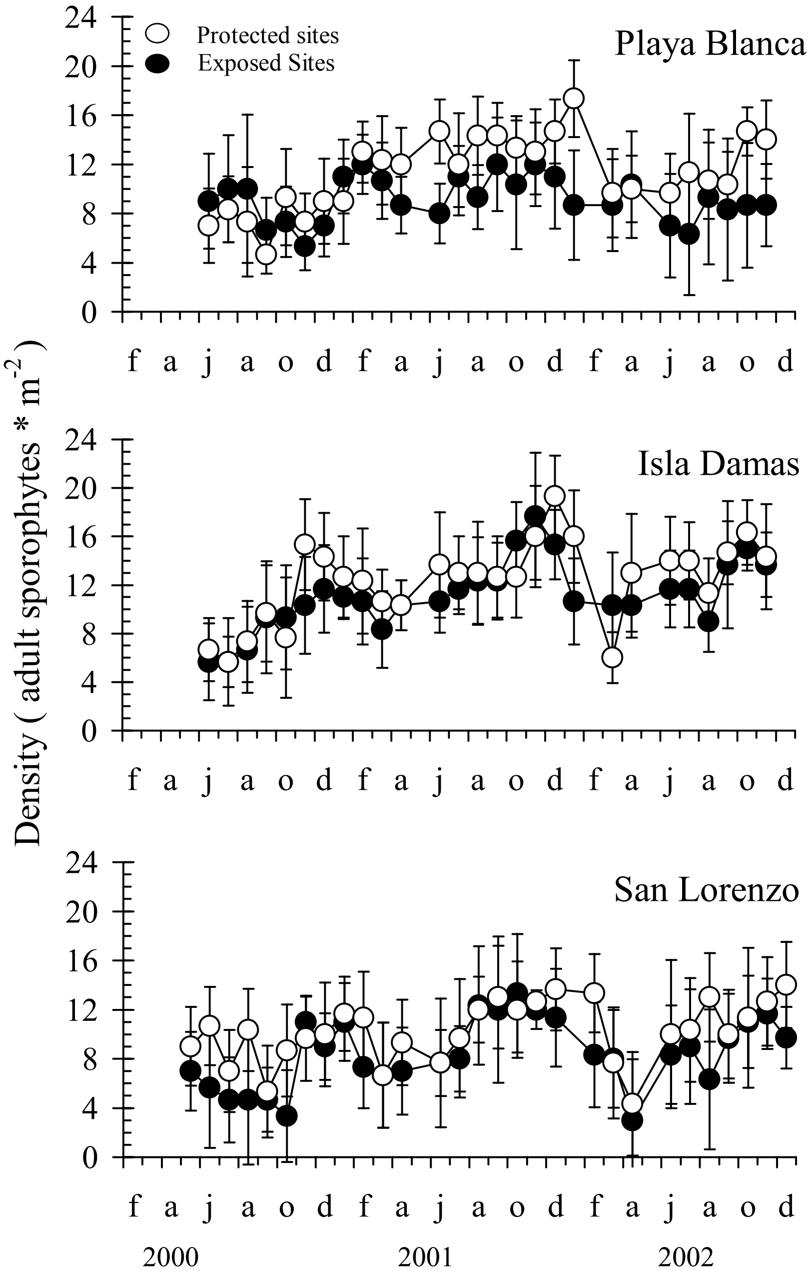


Figure 6. Temporal patterns of abundance of *Macrocystis integrifolia* adult sporophytes by sampling site. Mean ± SD.

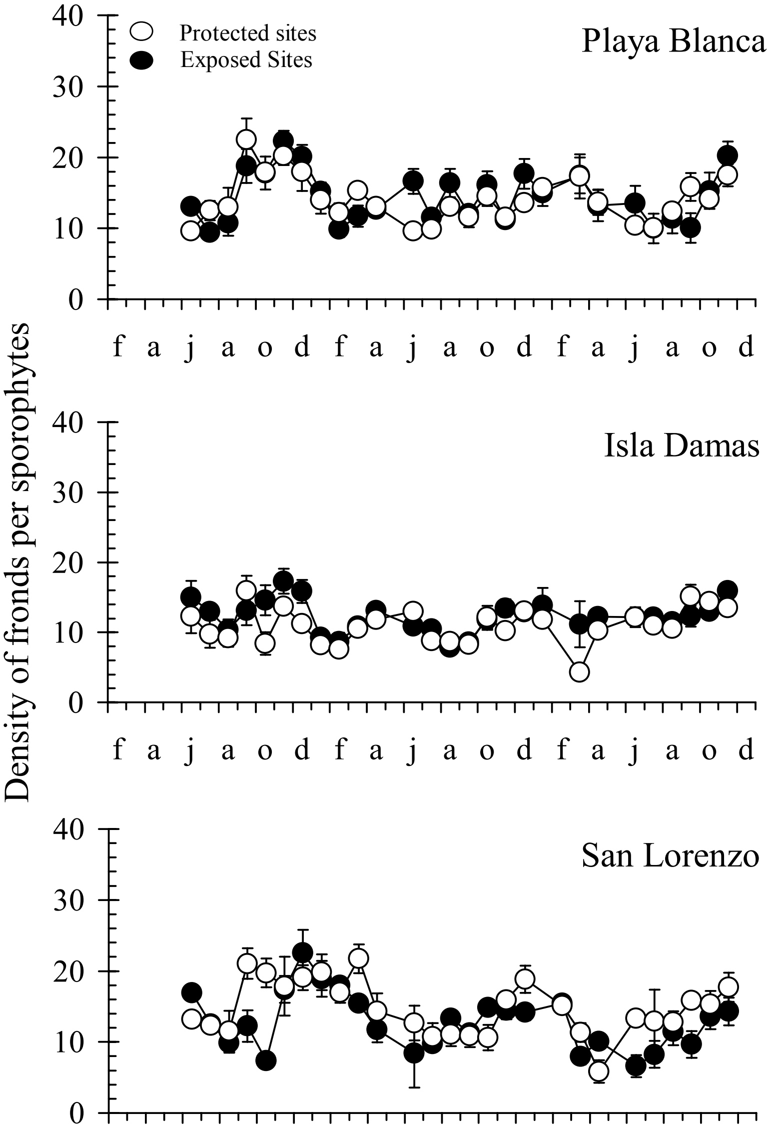


Figure 7. Temporal patterns of the frond densities of *Macrocystis integrifolia* sporophytes by sampling site. Mean ± SD.

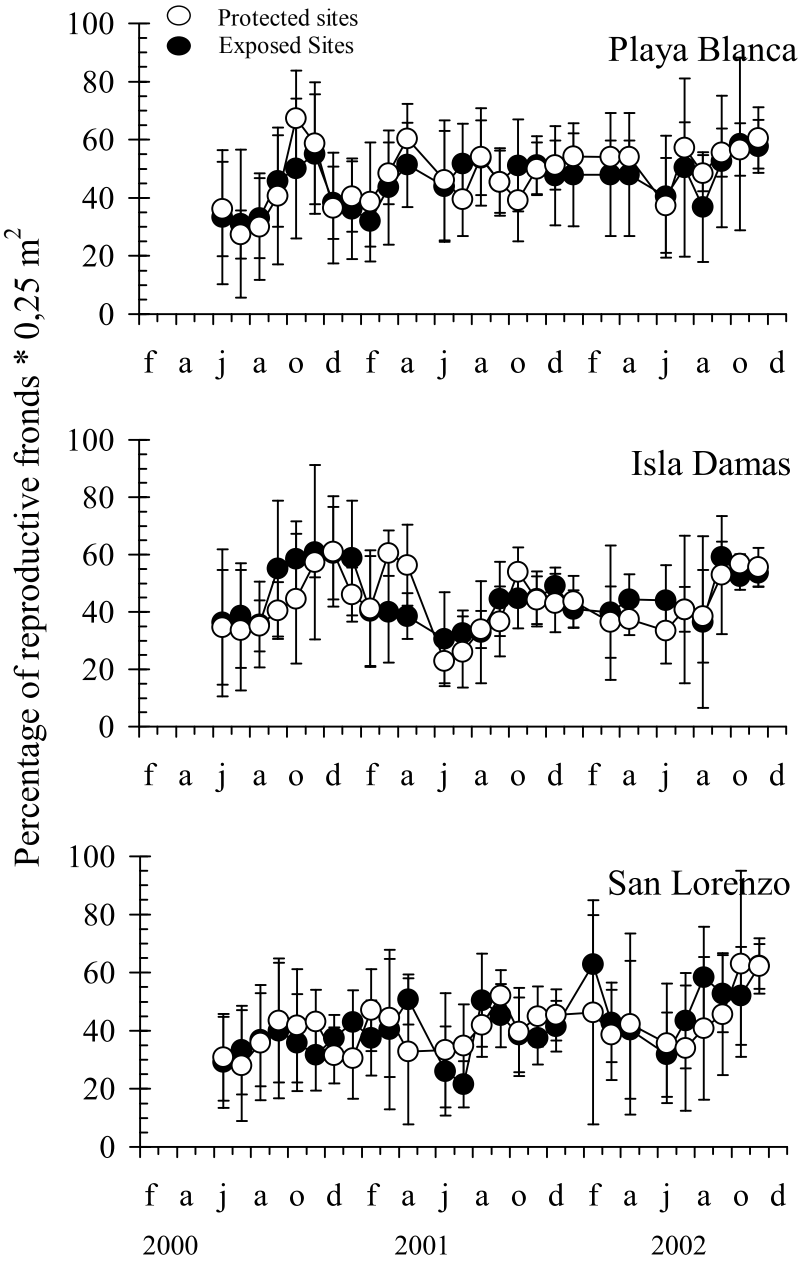


Figure 8. Temporal patterns in the frequency of reproductive fronds of *Macrocystis integrifolia* sporophytes by sampling site. Mean ± SD.

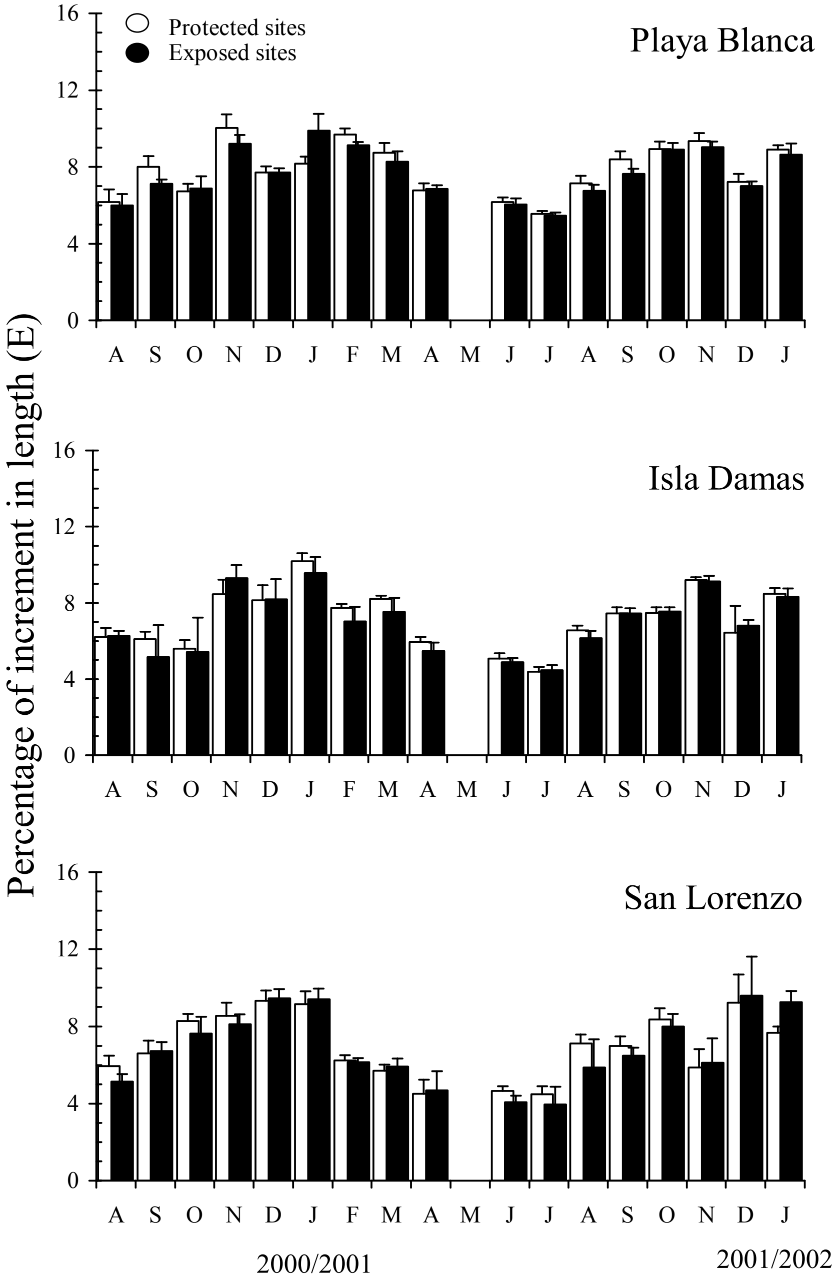


Figure 9. Monthly rate of frond elongation "E" (percent daily in cm) of *Macrocystis integrifolia* by sampling site. Mean ± SD.

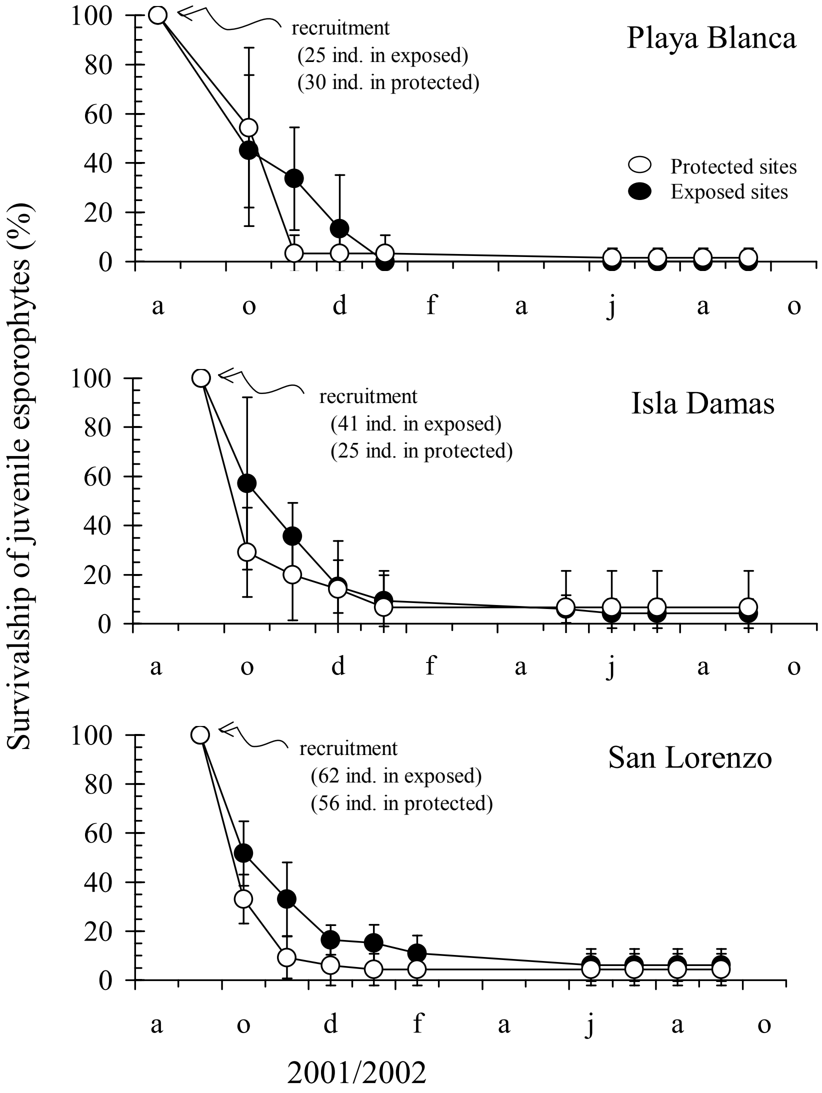


Figure 10. Temporal sequence in the survival *Macrocystis integrifolia* juvenile cohorts evaluated at each location and study site. Mean ± SD.

( )= initial density of recruits.

Table 1. Geographic location of study sites and bathymetric distributions of *Macrocystis integrifolia* populations.

Locality	Distance (km) from upwelling centers	Site	Geographyc ubication		Bathymetric distribution		Coast Orientation
			Latitude	Longitude	in shore	off shore	
Playa Blanca	150	Exposed	28º 11' 22,2"	71º 09' 48,1"	0.5 m	4 m	SW
		Protected	28º 11' 18,0"	71º 09' 53,3"			NW
Isla Damas	30	Exposed	29º 14' 08,3"	71º 31' 12,4"	0.5 m	8 m	SW
		Protected	29º 14' 29,7"	71º 31' 05,6"			SE
San Lorenzo	10	Exposed	30º 20' 10,9"	71º 40' 07,4"	0.5 m	5 m	SW
		Protected	30º 21' 29,8"	71º 40' 30,0"			NW

Table 2. Standard growth rate "G" (percent daily elongation in cm) for sporphyte fronds ubicated in exposed and protected sites in three localities of northern Chile near and away of upwelling centers Mean (Standard Desviation)

		Site	
locality	**Location from upwelling center**	**Exposed**	**Protected**
Playa blanca	away upwelling	5.18 (0.16)	5.27 (0.18)
Isla Damas	near upwelling	4.92 (0.27)	4.96 (0.23)
San lorenzo	near upwelling	4.86 (0.18)	4.91 (0.17)

CAPITULO 4

Local processes compound the latitudinal variability in the collapse and recovery of Chilean *Macrocystis integrifolia* populations (Laminariales, Phaeophyta) following 1997-1998 El Niño

Procesos locales producen variabilidad latitudinal en el colapso y recuperación de las poblaciones chilenas de *Macrocystis integrifolia* (Laminariales, Phaeophyta) después de El Niño 1997-1998

J. M. ALONSO VEGA[1][2], NATALIO GODOY[1], JULIO A. VASQUEZ[1][2]

[1] Facultad de Ciencias del Mar, Departamento de Biología Marina, Universidad Católica del Norte, Casilla 117 Coquimbo, Chile.

[2] Centro de Estudios Avanzados en Zonas Áridas (CEAZA).

ABSTRACT

An integrated, synchronic study is presented on interactive effects of two different-scale oceanographic processes including large-scale El Niño Southern Oscillation (ENSO) and mesoscale coastal upwelling, as they affect distribution and abundance patterns of kelp *Macrocystis integrifolia* Bory along temperate South American Pacific coast. Seasonal monitoring was carried out between 1996 and 2000 of abundance of adult and juvenile sporophytes at seven locations in northern Chile, encompassing 1500 km of coastline between 18°S and 32°S. Monthly records of different climatic indices, including Multivariate El Niño Index (MEI), Southern Oscillation Index (SOI), and Offshore Ekman Transport (OET), as well as continuous records of seawater temperature, were used to monitor the oceanographic climate. The high intensity 1997-1998 El Niño event occurred during the study period, as well as a moderate-intensity 1998-2000 La Niña event. These events were clearly detected at all sites included in the present study, based on seawater thermal anomalies. The upwelling events varied seasonally, with maximum in spring and summer, and interannual variability depending on ENSO events. The 1997-1998 El Niño produced mortalities of *M. integrifolia* at lower latitudes (18-20º S), associated with a decrease in upwelling events. At latitudes ≥ 23º S, the abundance of adult sporophytes decreased during the 1997-1998 El Niño, without causing local extinctions, and was correlated with persistence of upwelling events and a latitudinal decrease in sea surface warming. The increase in upwelling during spring of 1997, fully within the presence of the 1997-1998 El Niño, favored recruitment of juveniles in all the populations, although this recruitment did not result in the recovery of the abundance of adult populations. In contrast, intensification of upwelling processes from beginning of the 1998-2000 La Niña produced population dynamics for *M. integrifolia* determined by abiotic and biotic forcing factors, which were location-dependent. Our results suggested that alteration of geographical structure post-El Niño, are translated in an increase of regional heterogeneity of the patterns of distribution and abundance of *M. integrifolia*. This, possibly generates differences in the strategies of life of *M. integrifolia* between the north (18º-30ºS) and central (30º-37ºS) region of Chile or with con-generics species (*M. pyrifera*) located to southern Chile (> 40º S).

Keywords: population dynamics, kelp, *Macrocystis integrifolia*, Phaeophyta, latitudinal gradients, limiting factors, El Niño, Chile coast

INTRODUCTION

Kelp beds persist in a delicate balance between ecological processes driving their development and their extinction. These processes operate over a broad spectrum of temporal and spatial scales (Carlile *et al.* 1989, Wiens 1989). For *Macrocystis pyrifera* hierarchically nested scales have been distinguished (*sensu* Camus 1992), which are related to the most important factors that explain the spatio-temporal variability of kelp beds (Edwards 2004). The discrimination of scale-dependent variability patterns helps to unify patterns of distribution and abundance with the forcing factors operating at given scales (Dayton *et al*. 1992, 1999). Although in population studies the spatial inference is as diverse as the name assigned to the scale occupied, there is consensus that ecological processes, which act on a local scale (10^2 -10^3 m), are subordinate to others acting on a geographic scale (10^6 m), including a significant part of, or the entire latitudinal range of a species (Levin 1992).

On a local scale, the patterns of distribution and abundance of kelp are the net result of recruitment, growth and mortality, which are regulated by abiotic and biotic factors (North 1994). Temperature, light and nutrients are the principal abiotic factors controlling population dynamics of kelp (Jackson 1977, Graham 1996, Tegner *et al.* 1997, Hernández-Carmona *et al.* 2000, 2001), and covary to produce synergistic interactions (Kain 1989). Extrinsic biotic factors, which affect the kelp dynamics on this scale, include competition, herbivory and epiphytism (Vásquez & Buschmann 1997, Hurd *et al.* 2000), while intrinsic biotic factors are determined by intraspecific interactions, which generate processes of populational self-regulation dependent on the carrying capacity of the system (Reed & Foster 1984, Dayton *et al*. 1984, 1992).

On a geographic scale, the extension and persistence of kelp beds in the South American Pacific is correlated with the negative thermal anomaly in sea surface temperature (SST) of the coastal branch of the Humboldt Current, which flows towards the equator (Halpin *et al.* 2004). This anomalous negative condition is reinforced in spring and summer by the upwelling process of cool subsuperficial water, nutrient-enriched and poor in oxygen (Strub *et al.* 1998). In coastal areas having prominent geographic features such as points and peninsulas, upwelling may be stable and permanent throughout the year (Martínez *et al.* 2003). The topographic variability in the intensity and frequency of upwelling events is the main source of variation at a mesoscale of the SST and also nutrient concentrations along of this region (Strub *et al*. 1998, Nielsen & Navarrete 2004). Variability in the SST covaries inversely with the availability of nutrients (Zimmerman & Kremer 1984, Zimmerman & Robertson 1985), generating locality-dependent patterns in distribution and abundance of kelp, other macroalgae and consumers (Broitman *et al.* 2001, Martínez *et al.* 2003, Nielsen & Navarrete 2004, Vega *et al.* 2005). Together, these preceding processes generate a cascade-type "bottom up" trophic control, which locally regulates the composition and structure of the biota (Nielsen & Navarrete 2004), producing a highly diverse mosaic of submarine seascapes. This includes localities where benthic communities are strongly affected by large-scale oceanographic events such as the El Niño Southern Oscillation (ENSO), whereas in other localities the impact of these events is buffered, by areas with persistent upwelling (Martinez *et al.* 2003, Vega *et al.* 2005).

ENSO is an irregular fluctuation that involves the entire tropical Pacific Ocean and the global atmosphere generating interannual variability in the oceanographic climate, alternating periods with positive thermal anomalies (El Niño events) and negative thermal anomalies (La Niña events) of the SST in feedback cycles every two to seven years (Fiedler 2002). The changes in oceanographic climate caused by El Niño events have an important role as a process modulator in temperate latitudes of the South American Pacific, producing bathymetric migrations, invasions of exotic species, behavioral alterations, and changes in abundance which can range from reductions in population density to local extinctions (Glynn 1988, Camus 1994), modifying the composition of the biota on local and geographic scales (Camus 2001). Reductions in populations and local extinctions based on conditions generated by El

Niño events are important to the "engineer species" (*sensu* Jones *et al*. 1994) as kelps, since their presence or absence directly affects the diversity, structure, and functioning of cold temperate coastal ecosystems (Graham 2004, Vásquez *et al*. 2005).

El Niño events modify the geographic distribution range of kelps along a latitudinal gradient, generating processes of local extinction correlated with latitude (Camus 1994). Increase in the SST during El Niño, decreases the availability of nutrients producing physiological stress in the plants (Zimmerman & Robertson 1985, Gerard 1997). The nutrient deficit increases respiration rates, increasing the rate of tissue erosion above the growth rate, ultimately producing the deterioration and death of sporophytes (Gagne *et al.* 1982). Also, conditions during El Niño inhibit the growth and reproductive activity of the gametophytes, avoiding or decreasing the recruitment (Dean & Deysher 1983, Hernández-Carmona *et al*. 2000, 2001). Local conditions acting on a mesoscale, however, may alleviate the effects of El Niño events on some kelp beds, for example in locations with permanent coastal upwelling (Vega *et al*. 2005). Persistence of these local kelp beds and the post-Niño transition to a cool, nutrient-enriched condition (La Niña) facilitates and improves recolonization (Edwards 2004), although the recovery process may proceed slowly often requiring many years (Camus 1994, Martínez *et al.* 2003).

The 1997-1998 El Niño event on the northern coast of Chile produced two pulses of positive anomalies in SST, associated with strong poleward flow of warm nutrient-depleted water masses in the first 100 m (Carr *et al.* 2002). During these events, the thermocline, oxycline and nutricline, normally positioned at 40-60 m water depth, were depressed to 150-200 m (Ulloa *et al*. 2001). Nevertheless, during the 1997-1998 El Niño event, upwelling processes remained active in some coastal localities (Lagos *et al.* 2002). The 1997-1998 El Niño was immediately followed by a La Niña condition, characterized by a weak to moderate cooling of surface waters from 1998 to 2000 (Takesue *et al*. 2004). The 1998-2000 La Niña promoted the development of South Western winds, which drive coastal upwelling along the length of the South American Pacific coastline (Lagos *et al*. 2002). Given this scenario of some localities impacted by the 1997-1998 El Niño event and others relatively unaffected by changing oceanographic conditions. We predicted that kelp beds near at areas with permanent upwelling would persist during and before El Niño conditions, whereas kelp beds away from upwelling areas occur extinction and recolonization processes latitude-dependent. In this context, we carried out a monitoring program on seven subtidal populations of *M. integrifolia* Bory between 1996 and 2000. *Macrocystis integrifolia* presents a bipolar distribution on the American Pacific, forming beds from the intertidal zone to 15-20 m depth, both in protected and semi-exposed habitats (Alveal *et al*. 1973). In the Southern Hemisphere, the center of distribution of *M. integrifolia* beds is in northern Chile (18°-32° S), although the recorded distributional range for the species ranges from northern Peru (ca. 4º S) to central Chile (ca. 37º S) (Ramírez & Santelices 1991). In the Chilean northern coast, the sites were scattered along more than 1500 km of coastline, which permitted evaluation of the interactive effects between coastal upwelling and an ENSO cycle (1997-1998 El Niño event and 1998-2000 La Niña event) on the dynamics of subtidal kelp beds over a latitudinal gradient on the South American Pacific coast (18°-32° S).

This study examines, in an integrated and synchronous manner, the interactive effects of scale-dependent oceanic processes (ENSO cycle and coastal upwelling) on patterns of distribution and abundance of *M. integrifolia* sporophytes in northern Chile (18-32ºS). Both coastal oceanographic processes are important in the dynamics and organization of populations and communities on rocky shores in northern Chile (Camus 1990, 2001). In general, we postulate that the ENSO cycle and coastal upwelling are forcing agents in the development and persistence of subtidal kelp beds of *M. integrifolia* in the South East Pacific temperate coast.

MATERIALS AND METHODS

Study Area

The study area is located between 18° S and 32° S on the Chilean coast of the SE Pacific Ocean, representing an extension of about 1500 km (Fig.1). On a geographic scale, this part of the Chilean coastline is nearly straight, interrupted by a few small peninsulas and semi-protected bays. It is mostly wave-exposed rocky coastline, experiencing predominant SW winds (Strub *et al*. 1998). On a mesoscale, topographical complexity of this section of the coast increases toward the north, with a few inshore islands and coastal indentations open to the north, including small points, isthmuses, and peninsulas producing wave-protected sites (Vega & Vásquez 2005). Seasonal studies were carried out within this context between June 1996 and December 2000 on the patterns of distribution and abundance of *Macrocystis* subtidal beds at seven sites along this coast (Fig. 1A). The geographic location, wave-exposure, and bathymetric distribution of each of kelp beds are listed in Table 1.

With the exception of the Camarones site (Results, below), all the kelp beds consisted of a dominant stratum formed of *M. integrifolia* fronds extending to, and spreading at the sea surface. When present, shrub-like plants of the kelp *Lessonia trabeculata* formed a second, subsurface stratum (Vega *et al*. 2005). A third or basal stratum was variable in composition and structure. In some kelp beds, only crustose coralline algae were dominant, or were mixed with a turf of Gelidiales, Ceramiales and/or articulated corallines, while in others there were also monospecific stands or assemblages of foliose macroalgae (Vásquez *et al.* 2001a). There was a high diversity of invertebrates and fishes associated with the kelp beds (Godoy 2000). The most representative herbivores of this kelp beds in northern Chile are the snails *Tegula* spp and *Prisogaster niger*, the Decapod Crustaceans *Taliepus* spp. and the sea urchins *Tetrapygus niger* and *Loxechinus albus* (Vásquez & Buschmann 1997, Vásquez *et al*. 2001b).

Oceanographic conditions

Consultation with global climatic indices permitted characterization of general oceanographic conditions in the study area between 1996 and 2000, and are useful for making comparisons among oceanographic events and ecological processes which act on different spatio-temporal scales (Stenseth *et al*. 2003). The warm and cold phases of ENSO phenomena were estimated using the Southern Oscillation Index (SOI) and the Multivariate El Niño Index (MEI) obtained from the Australian Metereological Bureau (www.bom.gov.au/climate/current/) and the NOAA climatic diagnostic center (www.cdc.noaa.gov/~kew/MEI/mei.html), respectively. In order to evaluate the interannual and latitudinal variability in thermal anomalies in the study area we used the 1996-2000 SST time series recorded at five Chilean ports including Arica (18º), Iquique (20º), Antofagasta (23º), Caldera (27º) and Coquimbo (30º) available from the Chilean Navy Hydrographic Service (www.shoa.cl/index.jsp). *In situ* mean water temperatures were obtained at each sampling location in our study using continuous-recording thermographs (Onset Computer Corp., Bourne, Maine, USA), placed at 3 m depth within each kelp bed. Monthly thermal anomalies were calculated from monthly averages of SST for the study area and from the *in situ* temperature records for each sampling site, respectively. For both cases, the average mean monthly anomaly from January 1996 to December 2000 was calculated as a function of the monthly average of the historical time series over 53 years, obtained from the Chilean Navy Hydrographic Service (www.shoa.cl/index.jsp). To determine the spatial and temporal variability of upwelling events in the study area, we used the monthly average of the upwelling index (Offshore Eckman Transport, OET) between 1996 and 2000 for the stations located at 18º, 21º, 24º, 27º and 30º S. The monthly averages were obtained from the Pacific Environmental Laboratory of NOAA (www.pefg.noaa.gov/products/ PFELindices.htm; PFEL). A detailed description of the calculation, characteristics and area of influence of the SOI, MEI and OET indexes for the South American Pacific has been given by Navarrete *et al*. (2002).

Temporal patterns of abundance of *M. integrifolia*

The temporal patterns of abundance in the *M. integrifolia* subtidal kelp beds at each sampling location were evaluated on a seasonal basis, employing transects perpendicular to the coastline, and occupied once during each of the four seasons of the year. Sampling was done throughout the entire extension of each kelp bed sampled. Four replicate transects (n=4) were sampled within each kelp bed, each measuring between 50 and 160 m length, depending on the size of the bed, by one meter in width. Juvenile and adult sporophytes of *M. integrifolia* were counted within each transect, with abundances of adult and juvenile sporophytes expressed in numbers of individuals per m^2. Sporophytes with one or two laminar, lanceolate fronds without sporophylls, and having a holdfast $\leq$ 4 cm were considered to be juveniles. The seasonal monitoring in rocky habitats at Camarones (18º) during the study period was carried out to evaluate the potential long-term recolonization of *M. integrifolia*. At the San Marcos location, sampling of an intertidal population of *M. integrifolia* which appeared after the 1997-1998 El Niño was carried out using the same methodology as described for the subtidal kelp beds.

Data analysis

Our study rests mainly on the weight of the evidence, more than on a test of a statistical hypothesis. This line of thought has been previously applied to kelp population studies where the spatio-temporal variability was dependent on the accessibility, logistics, sea state, diving conditions, and evaluation methods (Tegner *et al*. 1997, Dayton *et al*. 1999), which as a group produced discontinuities in data collection such that the data did not meet the requisites for carrying out analyses of variance or of time series. The annual variation of the upwelling index by latitude was compared with ANOVA, using SYSTAT 8.0® software for Windows; after subjecting the data to a log + 1 transformation (Sokal & Rohlf 1981). The relations between the different climatic indices (SOI, MEI and OET), and local thermal anomalies were determined using a Pearson correlation analysis (Sokal & Rohlf 1981).

RESULTS

Oceanographic conditions

The oceanographic climate, based on the SOI and MEI indices, showed normal to slightly cool conditions during 1996, which persisted until summer 1997. From April 1997 to April 1998, the SOI showed negative values due to a high magnitude El Niño event. According to the MEI, the maximum intensities of the El Niño occurred during August/September 1997 (> 2.8 MEI) and February/March 1998 (> 2.7 MEI) (Fig. 1B). Immediately after the anomalous warm condition, La Niña condition began in August 1998 which was moderately cool (SOI range: 22.4 to –5.5; MEI range: 0.0 to –1.2) and remained until the end the study period (December 2000), although during the winter of 2000 the condition tended towards normality (Fig. 1B). The thermal anomalies calculated as a function of the *in situ* seawater temperature records for in all the kelp beds studied were negatively correlated with the SOI and positively correlated with the MEI (Table 2). During the 1997-1998 El Niño event, the positive thermal anomalies in seawater temperature decreased with increasing in latitude (Fig. 2). Between 18º S and 21º S the mean values of the thermal anomalies during the El Niño period were +2.5ºC, with maximum in the winter of 1997 (+2.6ºC) and summer of 1998 (+3.8ºC to +4.4ºC) (Fig. 2). At 23º S the mean thermal anomaly was +1.9ºC, with a maximum of +2.9ºC in winter 1997 and summer 1998 (Fig. 2). In contrast, at 27º S and 30º S the mean values for the thermal anomalies during the El Niño were +1.0ºC, with maximum of +2.1ºC in winter 1997 for both latitudes, with a second maximum of +2.2ºC, which was observed in summer 1998 at 27º S and +2.0ºC in winter 1998 at 30º S, respectively (Fig. 2). No latitudinal pattern was detected in negative thermal anomalies in sea temperature during the 1998-2000 La Niña condition (Fig. 2). The mean values for the thermal anomalies observed during the La Niña condition were -0.2ºC ± 0.6 at 18º S, -0.6 ± 0.5 at 21º S, -0.4 ± 0.8 at 23º S, -0.7 ± 0.7 at 27º S, and -0.3 ± 0.7 at 30º S, suggesting moderate cooling of the water during 1998-2000. However, the lowest negative values for the water temperature anomalies fluctuated between –1.6ºC and –2.5ºC, but became apparent during different seasons depending on latitude (Fig. 2).

The upwelling indices for northern Chile (estimated from the OET for different latitudes within the study area) showed maximum values in spring and summer, reaching conditions near neutrality or with downwelling of surface water in fall and winter (Fig. 2). However, annual temporal tendencies in the upwelling index differed significantly with latitude (Table 2). At 21°S the annual temporal tendency of the upwelling index is always significantly less when compared with all the other latitudes evaluated (Tukey test, $p<0.05$), with the OET reaching negative values during 1998 mainly in fall and winter (Table 3, Fig. 2). This suggests stratification of the water column, and deepening of the thermocline. At 18º S, the mean annual upwelling index was significantly lower during 1997, but slightly higher during 1996, 1999 and 2000 than at latitudes greater than 23º S (Table 3, Fig. 2). In contrast, a temporal tendency similar to the OET index was observed at 23º S, 27º S and 30º S (Fig. 2), with a weak but significant latitudinal tendency with increases in the mean upwelling indexes with latitude. This tendency was consistent among years (Table 3). In general, upwelling events during the El Niño condition througthout the study area, mainly in spring 1997 and summer 1998, in part buffered the warming at the sea surface (Fig. 2). This modulation of the effects of the 1997-1998 El Niño increased with latitude due to the increase in the frequency and magnitude of upwelling and the dilution of the El Niño event towards the higher latitudes (Fig. 2).

Population dynamics

The 1997-1998 El Niño had a differential impact over the latitudinal gradient included in the present study (18°-32°S). High impact of the El Niño conditions are observed in kelp beds located at higher latitudes (18º-21º S). Whereas, positive thermal anomalies have smooth effects in kelp beds located at lower latitude (23º-32º S). Thus, varied spatio-temporal patterns of abundance of *M. integrifolia* were observed at study area (Fig. 3).

During 1997-1998 El Niño, the density of adult sporophytes of *M. integrifolia* in San Marcos (21º S) decreased rapidly and linearly with increase in positive thermal anomalies (Fig. 3). Six months later, no adult sporophytes were found, marking local extinction of subtidal kelp bed, with no recolonization process observed during the study period (Fig. 3). In Camarones (18º S) during 1970's, the kelp bed occupied an area approx. 40 ha (IFOP, 1977), but the 1982-1983 El Niño event caused the local extinction (Soto 1985). Fifteen years later, the 1997-1998 El Niño generated substrate suitable for that occurs process of recolonization. In spite of favorable growth conditions produced by 1998-2000 La Niña event at this latitude, the kelp bed did not become re-established at that time (Fig. 3).

In contrast, from 23º to 32º S, the adult segment of the kelp populations persisted in subtidal habitats during period of positive thermal anomalies of the 1997-1998 El Niño. Inside this latitudinal range, the positive thermal anomalies did not significantly affect the abundance patterns of kelp bed located in areas with permanent upwelling (Constitución, Los Choros y San Lorenzo; Fig. 3). On the other hand, slight decreases in abundance of sporophytes were observed in kelp bed of Playa Blanca and Los Vilos (Fig. 3), both located in areas without permanent upwelling.

During the beginning of the 1998-2000 La Niña conditions, low abundances ($\leq$0.01 ind./m^2) of adult sporophytes of *M. integrifolia* were observed at an intertidal site near the subtidal sampling site at San Marcos, which in the following year a kelp bed was established persisted until the end of the study (Fig. 3). In Constitución, however, the abundance of sporophytes gradually diminished until the kelp bed disappeared in 1999 (Fig. 3), although a few adult sporophytes persisted in the deepest portion of the study site (0.1-0.6 plants/m^2). At higher latitudes (28º-32º S), the local abundance patterns of *M. integrifolia* adult sporophytes were temporally stable during negative thermal anomalies (Fig. 3).

With the exception of San Marcos, in all kelp beds evaluated a great recruitment of juveniles is observed during 1997-1998 El Niño conditions up to the beginning La Niña condition (1998), but during subsequent years a decrease in the abundance of juveniles sporophytes occurred at all the localities evaluated until the year 2000 (Fig. 4). The strong increase in the abundance of juvenile *M. integrifolia* at all study sites suggests that the attenuation of positive thermal anomalies induced by increase of upwelling process during spring 1998 favors a synchronous and massive recruitment (Fig. 4). The lower density of juvenile at San Marcos might explain the extinction of the kelp bed in this locality, but these cohorts were unable to contribute to the recovery of subtidal kelp beds located in higher latitudes during the following year (Fig. 4).

The beginning of La Niña conditions, indicated by negative thermal anomalies due to increase in seasonal upwelling processes, favored the synchronic development of a second cohort of recruits (fall-winter 1998) at all the study locations, including a emergent intertidal kelp bed at San Marcos (Fig. 4). This cohort could be clearly noted during spring 1998 when the abundance of juvenile sporophytes of *M. integrifolia* presents a second great increase in all the kelp beds (Fig. 4). Thus, with the exception at Caleta Constitución, the establishment and/or persistence of the *M. integrifolia* at the sampling sites during 1998-2000 appeared to be due to successful recruitments during initiation of La Niña conditions. Conversely, the low but constant abundance of juveniles during 1999-2000 (Fig. 4), suggested that continuous recruitment throughout the year explained the stability in the temporal patterns in the abundance of the adult fraction in the rest of the kelp populations monitored (Fig. 4).

DISCUSSION

In the design of ecological studies it is of increasing importance to identify the different temporal-spatial scales at which ecological processes act and how these affect relevant population parameters (Dayton and Tegner 1984, Carlile *et al*. 1989, Levin 1992, Dayton *et al*. 1999). Some studies have shown the utility of using space as a discrete variable based on an *a priori* hypothesis of logistical contrasts by means of a hierarchical sampling design with analysis of variance components (Wiens 1989). This design has been used in the study of scale-dependent process and patterns in the dynamics of kelp species (Camus & Ojeda 1992, Edwards 2004). However, when the sampling design is unable to fulfill with the statistical requisites needed, qualitative analyses can be used, which treat space as a continuous, and data are collected on the abundance of kelp at randomly selected intervals for indirect identification of scale-dependent processes.

Effects of the ENSO in abundance patterns

Based on the historical record of positive thermal anomalies, those produced by 1997-1998 El Niño have been the strongest recorded (Stenseth *et al*. 2002). As a direct consequence, this event modified the circulation patterns and water properties, with increased sea level and isotherm depths (Carr *et al*. 2002). Also during this period, the coastal upwelling processes are diminished or inhibited, particularly at low latitudes of the South American Pacific (Ulloa *et al*. 2001). Additionally, unusually high swells occurred during winter and spring (1997) and summer and fall (1998) (Halpin *et al*. 2004). These oceanographic conditions caused mass mortalities of adult sporophytes of *M. integrifolia*, correlated with latitude, which in many locations resulted in extinctions of local kelp populations (Godoy 2000, Llellish *et al*. 2001, and present study).

The transition and first peak of El Niño conditions generated available substrate, due to the decrease in abundance of adult sporophytes. However, the re-establishment of seasonal upwelling process in spring 1997 moderated surface warming and nutrient deficit (Carr *et al.* 2002, Takesue *et al*. 2004). This relaxation of El Niño condition favored a synchronic and massive recruitment, which was reflected by the proliferation of juvenile sporophytes along the northern Chilean coast. However, this recruitment pulse did not lead to a recovery of the populations during the following year, due to a second peak of El Niño conditions in summer 1998. *In situ* experiments showed that the recruitment and growth of kelp juveniles during El Niño condition was mainly limited by the availability of nutrients produced during the positive thermal anomalies of the 1997-1998 El Niño (Hernández-Carmona *et al*. 2000, 2001). This can be considered as circumstantial evidence of the importance in the continuity of seasonal upwelling for the persistence of *Macrocystis integrifolia* populations in the northern Chile during El Niño events. The synergistic effect of positive thermal anomalies, reduced availability of nutrients, and increased wave intensity, which act on a large scale can be buffered on mesoscale by other oceanographic process such as permanent coastal upwelling (Martínez 1999, Vega *et al*. 2005), producing different stages of development and persistence of local kelp beds over a latitudinal gradient. Immediately after the 1997-1998 El Niño, the South American Pacific coast experienced a period of oceanic conditions, which were anomalously cool, and nutrient-enriched (Carr *et al.* 2002, Takesue *et al.* 2004). The 1998-2000 La Niña event facilitated the recolonization processes of *Macrocystis* beds. However, the recovery rate of populations depended on local factors and the availability of reproductive propagules (Ladah *et al*. 1999). The local extinction and recolonization processes produced a change in the spatial distribution of the remaining local populations of *M. integrifolia*, similar as has been reported for other kelps (Camus 1994, Martínez 1999).

The 1997-1998 El Niño had a differential impact over the latitudinal gradient included in the present study (18°-32°S). The processes of recolonization and recovery of kelp beds are discussed separately. (a) Recolonization: Immediately after the 1997-1998 El Niño, recovery of the kelp beds between 18º S and 21º S was generally poor and geographically variable. At San Marcos (20º S) the recolonization process of the kelp bed occurred post-El Niño event (albeit recruitment occurred at an intertidal site), whereas to kelp bed documented in 1977 at Camarones (18º S) never re-established. Local extinction processes of *Macrocystis* in Peru were also documented after the 1997-1998 El Niño, extending our results to 11° S (Llellish *et al*. 2001). These local differences in the recolonization processes of kelp beds have been widely associated with the availability of microscopic stages (Ladah *et al*. 1999; Hernández-Carmona *et al.* 2000, 2001), or the survival of low-density patches of adult sporophytes in deepwater refuges (Ladah & Zertuche-González 2004, Vega *et al*. 2005) and possibly in intertidal areas (present study). During the return to cold conditions, with nutrient-rich waters and an adequate availability of propagules, local differences in recolonization of the kelp beds appear to be the result of variability in factors such as competition with sessile invertebrates, other macroalgae, and substrate availability for settlement (Ladah *et al*. 1999; Godoy 2000, *et al*. 2001, Llellish *et al*. 2001, Edwards 2004, Edwards & Hernández-Carmona 2005, Vega *et al*. 2005). (b) Recovery: This occurred rapidly in kelp beds at high latitudes (23º-32º S) during winter-spring 1998. Six months after of the 1997-1998 El Niño, all the locations evaluated, showed recovery, and increase in the abundance of sporophytes. The rapid recovery was facilitated by cool conditions of the 1998-2000 La Niña (Ulloa *et al*. 2001, Takesue *et al.* 2004), and by the presence of microscopic life stages (Ladah *et al.* 1999, Buschmann *et al*. 2004).

Effects of local factors and mesoscale process in abundance patterns

Under "normal" oceanographic conditions, the kelp abundance is modulated by abiotic factors, as well as by intrinsic and extrinsic biotic factors acting on a local scale (North 1994, Dayton *et al*. 1984, 1992, Graham *et al.* 1997, Graham 2002, Buschmann *et al*. 2004, Vega & Vásquez 2005). In contrast, patterns of distribution and abundance of kelp during the 1997-1998 El Niño condition were modulated mainly by oceanographic factors acting on a geographic scale (Tegner *et al.* 1997; Dayton *et al.* 1998, 1999; Edwards 2004). However, during this El Niño event, processes that acted on a mesoscale such as permanent upwelling next to some peninsulas aided in the local persistence of some *M. integrifolia* populations (Vega *et al.* 2005). This was the case representing the kelp beds at Caleta Constitución (23ºS), where the population dynamics of *M. integrifolia* were not modified during the 1997-1998 El Niño because upwelling activity was not interrupted in this area (Lagos *et al.* 2002, Takesue *et al.* 2004; Vega *et al.* 2005, present study). Based on this results it can be suggested that the persistence of kelp populations in the above mentioned upwelling areas during the higher positive thermal anomalies might function post-El Niño as local sources which "export" propagules to other localities "sinks" without upwelling where extinction process of kelp have occurred (Camus 1994). The propagules export may be realized throughout reproductive sporophylles in drift kelp raft (Macaya *et al.* 2005).

The return to the processes that had acquired local importance after the 1997-1998 El Niño, and during the 1998-2000 La Niña, was characterized by the development of different *Macrocystis* population dynamics detectable as a function of the scale of observation employed (geographic, mesoscale, or local). This reveals a differentiation scale-dependent in the relative importance of factors, which determine recruitment, growth, and survival of *Macrocystis* (Edwards 2004, present study). In this context, numerous studies suggest that these processes are driven by interactions of multiple biological and physical factors which act on mesoscale (*e.g.* ocean temperature, vicinity to areas of coastal upwelling) and on a local scale (*e.g.* availability of reproductive propagules, grazing, and competition) (Reed and Foster 1984, Deysher and Dean 1986, Graham *et al.* 1997, Dayton *et al.* 1999, Tegner *et al.* 1997, Ladah *et al.* 1999, Hernández-Carmona *et al.* 2000, 2001, Nielsen & Navarrete 2004, Buschmann *et al.* 2004, Vega *et al.* 2005, Vásquez *et al.* 2005). At Caleta Constitución (23º S), increases of the sea urchin abundance produced the local extinction of *M. integrifolia* in La Niña conditions (Vásquez *et al.* 2005). Local, low frequency and stochastic events of this type generate decreases in the kelp abundance, adding another level of complexity to its' dynamics on a geographic scale (Graham 2002, Edwards 2004, Vega *et al.* 2005).

Hemispherical comparisons

The present study analyzed qualitatively and indirectly the dependence on scale of the population dynamics of *M. integrifolia* over a geographic gradient in northern Chile. Our results compliment the analysis of geographic variance presented by Edwards (2004) on the population dynamics of *M. pyrifera* in the California upwelling ecosystem. The impact of 1997-1998 El Niño event was catastrophic for *Macrocystis* beds at low latitudes in both hemispheres, with almost complete loss of kelp beds along the coasts of Central and Baja California (Ladah *et al*. 1999, Hernández-Carmona *et al*. 2001, Edwards 2004), and in Peru and the extreme northern of Chile (Godoy 2000, Llellish *et al*. 2001, present study).

On the Pacific coast of South America, the almost complete disappearance of the kelp beds between 6° and 21°S produced a temporal suppression of the distributional limit of *M. integrifolia* towards high latitudes, similar to that described for *M. pyrifera* in the North American Pacific (Edwards 2004). These patterns have been commonly described for previous El Niño events in both hemispheres (Dayton and Tegner 1984, Tomicic 1985, Glynn 1988; Camus 1994, Hernández-Carmona *et al*. 2001). On the other hand, our results show an important variability in the impact of El Niño on a local scale, suggesting that processes acting on this scale are relevant along the latitudinal gradient of kelp distribution. Evidence for this, although not analyzed within the present context can be found in the studies of Camus (1994), Camus *et al.* (1994), Dayton *et al*. (1998, 1999), and Martínez *et al*. (2003). This authors described, in example, decrease the kelp genetic variability and low recovery process at sites located to lower latitudes and local importance of the presence or absence of ecosystem engineer or habitat-forming species.

In conclusion, during the 1997-1998 El Niño, the intensity and frequency of coastal upwelling processes were latitudinally modified, interacting inversely with intensity and magnitude of positive thermal anomalies. Here, persistence of kelp beds in low latitudes occurs only in coast areas having permanent upwelling. In other areas the El Niño event modifies the population dynamics due to inhibition of seasonal upwelling, producing short-term processes of local extinction and locality dependent recolonization processes. The permanent upwelling areas play an important role in reproduction and survival of kelp, especially during El Niño events. These areas favor the recolonization process in near areas where massive kelp mortalities occur. Nevertheless, while local patterns of recolonization depend directly on the re-establishment of seasonal upwelling along the Pacific coast of South America, the recolonization processes at other locations are more complex, suggesting that impact of the disturbance intensifies between the extreme northern Chile and the Peruvian coast (6º-23º S). The alteration of geographical structure post-El Niño, are translated in an increase of regional heterogeneity of the distribution and abundance patterns of *M. integrifolia*. This, finally, generates differences in the strategies of life of *M. integrifolia* between the north (18º-30ºS) and central (30º-37ºS) region of Chile or with con-generics species (*M. pyrifera*) located to southern Chile (> 40º S).

ACKNOWLEDGEMENTS

The authors acknowledge the help, in the field and in the laboratory, of D. Véliz, L. M. Pardo, F. Véliz, C. Cerda, S. Rubilar, E. Gelsich, A. Masuero, P. Flores, F. Díaz, J. Rivera, E. Rojas, A. L. Valdivia, B. Rubina, S. Ramos, N. Piaget and C. Olivares. We also wish to recognize the advice and constructive criticism of M. Thiel on various aspect of this manuscript. This study was supported by FONDECYT-SECTORIAL 5960001, FONDAP O&BM Nº3, FONDECYT 1000044-1040425 granted to JAV. This research is part of JMAV Masters of Sciences Thesis, and NG Marine Biologist Thesis.

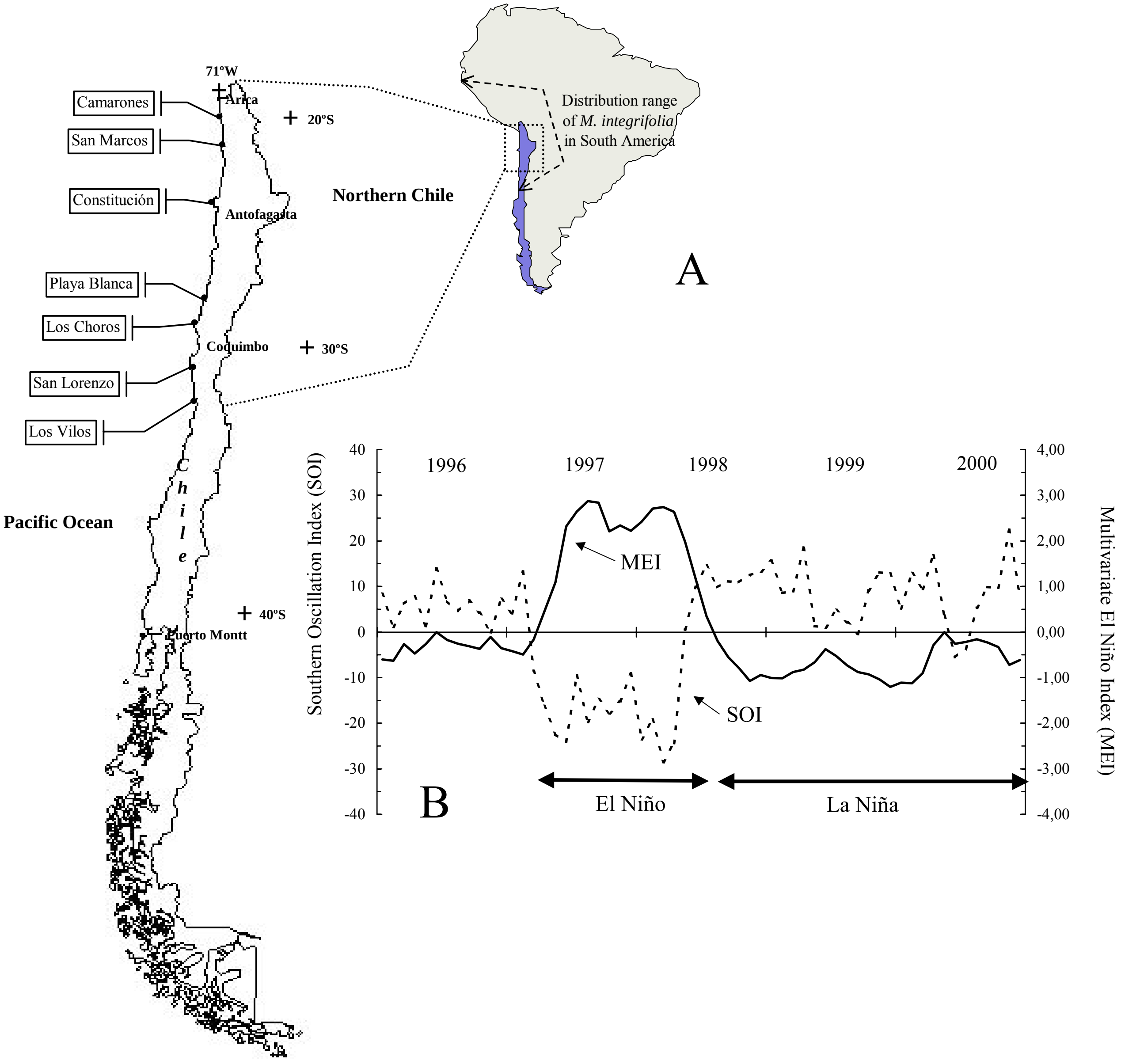


Figure 1. (A) Study area in northern Chile to show sampling locations and latitudinal distribution of *M. integrifolia* along the South American Pacific coastline. (B) Temporal characterization (1996-2000) of the oceanographic climate in the study area as a function of global climatic indices including the El Niño Multivariate Index (MEI) and the southern oscillation index (SOI).

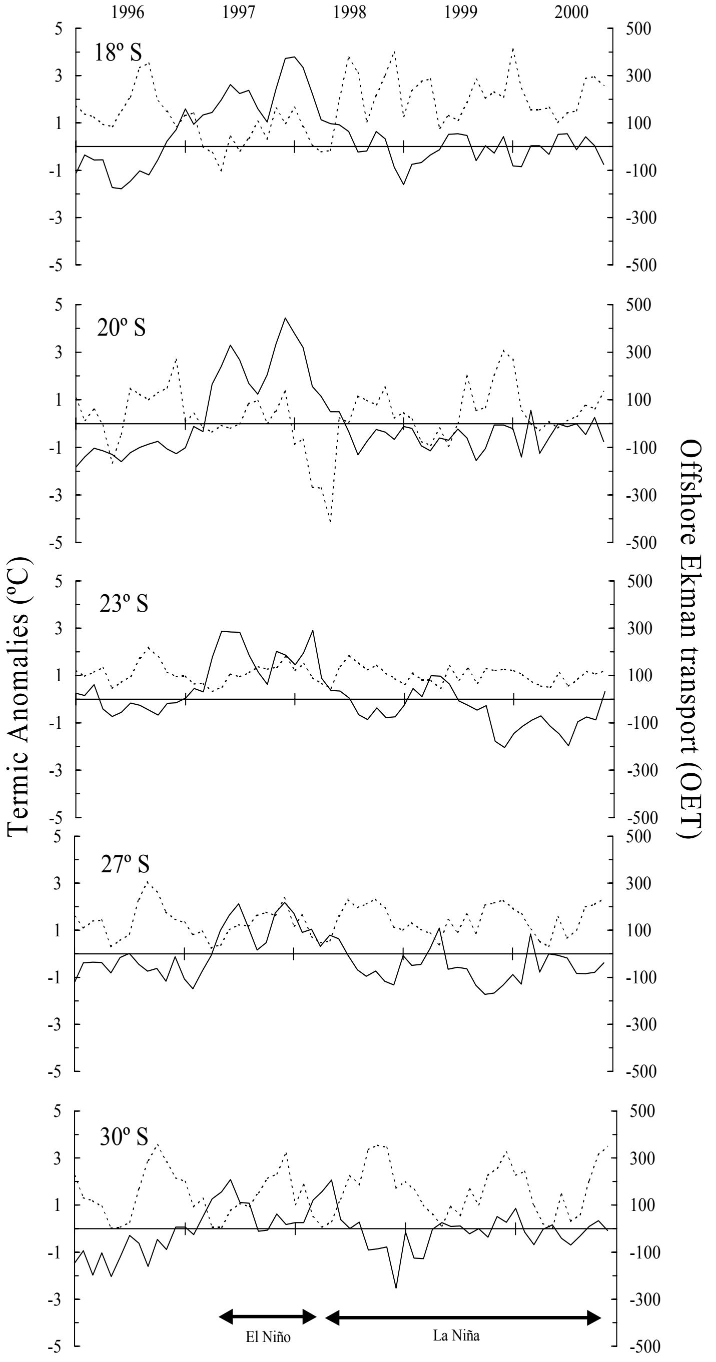


Figure 2. Temporal characterization (1996-2000) of the local oceanographic climate on a latitudinal gradient in northern Chile as a function of thermal anomalies in the sea surface temperature (SST; solid line) and the index of coastal upwelling (OET; broken line).

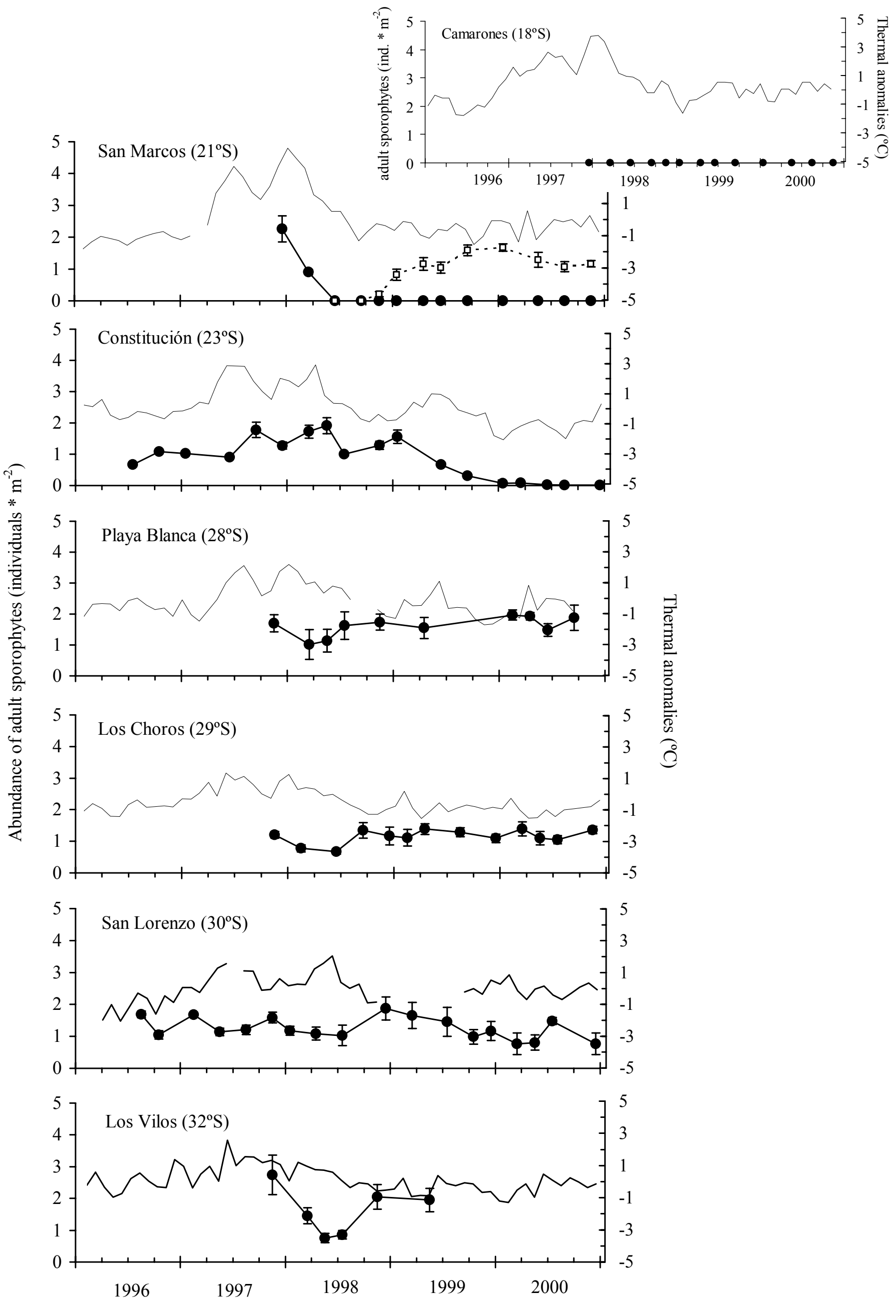


Figure 3. Temporal variation (1996-2000) in the abundances of adult sporophytes of *M. integrifolia* (●) and thermal anomalies estimated *in situ* (line) over a latitudinal gradient in northern Chile. *Note*: At San Marcos an intertidal kelp population appeared after an El Niño event (□), while the subtidal kelp bed did not recover. At Camarones (top) no sporophytes were observed during the study period.

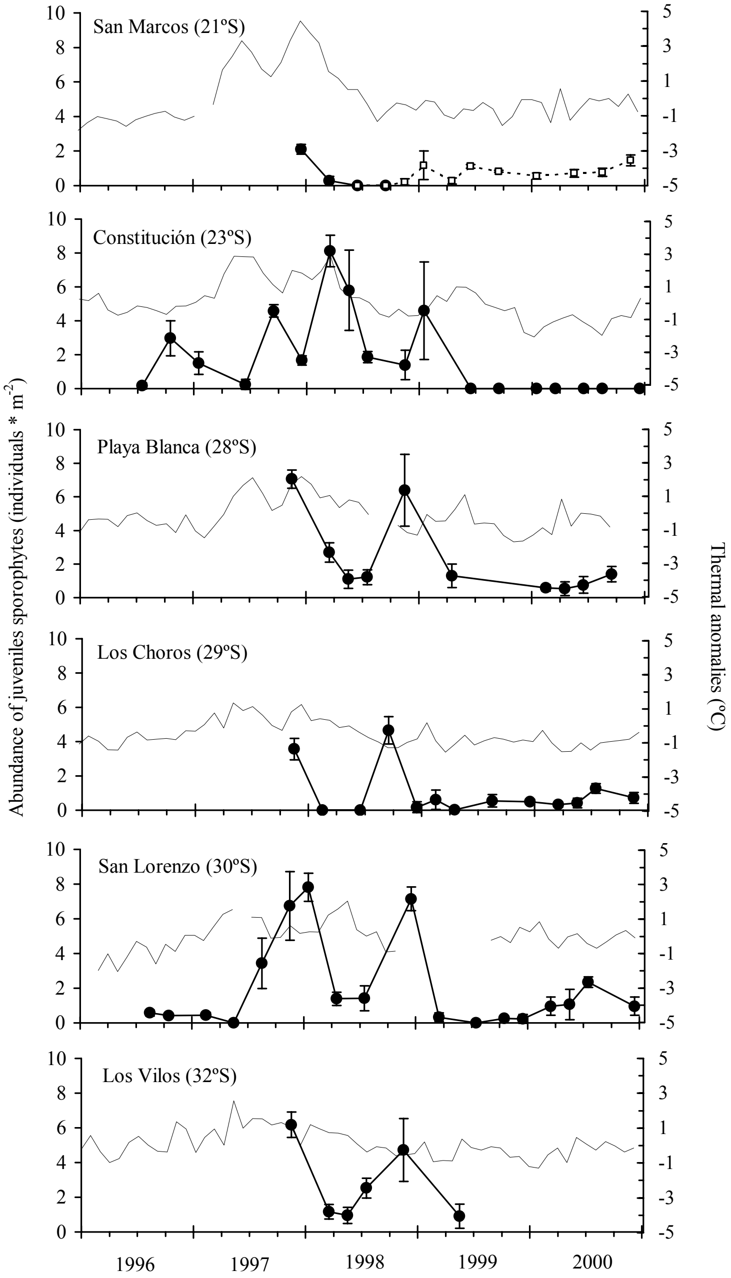


Figure 4. Temporal variation (1996-2000) in the abundances of juvenile sporophytes of *M. integrifolia* (●) and thermal anomalies estimated *in situ* (line) over a latitudinal gradient in northern Chile. *Note*: At in San Marcos an intertidal kelp population appeared post-El Niño event (□).

Table 1. Location, degree of exposure, and geographic coordinates of the study sites, with bathymetric distributions of kelp beds of *Macrocystis integrifolia* monitored in northern Chile.

kelp beds of *M. integrifolia*		Geographic coordinates		Bathymetric distributions		Orientation
Locality	site	Latitude	Longitude	shallow	deep	of the coast
Camarones	Protected	19°12' 48"	70º 17' 21"	-	-	NW
San Marcos	Exposed	21º 18' 33"	70º 15' 18"	0.5 m	12 m	SW
Constitución	Semi-exposed	23° 26' 30"	71º 36' 30"	1.0 m	15 m	SW
Playa Blanca	Exposed	28º 11' 22"	71º 09' 48"	0.9 m	4 m	NW
Los Choros	Exposed	29º 14' 08"	71º 31' 12"	0.5 m	8 m	SE
San Lorenzo	Protected	30º 21' 30"	71º 40' 30"	0.7 m	5 m	SW
Los Vilos	Exposed	31º 54' 28"	71º 31' 07"	1.0 m	5 m	NW

Table 2. Pearson correlation coefficient (probability in parenthesis), between climatic indexes (SOI and MEI) and thermic anomalies calculated from *in situ* records of seawater temperature of each locality study per latitude. Significant association at alpha = 0.05.

	Thermic anomalies from *in situ* records of seawater temperature per latitude						
Climatic index	18º	20º	23º	28º	29º	30º	32º
SOI	-0.398	-0.720	-0.733	-0.629	-0.724	-0.466	-0.670
	(0.0017)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0002)	(0.0001)
MEI	0.447	0.858	0.804	0.818	0.769	0.562	0.749
	(0.0003)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)	(0.0001)

Table 3. Yearly mean (SD) upwelling indexes (Offshore Eckman transport, m^3 s^{-1} per 100 m of coastline) for quadrants of 3º * 3º of latitude by longitude along northern Chile. Results of two-way ANOVA comparing upwelling indexes among latitudes and years. Significant differences at alpha of 0.05.
(df, degrees of freedom; MS, mean square)

	YEAR				
Latitude (º S)	**1996**	**1997**	**1998**	**1999**	**2000**
18	174.0 (25.5)	49.2 (22.7)	152.3 (38.5)	212.7 (26.6)	214.9 (25.4)
21	73.0 (32.1)	39.4 (24.2)	-41.3 (53.5)	27.6 (28.5)	75.3 (31.5)
23	123.2 (13.8)	93.3 (9.7)	125.4 (12.1)	94.3 (8.8)	93.6 (8.2)
27	153.6 (23.6)	113.6 (13.9)	159.8 (20.3)	123.8 (15.0)	145.3 (20.7)
30	160.5 (34.0)	127.3 (22.5)	189.2 (37.2)	134.3 (21.7)	168.5 (36.4)

Source of variation	**df**	**MS**	***F***	***P***
Year	4	99.339	3.291	0.0118
Latitude	4	741.583	24.567	0.0001
Year * Latitude	16	56.551	1.873	0.0228
Residual	275	30.186		

DISCUSIÓN GENERAL

Aspectos metodológicos, resultados y fenómenos del estudio

El objetivo general de esta tesis fue el estudio de los efectos del evento El Niño y de la surgencia costera permanente en la dinámica de las poblaciones de *M. integrifolia* en el norte de Chile. Es por esta razón que cada uno de los distintos Capítulos contiene alguno de los objetivos específicos planteados en la presente tesis, que constituyen diferentes aspectos de un mismo tipo de fenómenos, la regulación de los patrones de distribución y abundancia de *M. integrifolia* por procesos que operan a escala regional (ENOS) que inciden en otros que actúan a mesoescala (surgencia costera permanente) y a escala local (factores abióticos y bióticos). Sin embargo, existen otros factores forzantes no considerados en este estudio (Ej. Cambio global, Oscilación Decadal del Pacífico, áreas intervenidas antrópicamente, etc.), que actúan a distintas escalas espacio-temporales generando procesos que podrían influir en la dinámica de poblaciones de *M. integrifolia* en el norte de Chile (Castilla *et al.* 1993, Vásquez *et al.* 1999, 2000, Fernández *et al.* 2000, Graham 2004, Faugeron *et al*. 2005).

Para cumplir con el objetivo general fue necesario desarrollar un enfoque mixto, usando distintas metodologías para caracterizar el ámbito de variación tanto del sistema (norte de Chile) como de la especie (*M. integrifolia*) en estudio. En primer lugar, este enfoque involucra desechar *a priori* la idea de homogeneidad y de estabilidad en equilibrio (Fariña *et al.* 1997, Lima 2001). En segundo lugar, se modificó y combinó elementos de marcos teóricos distintos relacionados al problema de la heterogeneidad espacio-temporal de la biodiversidad. Algunos aspectos de la ecología de comunidades de huirales submareales (Vásquez 1992, Dayton *et al.* 1998, 1999), se han usado en esta tesis para analizar aspectos biológicos de *M. integrifolia*, como una entidad observable simultáneamente a distintos niveles de resolución. Esta aproximación se asemeja parcialmente a la reciente propuesta de Edwards (2004), que enfatiza la variabilidad de los patrones en función de procesos dependientes de escalas jerárquicamente anidadas. Además de lo anterior, en esta tesis se reconocen múltiples unidades de escala con características propias, que no necesariamente deben ser naturales (Camus 1992). Así un patrón resulta de la interacción entre factores generadores de procesos que ejercen un control local (factores bióticos y abióticos) junto a otros que ejercen un control a mayores escalas (surgencia costera y ENOS). Además, en esta tesis se han utilizado distintos aspectos de la teoría ecológica que trata la heterogeneidad espacial como un factor que regula los patrones de biodiversidad en múltiples escalas (Whittaker 1972). Esta teoría ha sido aplicada para la dinámica de poblaciones de *M. integrifolia* en el norte de Chile considerando que cualquiera de los conceptos teóricos de heterogeneidad espacial desarrollados para ecología de comunidades es aplicable, de manera particular, a cualquiera de los componentes específicos del sistema ecológico analizado (Carlilie *et al.* 1989, Wiens 1989, Levin 1992).

Los resultados más importantes entre los obtenidos en esta tesis y que se destacan a modo de Conclusión, serian:

A) En el norte de Chile, los patrones temporales de la abundancia de *M. integrifolia* son anualmente estables, con un claro patrón estacional de reproducción y crecimiento (Capítulo 1 y 3), característico de años con condiciones normales o La Niña (Capítulo 3). A largo plazo, la manifestación de una condición El Niño, de gran intensidad y magnitud, produce variabilidad interanual (Capítulo 2), debido a que disminuye la abundancia o produce procesos de extinción y recolonización local dependientes de la latitud (Capítulo 4). Aunque en condiciones normales o La Niña, disturbios estocásticos locales de baja predictibilidad (Ej. Aumento de la presión de herbivoría) también generan variabilidad interanual (Capítulo 2).

B) En el norte de Chile, los patrones de organización espacial de los huirales de *M. integrifolia* están determinados por factores y procesos que actúan a distintas escalas jerárquicamente anidadas (Capítulo 4). Una condición El Niño, de gran intensidad y magnitud, genera procesos de extinción local dependiente de la latitud, modificando (1) el límite norte de distribución y (2) el arreglo geográfico de las poblaciones de *M.*

integrifolia (Capítulo 4). Así, El Niño 1997-1998, produjo procesos de extinción o cambios en los patrones de distribución local de *M. integrifolia* entre los 6º S y 21º S, mientras que en latitudes más altas (23º-32º S) los huirales sólo disminuyeron sus abundancias (Capítulo 4). Inmediatamente después, durante La Niña 1998-2000, los procesos de recolonización y/o la recuperación de las abundancia en los huirales dependió de procesos de inhibición y facilitación modulados por factores abióticos y bióticos locales (Capítulo 2 y 4). La continuidad de los procesos de surgencia costera permanente en algunas áreas particulares durante El Niño 1997-1998 fue un factor determinante para la persistencia local de *M. integrifolia* (Capítulo 2), generando a mesoescala una diferenciación latitudinal del impacto, con zonas poco o no afectadas (Capítulo 4), no observadas en condiciones normales o La Niña (Capítulo 3). Finalmente, el efecto interactivo entre el ciclo ENOS y la surgencia costera en el norte de Chile produce una diferenciación regional inmediata de respuesta al comparar los patrones de abundancia y fenología reproductiva de *M. integrifolia* con los patrones de *M. pyrifera* en el sur de Chile (Capítulo 1).

Factores que generan procesos ecológicos de control local *versus* factores que generan procesos ecológicos de control regional y mesoescala como moduladores de la variación latitudinal de la dinámica de poblaciones de *M. integrifolia*

En relación con la sección anterior, el análisis en conjunto indica que los factores forzantes que ejercen el control de los patrones de distribución y abundancia de *M. integrifolia* son dependientes de la escala. Los resultados sugieren que, en Sudamérica, *M. integrifolia* persisten en un balance de procesos ecológicos que conducen a su desarrollo y mantención o extinción, con dinámicas poblacionales que dependen del reclutamiento exitoso, y del crecimiento y mortalidad de los esporofitos.

La dinámica poblacional de Laminariales, a escala local, esta controlada por factores abióticos y bióticos extrínsecos e intrínsecos (North 1986, 1994, Edwards

2004). En el norte de Chile, los factores abióticos, más relevantes, que controlan la dinámica poblacional de *M. integrifolia* son la disponibilidad de sustrato y de sitios con bajo movimiento del agua, en conjunto con el efecto sinérgico de la luz, la temperatura y los nutrientes. Mientras que los factores bióticos extrínsecos, más importantes, son la competencia (Ej. *Lessonia trabeculata*) y la herbivoría (Ej. Erizo negro, *T. niger*). Los factores bióticos intrínsecos determinados por interacciones intraespecíficas que generan procesos de auto-raleo (Ej. Disponibilidad y viabilidad de propágulos, capacidad y potencial reproductivo) dependientes de la capacidad de carga del sistema (Reed & Foster 1984, Dayton *et al.* 1984, 1992), parecen ser más importantes en condiciones normales o La Niña, cuando la abundancia en los huirales de *M. integrifolia* es temporalmente estable. Aunque factores de origen antrópico (Ej. cosecha, uso del borde costero, especies invasoras) no evaluados en esta tesis, también pueden ejercer un control local (Vásquez 1995, 1999, Tegner & Dayton 2000).

La expansión de *M. integrifolia* desde su foco original de distribución hacia latitudes bajas se correlaciona con la anomalía térmica negativa causada por la rama costera de la corriente de Humboldt (Camus 1990, 2001). Esta condición es reforzada por el afloramiento estival de aguas frías subsuperficiales ricas en nutrientes y pobres en oxígeno en todo el litoral del norte de Chile y Perú (Halpin *et al.* 2004). Esto produce un patrón estacional común acoplado de respuesta de las poblaciones de *M. integrifolia* establecidas en el norte de Chile, y quizás en Perú. Es en esta condición (años normales) o en presencia de un evento La Niña (que incrementa la surgencia costera), cuando los factores locales (Ej. herbivoría, competencia, sustrato, disponibilidad de propágulos para reclutamiento) adquieren una mayor relevancia en el control de los patrones de distribución y abundancia de *M. integrifolia*.

El Niño es un evento oceanográfico de gran escala, que genera variación interanual del clima oceanográfico costero en latitudes bajas del Pacífico Americano, modulando la dinámica poblacional de *Macrocystis* a escala regional (Tegner &

Dayton 1987, Dayton *et al.* 1998, 1999, Edwards 2004). En el Hemisferio Sur, El Niño tiene un importante papel como proceso perturbador y generador de un área de alta inestabilidad e impredictibilidad entre los 6ºS y los 30ºS, sometiendo a los componentes de la biota de esta región, a extinciones locales no selectivas (Camus 1990, 2001). Es en este contexto, que la condición El Niño se transforma en un factor que controla los procesos ecológicos a escala regional, debilitando o inhibiendo los procesos de surgencia, aumentando la temperatura y el nivel del mar, profundizando la termoclina y disminuyendo la concentración de nutrientes (Strub *et al*. 1998, Ulloa *et al*. 2001, Halpin *et al.* 2004). En 1997-1998, esta perturbación de gran escala y baja frecuencia, generó procesos de extinción local correlacionados con la latitud, modificando el arreglo geográfico de las poblaciones de *M. integrifolia*. Aún cuando en presencia de La Niña o en años normales, las poblaciones pudieron volver a colonizar sitios rápidamente, en otros demora años, o nunca más han sido restablecidas. Esto se debe a que procesos sucesionales regulados por factores de control local inhiben o facilitan el desarrollo del huiral (Camus *et al.* 1994; Martínez 1999).

Durante El Niño 1997-1998, las áreas con surgencia permanente en el norte de Chile mantuvieron su actividad amortiguando los efectos de las anomalías térmicas positivas del mar (Lagos *et al.* 2002, Takesue *et al*. 2004). La surgencia costera permanente produjo un control a mesoescala que favoreció la persistencia de los huirales de *M. integrifolia* ubicados en estas áreas. Estas poblaciones remanentes funcionarían como áreas fuentes productoras de propágulos disponibles para recolonizar áreas sumideros, donde el efecto catastrófico de la perturbación causada por El Niño generó procesos de extinción local (Camus 1994, Martínez *et al.* 2003). Sin embargo, aunque los huirales de *M. integrifolia* establecidos en estas áreas facilita el desarrollo de otros huirales a través de la producción y dispersión de propágulos reproductivos por distintas vías (Macaya *et al.* 2005), son los factores de control local los que finalmente determinan la factibilidad de recolonización de estos huirales.

La importancia de conectar escalas en estudio de dinámica de poblaciones: El caso de *M. integrifolia* en el norte de Chile

En el diseño de estudios ecológicos siempre ha sido importante identificar y conectar las distintas escalas espaciales y temporales en que actúan los procesos que se pretenden evaluar con las distintas escalas en que los parámetros poblacionales o comunitarios sometidos a prueba pueden responder. En general, las poblaciones están reguladas por procesos que actúan a una escala particular en un tiempo dado, pero estas mismas poblaciones también pueden ser reguladas por procesos que operan a otras muy diferentes escalas en otros momentos (Dayton & Tegner 1984, Wiens 1989, Levin 1992). Así, comprender la naturaleza espacial y temporal de esta dependencia de la escala, provee una visión más clara de la importancia relativa de estos procesos en la dinámica total del ecosistema (Camus 1992, 1998, Edwards 2004).

Los eventos El Niño, tienen un gran impacto en las poblaciones y comunidades marinas litorales del Pacífico Sudamericano a través de efectos simultáneos en distintas escalas (Camus 2001). El Niño 1997-1998, fue una perturbación de gran escala que ofreció una oportunidad única para examinar en forma directa la dinámica geográfica de las poblaciones de *M. integrifolia*, y la propagación de sus efectos entre escalas jerárquicamente anidadas (Whittaker 1972, Camus 1992). Este evento impactó principalmente el norte de Chile (18º-30º S; Ulloa *et al.* 2001, Carr *et al.* 2002), generando una diferenciación geográfica inmediata en términos de efectos regionales (Fig. 1). A escala regional, El Niño 1997-1998 causó mortalidad y procesos de extinción de *M. integrifolia* correlacionada con la latitud, con efectos que descienden directamente a escalas menores que se tradujo en cambios locales de los patrones de distribución y abundancia (Fig. 1). Sin embargo, debido a la variación geográfica en las características físicas del hábitat modificado por la surgencia costera permanente, algunos efectos fueron amortiguados en localidades aisladas produciendo variabilidad a mesoescala en la dinámicas poblacionales de *M. integrifolia* (Fig. 1). En términos de escala, estos efectos son causados por procesos que operan a escala regional (El Niño) que incide en todas las escalas espaciales menores (efectos descendentes). Este proceso regional en pocos meses altera en mayor o menor grado los patrones de abundancia de *M. integrifolia* en todas las escalas, dejando al sistema completo en una nueva configuración, que en algunas localidades puede ser irreversible (Fig. 1). Una vez pasada la perturbación causada por El Niño, se inician procesos de recolonización que restablecen los patrones de distribución y abundancia de *M. integrifolia*, ocurriendo primero a escala local y posteriormente propagando su efecto hacia escalas mayores (efectos ascendentes). Sin embargo, dependiendo de los cambios ocurridos en la abundancia local de *M. integrifolia*, aspectos de organización comunitaria post-disturbio pueden también variar en direcciones que limitan la posibilidad de recuperar la situación previa a la perturbación causada por El Niño. La extinción local de *M. integrifolia* produce cambios comunitarios, y el eventual retorno a condiciones pre-El Niño necesariamente implica el restablecimiento del huiral, el cual esta limitado por la disponibilidad de propágulos (Ej. gametófitos y esporofitos), presión de herbivoría (Ej. *T. niger*), e inhibición sucesional causada por otras macroalgas dominantes (Ej. *L. trabeculata*). Así, la recolonización depende casi exclusivamente de procesos de facilitación (Ej. refugio generados por algas o el hábitat, parches flotando a la deriva, estados microscópicos latentes, entre otros; ver Ladah *et al.* 1999, Kilan *et al*. 2003, Edwards & Hernández-Carmona 2005, Macaya *et al*. 2005). Sin embargo, la recolonización de *M. integrifolia* puede experimentar un retardo o detención debido a interacciones locales que antes del impacto regional no eran limitantes. Así se altera la estructura geográfica poblacional, con efectos que se propagan hacia escalas espaciales mayores, que a su vez se traducen en distintas dinámicas poblacionales y en un aumento de la heterogeneidad regional de los patrones de distribución y abundancia de *M. integrifolia* (Fig. 1). Esto genera diferencias en las estrategias de vida de *M. integrifolia* entre las regiones norte y central del país o con especies congenéricas (*Macrocystis pyrifera*) ubicadas más al sur de Chile.

Comentarios finales

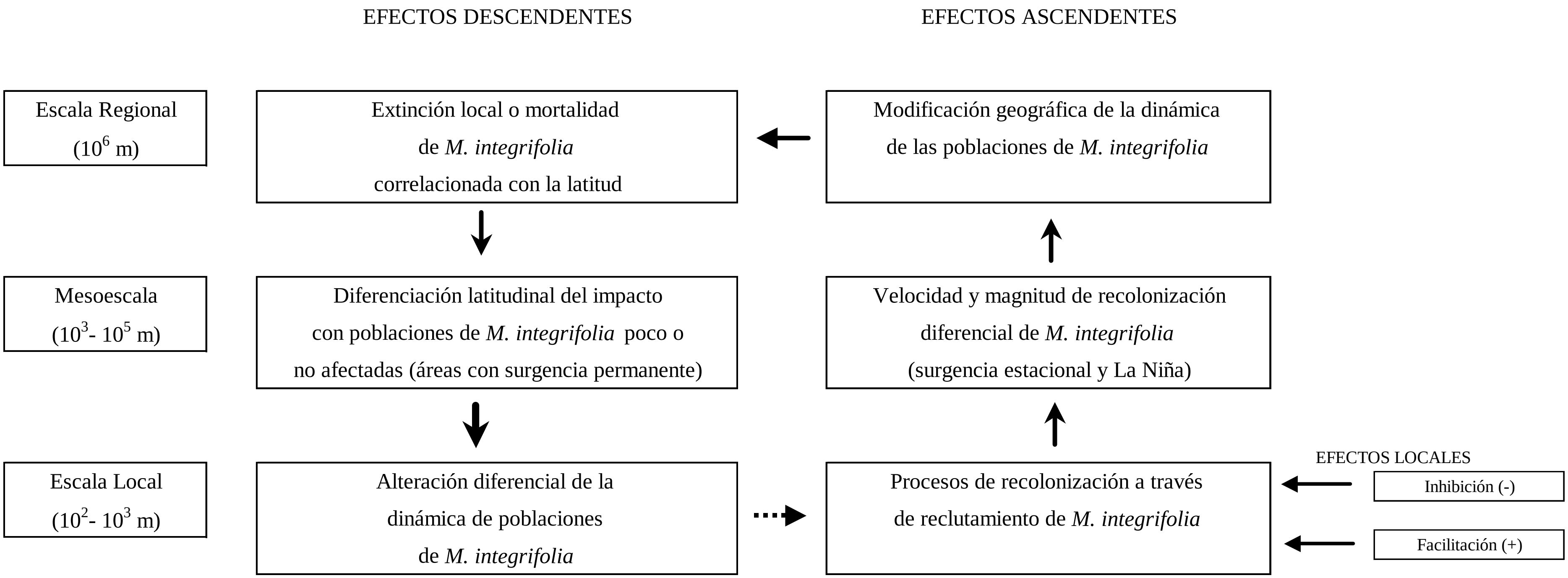
El estatus taxonómico de las especies de *Macrocystis* necesita ser revisado debido a que: (1) las especies son fértiles entre sí (Lewis *et al.* 1986); (2) existen morfologías intermedias *in situ* (Setchell 1932); (3) además de la morfología de las frondas (Hurd *et al.* 1997), los discos básales son fenotípicamente plásticos (Setchell 1932); y lo más importante, (4) los patrones de relación genética entre especies no concuerdan con la clasificación morfológica corriente (Coyer *et al.* 2001). Esta evidencia sugiere reconocer al género *Macrocystis* como una única especie morfológicamente plástica, con poblaciones globales unidas por flujos genéticos poco triviales (Graham *et al. in litteris*). Sin embargo, para propósitos de este estudio se ha conservado el nombre *Macrocystis integrifolia* clasificada en función de la morfología del disco básal (ver Hoffman & Santelices 1997).

Además de describir la dinámica de las poblaciones de *M. integrifolia* en el norte de Chile, la intención final de este estudio fue generar una línea base para futuras investigaciones porque a pesar de su importancia ecológica, social y económica (Vásquez & Vega 1996, Vásquez 1999), muy poco se sabe de este huiro en el Pacífico Sudamericano. Futuras investigaciones podrían estudiar aspectos fisiológicos de los esporofitos, o de sus constituyentes químicos. Por otra parte, *M. integrifolia* es una especie ingeniera autogénica (Vásquez *et al.* 2005), que podría ser usada como unidad ecosistémica replicable para evaluar efectos producidos por factores dependientes de la escala, o como un "indicador" de áreas aptas para la conservación (Vásquez & Vega 2005). También, las fases microscópicas (gametofitos femeninos y masculinos, y estados microscópicos esporofíticos) aún requieren de mucho más estudios. Aunque en esta tesis se entregan algunos antecedentes, nuevas investigaciones debieran centrarse en replicar experimentos *in situ* (Ej. Graham 1996), o en acoplar estos estados microscópicos con los factores multi-escala que controlan la dinámica de la fase macroscópica (Ej. Graham 2000, 2002; Kilan *et al*. 2003). Así, la información de esta tesis abre las puertas a nuevas interrogantes insertas en ámbitos tan variados como la autoecología, la ecología de poblaciones, de comunidades y de paisajes.

En el norte de Chile, los procesos de extinción y recolonización en parte importante del rango de distribución de las especies producen un patrón heterogéneo de la dinámica espacial y temporal de las poblaciones (Camus *et al.* 1994). En esta tesis se muestra parte del grado de variación entre poblaciones de una especie en este sistema, aplicable también a otras (Ej. Camus *et al.* 1994, Vásquez *et al*. 2005), permitiendo reconocer alguno de los factores y procesos involucrados. En la Figura 2, se presenta un esquema simple de los distintos cambios observados en la dinámica de poblaciones de *M. integrifolia*. Sin embargo, es importante considerar la dinámica poblacional que una especie como *M. integrifolia* desarrolla en función de la configuración resultante luego de un evento El Niño (Fig. 2). Considerando la configuración geográfica de la costa chilena, y suponiendo que existe algún grado de conectividad entre poblaciones, esta dinámica puede ser descrita como un tipo particular de metapoblación (Ej. Schoener 1991), con parches de tamaño similar dispuestos en una línea con hipotéticamente una dirección del flujo de migración (hacia el norte). Es en este contexto que los cambios en la estructura geográfica entre eventos El Niño podrían hacerla variar constantemente, afectando la dinámica de las poblaciones donde los procesos de extinción y recolonización se han producido.

Finalmente, la perspectiva jerárquica de los efectos en la dinámica de poblaciones de *M. integrifolia* causados por el ciclo ENOS (eventos El Niño y La Niña), por la surgencia costera, y por los factores que operan a escala local es tan necesaria para interpretar el funcionamiento del sistema litoral del Pacífico Sudamericano temperado como la de cualquier otro sistema. También es útil para comprender una variedad de otras perturbaciones naturales o antropogénicas (Fernández *et al.* 2000), o para estudiar la dinámica de poblaciones de otros recursos marinos explotados en estas latitudes (Castilla & Camus 1992).

Figura 1. Modelo funcional del impacto de El Niño 1997-1998 en la dinámica de poblaciones de *M. integrifolia* en el norte de Chile (Modificado de Camus 1994, Camus *et al.* 1994). El Impacto es representado como efectos de perturbación que descienden desde escalas mayores a menores (las flechas indican el orden de magnitud). Después de la perturbación factores locales controlan los procesos de recolonización de *M. integrifolia* , que se propagan de forma ascedente a través de de la jerarquía de las escalas.La flecha segmentada indica que los cambios pueden retroalimentarse al siguiente evento El Niño, dependiendo de los patrones de distribución y abundancia de *M. integrifolia* cuando ocurra esta nueva perturbación.



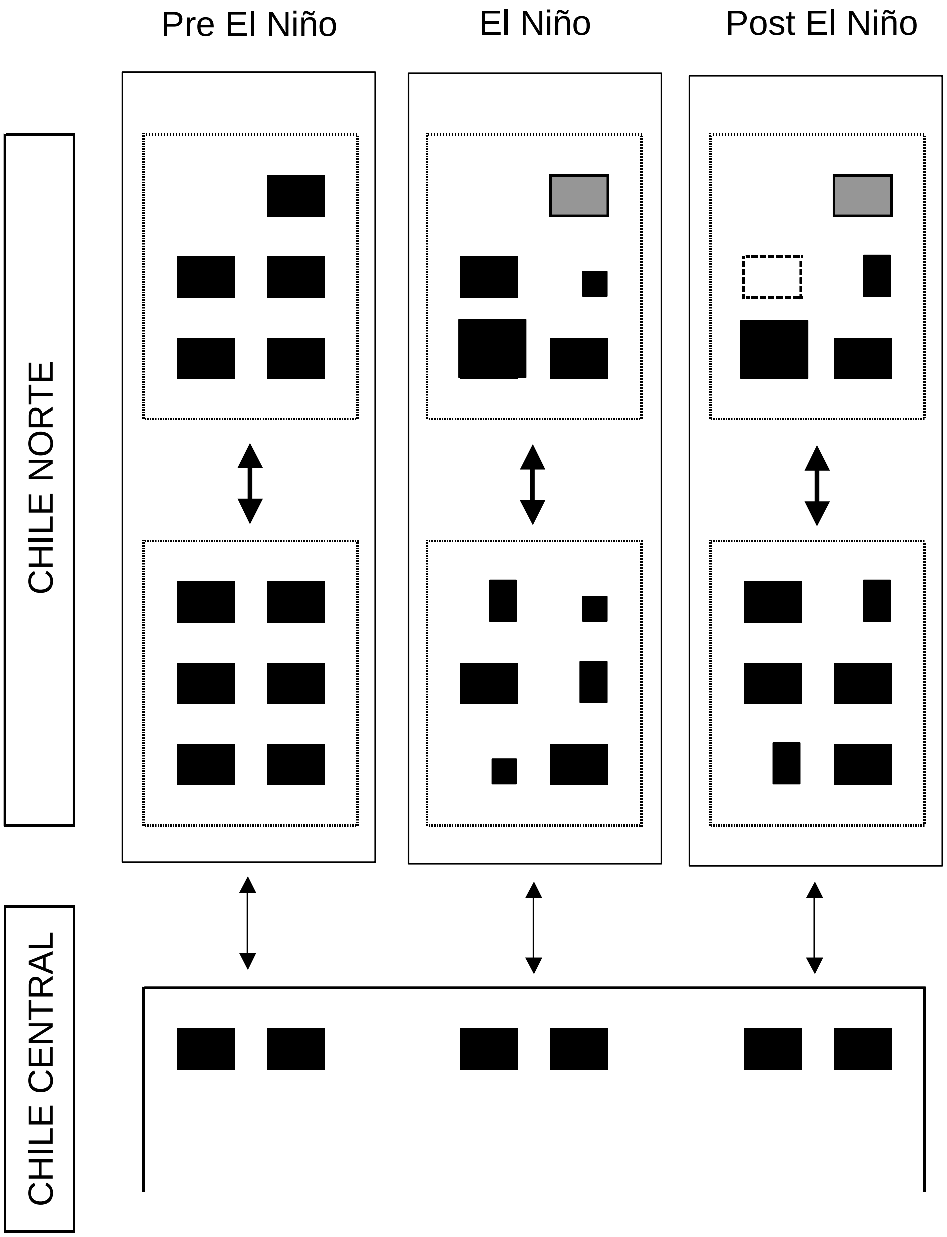


Figura 2. Esquema de los cambio espacio-temporales en los patrones de distribución y abundancia de las poblaciones de *M. integrifolia* en el litoral del norte de Chile antes, durante y despues de un evento El Niño.El rectangulo vertical representa el norte de Chile y el rectangulo horizontal abierto Chile central y sur. Los rectangulos segmentados representan efectos correlacionados con la latitud. Los cuadrados negros representan los procesos de extinción local, cambios de abundancia (aumento o disminución del tamaño del cuadrado) o en la distribución (cuadrado gris) local de las poblaciones de *M. integrifolia* en el tiempo. Los cuadrados blancos y segmentados representan procesos de extinción local causados por eventos estocásticos de baja frecuencia y predictibilidad. Espacios sin cuadrados representan procesos de extinción local durante El Niño anteriores y donde no se ha vuelto a producir procesos de recolonización. Los cuadrados negros sin cambios en el tamaño representan poblaciones insertas en áreas con surgencia permanente. El grosor de las flechas indica el grado de conectancia entre poblaciones dentro y entre regiones (modificado de Camus 1994, Jaksic 2000).

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