GOBIERNO DE CHILE
COMISION NACIONAL
DEL MEDIO AMBIENTE

ANT.: Revisión norma de emisión para la regulación de contaminantes asociados a las descargas de residuos líquidos a aguas marinas y continentales superficiales. Decreto Supremo N°90/2000.

MAT.: Cita a reuniones ordinarias y extraordinarias del Comité Operativo en el mes de abril 2009.

SANTIAGO, 0 2 ABR. 2009

DE : HANS WILLUMSEN ALENDE
Jefe Departamento Control de la Contaminación
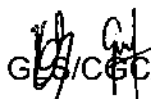Comisión Nacional del Medio Ambiente

A : SEGÚN DISTRIBUCIÓN

En relación con el proceso de revisión de la *"Norma de emisión para la regulación de los contaminantes asociados a las descargas de residuos líquidos a aguas marinas y continentales superficiales, Decreto Supremo N°90/2000"*, se invita a los representantes del Comité Operativo a participar de las reuniones ordinarias y extraordinarias del mes de abril, las cuales se realizarán según el siguiente cuadro:

REUNIÓN	FECHA	HORA	UBICACIÓN	TEMAS
Extraordinaria	Martes 07 abril 2009	10:30 a 13:00	CONAMA Teatinos 258 Piso 4	– Lagos – Estuarios – Cuerpo fluvial afluente de cuerpo lacustre
Ordinaria 22° Reunión	Martes 14 abril 2009	10:30 a 13:00	CONAMA Teatinos 258 Piso 4	– Parámetros – Otros
Ordinaria 23° Reunión	Martes 28 abril 2009	10:30 a 13:00	DIRINMAR Subida Cementerio N°300, Playa Ancha, Valparaíso	– Métodos de medición – Control y monitoreo – Otros

Agradeceré a usted confirmar su asistencia a la Srta. Claudia Galleguillos C., profesional del Departamento Control de la Contaminación de CONAMA Central, Teléfono: 02-2405706, correo electrónico cgalleguillos@conama.cl

Sin otro particular, saluda atentamente,

HANS WILLUMSEN ALENDE
Jefe Departamento Control de la Contaminación
Comisión Nacional del Medio Ambiente

GE/CGC/aat

DISTRIBUCIÓN:

- Sra. Nancy Cepeda, Encargada de la Unidad de Normas, Superintendencia de Servicios Sanitarios (SISS)
- Sra. Mesenia Atenas V., Jefa del Departamento de Conservación y Protección de los recursos Hídricos, Dirección General de Aguas (DGA)
- Sra. Teresa Agüero T., Profesional del Departamento Políticas Agrarias de ODEPA.
- Sr. Juan Berasaluce, Capitán de Navío Litoral, Dirección del Territorio Marítimo y Marina Mercante (DIRECTEMAR)
- Sr. Fernando Baeriswyl Rada, Jefe División Protección Recursos Naturales Renovables, Servicio Agrícola y Ganadero (SAG)
- Sra. Rossana Brantes Abarca, Profesional de de Dirección de Estudios de la Comisión Chilena del Cobre (COCHILCO)
- Sr. Pedro Riveros, Dpto. Salud Ambiental, Ministerio de Salud (MINSAL)
- Sr. Juan Ladrón de Guevara, Asesor de Medio Ambiente, Ministerio de Economía, Fomento y Reconstrucción.
- Sr. Cristian Andaur, Departamento de Administración Pesquera, Servicio Nacional de Pesca (SERNAPESCA).
- Sr. Rodrigo Iglesias A., Secretario Ejecutivo Comisión Nacional de Energía.
- Sr. Pablo Lagos, Departamento de Acuicultura, Subsecretaría de Pesca (SUBPESCA).
- Sra. Carmen Rivera Mardones, Profesional EVYSA, Comisión Nacional del Medio Ambiente (CONAMA)
- Sr. Miguel Stutzin, Jefe Departamento RRNN, CONAMA Central.

c.c:

- Dirección Ejecutiva CONAMA
- Archivo Departamento Control de la Contaminación, CONAMA.
- Expediente Norma DS 90

ORD. N° ~~091129~~ /

ANT.: Revisión norma de emisión para la regulación de contaminantes asociados a las descargas de residuos líquidos a aguas marinas y continentales superficiales. Decreto Supremo N°90/2000.

MAT.: Cita a reunión por el proceso de revisión del DS90.

GOBIERNO DE CHILE
COMISION NACIONAL
DEL MEDIO AMBIENTE

SANTIAGO,

0 2 ABR. 2009

DE : HANS WILLUMSEN ALENDE
Jefe Departamento Control de la Contaminación
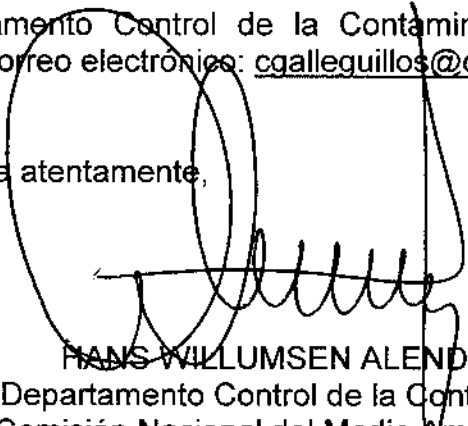Comisión Nacional del Medio Ambiente

A : SEGÚN DISTRIBUCIÓN

En relación con el proceso de revisión de la *"Norma de emisión para la regulación de los contaminantes asociados a las descargas de residuos líquidos a aguas marinas y continentales superficiales, Decreto Supremo N°90/2000"*, se invita a participar de reunión el día miércoles 22 de abril 2009, en CONAMA ubicada en Teatinos N°258, Piso 4.

El objetivo de la reunión es tratar los temas relacionados con "Métodos de Análisis" y "Monitoreo y Control" del proceso de revisión de la norma.

Agradeceré a usted confirmar su asistencia a la Srta. Claudia Galleguillos C., profesional del Departamento Control de la Contaminación de CONAMA Central, Teléfono: 02-2405706, correo electrónico: cgalleguillos@conama.cl

Sin otro particular, saluda atentamente,

HANS WILLUMSEN ALENDE
Jefe Departamento Control de la Contaminación
Comisión Nacional del Medio Ambiente

GLS/CGC/aat
DISTRIBUCIÓN:

- Sra. Nancy Cepeda, Encargada de la Unidad de Normas, Superintendencia de Servicios Sanitarios (SISS)
- Sra. Mesenia Atenas V., Jefa del Departamento de Conservación y Protección de los recursos Hídricos, Dirección General de Aguas (DGA)
- Sr. Juan Berasaluce, Capitán de Navío Litoral, Dirección del Territorio Marítimo y Marina Mercante (DIRECTEMAR)
- Sr. Fernando Baeriswyl Rada, Jefe División Protección Recursos Naturales Renovables, Servicio Agrícola y Ganadero (SAG)
- Sr. Alexander Chechilnitzky, Director AIDIS CHILE
- Sr. Aldo Tamburrino T., Jefe de División de Recursos Hídricos y Medio Ambiente del Dpto. Ingeniería Civil de la Universidad de Chile
- Sr. Jacobo Homsi, Consultora Kristal

c.c:
- Elizabeth Echeverría, AIDIS
- María Pía Mena, AIDIS
- Ana María Sacha, División de Recursos Hídricos y Medio Ambiente del Dpto. Ingeniería Civil de la Universidad de Chile
- Dirección Ejecutiva CONAMA
- Archivo Departamento Control de la Contaminación, CONAMA.
- Expediente Norma DS 90

GOBIERNODECHILE
COMISION NACIONAL
DEL MEDIO AMBIENTE

Dirección Ejecutiva
Departamento de Control de la Contaminación
Área Control de la Contaminación Hídrica

DOCUMENTO ENVIADO POR CORREO ELECTRÓNICO
"Proceso de Revisión DS 90"

Enviado por : SISS- Nancy Cepeda

e-mail : ncepeda@siss.cl

Fecha : Viernes, 03 abril 2009

Hora : 16:54 hrs

DOCUMENTOS ANEXOS

N°	DOCUMENTO
1	Parámetros Temperatura, SSED, Poder espumógeno y Coliformes Fecales

Claudia, esto es lo que entiendo sobre el tema de los parámetros Temp, SSed, Poder espumógeno y CF:

- EL DS 90 vigente considera como fuente emisora (FE), cualquier descarga de residuos líquidos que exceda los valores de la Tabla para los parámetros con valor característico, independiente del caudal descargado.

- En reunión del CA se planteó que la calificación como FE, para efectos de estos parámetros, se debe fundamentar en un volumen de descarga de aguas servidas para 100 habitantes, en forma similar a lo establecido para los demás parámetros de la Tabla de FE, cuyo límite está en términos de carga contaminante media diaria. En este contexto, se propuso que el volumen debiera ser 10 m3/día, que correspondería al volumen de aguas servidas de 100 habitantes, considerando los consumos medios país al 2007 según información SISS.

- Al respecto, lo que hemos analizado/conversado en el CO:
  - Es necesario establecer una condición adicional al lím. máx. de los parámetros con valor característico, para evitar que descargas muy pequeñas califiquen como FE
  - Si para establecer el volumen de descarga, se considera el criterio del volumen equivalente de aguas servidas de 100 habitantes, para mantener la coherencia que está implícita en los valores de carga contaminante media diaria de los demás parámetros de la Tabla, correspondería considerar 16 m3/día
  - Se debe tener presente, que cualquier descarga inferior al volumen (m3/día) que se proponga en la norma, podría tener los parámetros de valores característicos superiores a los límites de la Tabla y no calificaría como FE
  - Se ha estimado prudente considerar un volumen inferior al equivalente a 100 habitantes, para lo que se ha propuesto 5 m3/día

Saludos,

Comisión Nacional del Medio Ambiente
División Jurídica

Memorándum N°72

DE: Rodrigo Guzmán Rosen
       Jefe División Jurídica

A: Hans Willumsen Alende
       Jefe Departamento Control de la Contaminación

MAT: ZPL

Fecha: 02 de abril de 2009

Se ha consultado a esta División Jurídica sobre la factibilidad jurídica de la propuesta de modificación al D.S. N°90 relativa a la Zona de Protección Litoral, en particular la disposición que establece que dicha modificación no afecta a las fuentes que cuentan con autorización para descargar sus residuos líquidos conforme a la ley.

Al respecto, puedo informar a Ud. que no existe obstáculo legal para establecer respecto de determinadas fuentes un régimen diferenciado de aplicación de las norma de emisión, siempre y cuando dicha diferenciación no implique una discriminación arbitraria, es decir, que la distinción sea razonable, que persiga una finalidad, y que las consecuencias derivadas de esa distinción sean adecuadas y proporcionales a dicho fin. Bajo ese contexto las fuentes existentes generalmente son objeto de un mayor plazo para el cumplimiento de las normas o se les exime de tal exigencia, y el fundamento de tal proceder normalmente está asociado al impacto económico y social de la medida. En todo caso, las normas de emisión deben revisarse cada cinco años, por lo que tal criterio podría modificarse precisamente por existir nuevos antecedentes o circunstancias que exijan cambiarlo.

Sin perjuicio de lo anterior, hago presente a Ud., que una consideración de tal tipo, no puede basarse exclusivamente en que una fuente cuente con el otorgamiento de un permiso o autorización, pues el criterio del impacto económico y social de la medida exige que se trate de una fuente ya construida, es decir de una fuente respecto de la cual se ha generado un gran costo económico, que se considera pertinente tomar en consideración, por lo que se debe incluir tal criterio en la disposición en cuestión.

Sin otro particular, saluda atentamente a Ud.

Rodrigo Guzmán Rosen
Jefe División Jurídica

APR/CRB
CC.
Archivo

Dirección Ejecutiva
Departamento de Control de la Contaminación
Área Control de la Contaminación Hídrica

DOCUMENTO ENVIADO POR CORREO ELECTRÓNICO
"Proceso de Revisión DS 90"

Enviado por : Grupo 2 Comité Ampliado- CORMA- Pedro Navarrete

e-mail : pnavarrete@celulosa.cmpc.cl

Fecha : Lunes, 06 de abril 2009

Hora : 16:21 hrs

DOCUMENTOS ANEXOS

N°	DOCUMENTO
1	Reiteran observaciones al borrador 6 de la norma, las cuales fueron enviadas por CORMA, a través de un correo electrónico con fecha lunes 23 de marzo 2009, a las 11:32 hrs.

De: Pedro Navarrete (CMPC Celulosa G.Tecnica) [mailto:pnavarrete@celulosa.cmpc.cl]
Enviado el: Lunes, 06 de Abril de 2009 16:21
Para: Claudia Galleguillos
CC: Mariela Arevalo; Carlos Decourvieres G.; xrojas@salmonchile.cl; Carolina Vargas Gonzalez; Ximena Molina; alfonso.guijon@poch.cl; claudio.perez@essbio.cl; cquilodr@labchile.cl; Cesar Peredo L. (Esval S.A.); portiz@carozzi.cl; c_alex_quilodran@yahoo.es; JUAN LARENAS; María Pía Mena; Gladys Vidal; olga.espinoza@sag.gob.cl; jeanine.hermansen@sag.gob.cl; Maria Pia Mena
Asunto: RE: DS-90
Importancia: Alta

Estimada Claudia,

No había tenido un minuto para referirme a nuestra participación en la última reunión del Ampliado. Este correo tiene esa finalidad.

1. Presentación del GR2

Nuestros puntos fueron:

a) Ya 'hemos hecho llegar comentarios a otras versiones del AP por lo que sólo nos referimos al Borrador # 6
b) Consideramos que las aguas lluvia no pueden quedar incorporadas en el DS-90 por- ser de naturaleza completamente distinta de los RL (esporádicas, dentro de una época precisa del año calendario); variables en cantidad. No nos oponemos a que su calidad deba ser regulada, si la Autoridad lo estima; sin embargo creemos que esto es el resultado de un proceso dedicado a ello, ajustado al procedimiento estipulado en la LBGMA.
c) Nos preocupa que la metodología para la determinación del caudal de dilución no haya quedado formalmente referenciada, ya sea como estuvo en versiones anteriores del AP o bién explicitando el documento que la contiene.
d) No estamos de acuerdo con que la actual versión solicite caracterizar los efluentes de todas las fuentes emisoras porque ésto es algo que ya fue realizado por las fuentes que cuentan con Resoluciones de Monitoreo de la SISS emitidas el el contexto de un proyecto sometido al SEIA. Creemos que solamente deben caracterizar sus efluentes aquellas fuentes que no lo hayan hecho antes.
e) Nada de lo que el Comité Ampliado en pleno comentó sobre la no pertinencia del concepto contaminación, contaminante y otras expresiones similares, en el AP. En la versión # 6 sigue apareciendo tal como antes del comentario y no hemos recibido ninguna comunicación (ni notas al margen) que nos indique las razones de su no consideración ó bien se indique el estado de análisis en que se encuetra dicha moción.
f) Creemos que es necesario dedicar más tiempo que una parte de una reunión al tema económico.
g) Solicitamos se dejara constancia en el Acta de que el Comité Ampliado ha perdido 2 reuniones (Enero y Febrero 09) para dialogar con las autoridades, recibir información y/o hacer presente comentarios debido a la suspensión de dichas sesiones que nos fuera informada por Conama.

Sobre el punto f), designamos a don Carlos Descourvieres nuestro representante en el Grupo que se organizó en esta reunión del Ampliado, para integrarse al equipo de trabajo con el consultor Kristal.

2. Fichas del GR-2 con comentarios al Borrador # 6
Son las mismas que te envié con el correo adjunto sólo que ahora representan no sólo a Corma sino que al Grupo completo.
Para evitar malos ententendidos, adjunto las fichas que representan al Grupo 2.

Pedro Navarrete Ugarte
Superintendente de Gestión Ambiental
Gerencia de Medio Ambiente y Asuntos Públicos
CMPC Celulosa S.A.

Fono: 56-43-403930 -3979
Fax: 56-43-403914
Mail: pnavarrete@celulosa.cmpc.cl

GOBIERNO DE CHILE
COMISION NACIONAL
DEL MEDIO AMBIENTE

Dirección Ejecutiva
Departamento Control de la Contaminación

MEMORÁNDUM N° 136/2009

De   :   HANS WILLUMSEN ALENDE
Jefe Departamento Control de la Contaminación
Comisión Nacional del Medio Ambiente

A   :   RODRIGO GUZMAN ROSEN
Jefe División Jurídica
Comisión Nacional del Medio Ambiente

Mat.   :   Solicita análisis jurídico para el concepto "contaminante", en el marco del proceso de revisión del DS. 90.

Fecha :   06 de abril 2009

Por medio de la presente, solicito a usted, tenga a bien realizar un análisis respecto a la factibilidad jurídica de cambiar el concepto "contaminante", en el marco del proceso de revisión del DS 90.

La consulta se realiza en el contexto de las observaciones recibidas por parte de miembros del Comité Ampliado (las cuales se deben responder formalmente), quienes entregan los siguientes fundamentos:

– No es etimológicamente correcto identificar como "contaminante" al pH, la temperatura y otros elementos químicos y/ compuestos listados en las distintas Tablas del Anteproyecto.

– La Ley 19.300 define como Contaminante a todo elemento, compuesto, sustancia, derivado químico o biológico, energía, radiación, vibración, ruido, o una combinación de ellos, cuya presencia en el ambiente, en ciertos niveles, concentraciones o períodos de tiempo, pueda constituir un riesgo a la salud de las personas, a la calidad de vida de la población, a la preservación de la naturaleza o a la conservación del patrimonio ambiental.

Por lo tanto, en estricto rigor la palabra "contaminante" implica que la concentración del elemento es superior a la que puede constituir un riesgo para las personas o el medio ambiente.

– Desafortunadamente, la palabra "contaminante" conlleva un carácter peyorativo en el lenguaje común, que se asocia indefectiblemente a la actividad regulada por el DS-90, lo que es injustificable toda vez que la emisión en cantidades inferiores a los límites – que es la obligación legal de las fuentes emisoras – no tiene dicho carácter.

– El actual proceso de revisión y mejoramiento del DS-90 ofrece la oportunidad para rectificar este aspecto, que si bien no modifica los objetivos de regulación requiere cambios en gran parte del documento.
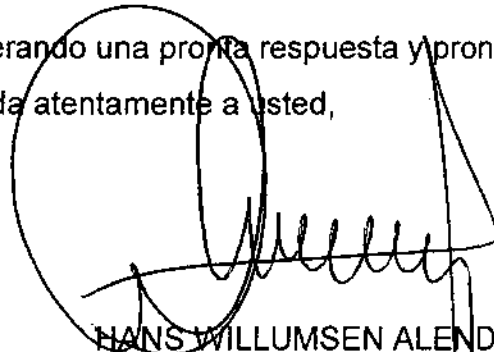
La propuesta de cambio realizada por el Comité Ampliado de la norma, es la siguiente:

1. Reemplazar el título actual de la Norma por "Norma de Emisión para la descarga de residuos líquidos a aguas marinas y continentales superficiales"

2. Reemplazar la palabra "Contaminante" por "Parámetro", "Compuesto", "Composición" y "Propiedad Física" a lo largo del texto del AP, utilizando cada una de estas palabras en consonancia con el sentido del artículo específico de que se trate.

3. Reemplazar primer párrafo del Articulo Primero por: "Establécese la siguiente norma de emisión para la regulación de descargas de residuos líquidos a aguas marinas y continentales superficiales."

4. Reemplazar OBJETIVO DE PROTECCION AMBIENTAL Y RESULTADOS ESPERADOS por: "La presente norma tiene como objetivo de protección ambiental prevenir la contaminación de las aguas marinas y continentales superficiales de la República mediante el control de la calidad de los residuos líquidos que se descargan a estos cuerpos receptores. Con lo anterior, se logra proteger la calidad ambiental de estos ecosistemas marinos y terrestres,

de conformidad a lo establecido en la Constitución y en la Ley de Bases Generales del Medio Ambiente."

5. Reemplazar DISPOSICIONES GENERALES por: "La norma establece los límites de emisión a los que deben ajustarse los parámetros, compuestos, la composición o propiedad física, de los residuos líquidos descargados por fuentes emisoras fijas a los cuerpos de agua marinos y continentales superficiales de la República de Chile."

Esperando una pronta respuesta y pronunciamiento jurídico frente a esta consulta, saluda atentamente a usted,

HANS WILLUMSEN ALENDE
Jefe Departamento Control de la Contaminación
Comisión Nacional del Medio Ambiente

GES/MAH/CGC/aat

<u>Distribución:</u>
- Archivo Departamento Control de la Contaminación.

c.c.:
- Alejandra Precht R., División Jurídica, CONAMA
- Conrado Ravanal F., División Jurídica, CONAMA.

MEMORÁNDUM N° 136/2009

De : HANS WILLUMSEN ALENDE
Jefe Departamento Control de la Contaminación
Comisión Nacional del Medio Ambiente

A : RODRIGO GUZMAN ROSEN
Jefe División Jurídica
Comisión Nacional del Medio Ambiente

Mat. : Solicita análisis jurídico para el concepto "contaminante", en el marco del proceso de revisión del DS. 90.

Fecha : 06 de abril 2009

Por medio de la presente, solicito a usted, tenga a bien realizar un análisis respecto a la factibilidad jurídica de cambiar el concepto "contaminante", en el marco del proceso de revisión del DS 90.

La consulta se realiza en el contexto de las observaciones recibidas por parte de miembros del Comité Ampliado (las cuales se deben responder formalmente), quienes entregan los siguientes fundamentos:

– No es etimológicamente correcto identificar como "contaminante" al pH, la temperatura y otros elementos químicos y/ compuestos listados en las distintas Tablas del Anteproyecto.

– La Ley 19.300 define como Contaminante a todo elemento, compuesto, sustancia, derivado químico o biológico, energía, radiación, vibración, ruido, o una combinación de ellos, cuya presencia en el ambiente, en ciertos niveles, concentraciones o períodos de tiempo, pueda constituir un riesgo a la salud de las personas, a la calidad de vida de la población, a la preservación de la naturaleza o a la conservación del patrimonio ambiental.

Por lo tanto, en estricto rigor la palabra "contaminante" implica que la concentración del elemento es superior a la que puede constituir un riesgo para las personas o el medio ambiente.

- Desafortunadamente, la palabra "contaminante" conlleva un carácter peyorativo en el lenguaje común, que se asocia indefectiblemente a la actividad regulada por el DS-90, lo que es injustificable toda vez que la emisión en cantidades inferiores a los límites – que es la obligación legal de las fuentes emisoras – no tiene dicho carácter.

- El actual proceso de revisión y mejoramiento del DS-90 ofrece la oportunidad para rectificar este aspecto, que si bien no modifica los objetivos de regulación requiere cambios en gran parte del documento.

La propuesta de cambio realizada por el Comité Ampliado de la norma, es la siguiente:

1. Reemplazar el título actual de la Norma por "Norma de Emisión para la descarga de residuos líquidos a aguas marinas y continentales superficiales"

2. Reemplazar la palabra "Contaminante" por "Parámetro", "Compuesto", "Composición" y "Propiedad Física" a lo largo del texto del AP, utilizando cada una de estas palabras en consonancia con el sentido del artículo específico de que se trate.

3. Reemplazar primer párrafo del Artículo Primero por: "Establécese la siguiente norma de emisión para la regulación de descargas de residuos líquidos a aguas marinas y continentales superficiales."

4. Reemplazar OBJETIVO DE PROTECCION AMBIENTAL Y RESULTADOS ESPERADOS por: "La presente norma tiene como objetivo de protección ambiental prevenir la contaminación de las aguas marinas y continentales superficiales de la República mediante el control de la calidad de los residuos líquidos que se descargan a estos cuerpos receptores. Con lo anterior, se logra proteger la calidad ambiental de estos ecosistemas marinos y terrestres,

de conformidad a lo establecido en la Constitución y en la Ley de Bases Generales del Medio Ambiente."

5. Reemplazar DISPOSICIONES GENERALES por: "La norma establece los límites de emisión a los que deben ajustarse los parámetros, compuestos, la composición o propiedad física, de los residuos líquidos descargados por fuentes emisoras fijas a los cuerpos de agua marinos y continentales superficiales de la República de Chile."

Esperando una pronta respuesta y pronunciamiento jurídico frente a esta consulta, saluda atentamente a usted,

HANS WILLUMSEN ALENDE
Jefe Departamento Control de la Contaminación
Comisión Nacional del Medio Ambiente

GES/MAH/CGC/aat

<u>Distribución</u>:
- Archivo Departamento Control de la Contaminación.

c.c.:
- Alejandra Precht R., División Jurídica, CONAMA
- Conrado Ravanal F., División Jurídica, CONAMA.

GOBIERNODECHILE
COMISION NACIONAL
DEL MEDIO AMBIENTE

Reunión EXTRAORDINARIA COMITÉ OPERATIVO
"Proceso de Revisión DS 90"

Fecha   : 07 abril 2009
Lugar   : CONAMA CENTRAL, 4° piso
Hora   : 10:30 a 13:00 hrs

DOCUMENTOS DE REUNIÓN

N°	CONTENIDO
1	Tabla de Reunión
2	Acta de reunión aprobada
3	Presentación DGA
4	Presentación WWF
5	Presentación RRNN CONAMA
6	Lista de Asistencia

GOBIERNODECHILE

COMISION NACIONAL
DEL MEDIO AMBIENTE

Reunión Comité Operativo
"Proceso de Revisión DS 90"

Fecha   : 07 abril 2009

Lugar   : CONAMA CENTRAL, PISO 4

Hora   : 10:30 a 13:00 hrs

<u>TABLA DE REUNIÓN</u>

HORA	CONTENIDO	RESPONSABLE
10:30	Bienvenida	Claudia Galleguillos CONAMA
10:40	Presentación estudio para medir caudal de dilución en estuarios	Fernando Aguirre DGA
11:00	Presentación estudio de Lagos	Paula Moreno WWF
12:00	Presentación de otros antecedentes	Ricardo Serrano RRNN CONAMA
12:45	Cierre	Claudia Galleguillos CONAMA

ACTA REUNIÓN
REUNIÓN "GRUPO ESTUARIOS" COMITÉ OPERATIVO
PROCESO DE REVISIÓN DS 90/00

Tema: COMITÉ OPERATIVO, PROCESO DE REVISIÓN DS 90/00
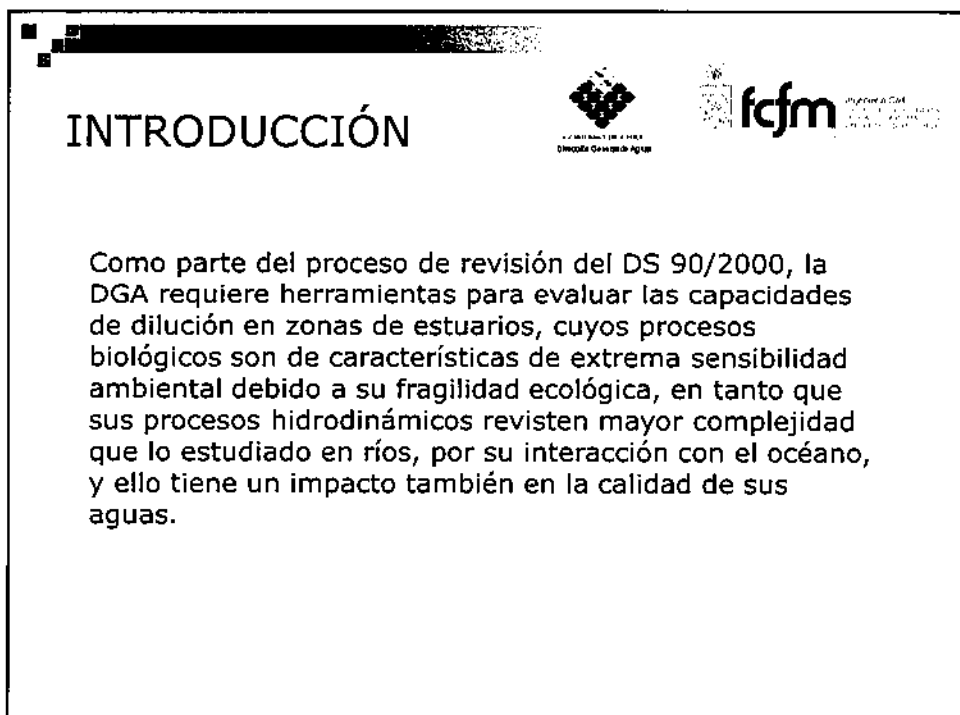**Fecha:** 07 de abril 2009   **Lugar:** CONAMA CENTRAL, SALON DE REUNIONES 4° PISO
Horario: 10:30 hrs a las 13:00 hrs.

LISTA DE ASISTENCIA		
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TABLA DE LA REUNION:
- Análisis del tema estuarios en el DS 90

ESTUARIOS:

- DGA: Realiza presentación respecto a los avances de la consultoría que se está ejecutando para medir caudal de dilución en estuarios. La presentación es realizada por el Sr. Fernando Aguirre de la DGA y el Sr. Yarko Niño de la Universidad de Chile.

LAGOS
- WWF: La Sra. Paula Moreno realiza presentación respecto a estudio de la WWF denominado "Salomonicultura en los lagos del sur de Chile". Se adjunta presentación.

OTROS:
- RRNN CONAMA: Realiza presentación respecto a otros antecedentes que se deben considerar en el tema de lagos y estuarios. Se adjunta presentación

COMPROMISOS ADOPTADOS:

1.

FECHA PRÓXIMA REUNIÓN COMITÉ OPERATIVO:

ANÁLISIS METODOLÓGICO PARA DETERMINAR CAUDALES DE DILUCIÓN EN ZONAS ESTUARINAS

Dirección General de Aguas
Universidad de Chile

INTRODUCCIÓN

Como parte del proceso de revisión del DS 90/2000, la DGA requiere herramientas para evaluar las capacidades de dilución en zonas de estuarios, cuyos procesos biológicos son de características de extrema sensibilidad ambiental debido a su fragilidad ecológica, en tanto que sus procesos hidrodinámicos revisten mayor complejidad que lo estudiado en ríos, por su interacción con el océano, y ello tiene un impacto también en la calidad de sus aguas.

OBJETIVOS

Objetivo General

Desarrollar una metodología para la determinación de caudales disponibles para dilución en zonas estuarinas del territorio chileno.

Objetivos Específicos

• Clasificar o caracterizar tipos de estuarios a nivel nacional.

• Desarrollar una metodología para determinar caudales disponibles para dilución en estuarios del territorio nacional.

• Aplicar metodología en estuarios piloto

• Definir modelo hidrodinámico para validar met. en 2da etapa

ALCANCES

Dotar a la DGA de metodologías claras y fundamentos técnicos para la determinación de caudales disponibles para la dilución en zonas estuariales, de manera simplificada, a través de herramientas uniformes, proponiendo recomendaciones que den coherencia a las políticas que desarrollan los distintos servicios.

ETAPAS

Etapa 1: Recopilación de antecedentes.

Etapa 2: Determinación de metodología para determinar los caudales de dilución, para cada tipo de estuario identificado

Etapa 3: Campañas de caracterización de sistemas seleccionados y aplicación piloto de metodología

Etapa 4: Definición preliminar del modelo hidrodinámico a utilizar para validación en segunda etapa.

Etapa 5: Conclusiones e Informe Final.

PRODUCTOS

Como productos del presente estudio, se entregará:

• Una metodología para la delimitación de la zona estuarina.

• Una metodología para determinar caudales disponibles para dilución de acuerdo al tipo de estuario definido en la clasificación a nivel nacional.

• Una aplicación de las metodologías a casos piloto.

REVISIÓN CLASIFICACIÓN DE ESTUARIOS

ESTRATIFICACIÓN

- **Fuertemente estratific**
  - Río > marea

- **Parcialmente estratific**
  - Curvas isosalinidad inclinada:
  - Mayor efecto de la marea.
  - Circulación baroclínica.

- **Mezclado**
  - Baja influencia del río

$$R = \frac{\Delta \rho g Q_R}{\rho W U^3}$$

PROPUESTA DEL SHOA

PRISMA DE MAREA: Variación de volumen del estuario asociado a la marea

- Tipo 1: El agua dulce es mucho mayor que el prisma de marea. Normalmente son estuarios profundos y de cuña bien definida y pronunciada.

- Tipo 2: Prisma mayor que agua dulce. La cuña avanza hasta la cabeza del estuario. El efecto de Coriolis es importante y la interfaz se inclina hacia un costado del estuario. Normalmente esto sucede en los fiordos.

- Tipo 3: Similar al 2, pero con menor agua dulce, por lo que la cuña intercepta la superficie en un costado del estuario. En este caso se dan gradientes laterales de salinidad.

- Tipo 4: Con barra o umbral en la Boca a veces no son ni de tipo 1, 2 ni 3. En estos casos, difieren del resto, ya que los procesos de mezcla se dan sólo en la superficie.

CLASIFICACIÓN GEOMORFOLÓGICA

Valle inundado	- Mayor aporte de río que de marea - Presencia de cuña salina - Relativamente someros - Normalmente amplios
De barrera	- Mayor importancia de la marea - Barra estacional o semisumergida - La interacción se da a través de canales - Bien mezclados, por bajas profundidades - Alta salinidad
Laguna costera	- Marcada cuña de sal - Agua salina intercepta la superficie - Gradientes laterales de salinidad (Coriolis)
Fiordo	- Origen glacial - Profundos (B/h <10) - Bordes pronunciados - Suelo rocos --> bajos sedimentos
Origen tectónico	- IX y X región, generados por hundimiento costero - Baja profundidad

TIPO	NOMBRE DEL ESTUARIO	JUSTIFICACION
	Limarí	Marea Pequeña

ESTUARIO	TIPO	TIEMPO AUTOLIMPIEZA (hrs)	LIMITES DE APLICACIÓN Desde boca límite hacia el río
Limarí	1	S/I	4000
Aconcagua	1	6.5	1000
Maipo	2	32.6	2000
Cahuil	3	60.8	3000
Mataquito	2	66.7	7000
Maule	2	10.2	5000
Bío-Bío	1	22.8	5000
Lebu	2	S/I	4000
Imperial	5	10.4	6000
Queule	5	S/I	4000
Lingue	5	S/I	5000
Valdivia	1	12.9	Completo
Maullín	1	115.9	12000
Reloncaví	4	S/I	Completo
Pudeto	1	S/I	8000
Cumau	4	S/I	Completo
Palana	4	S/I	9000
Gala	4	S/I	18000
Cisnes	4	1602	Completo
Aysén	4	2506.5	Completo
Baker	1	S/I	2000
Yendegaia	4	S/I	Completo

		después del terremoto del año 60
Tipo 5	Queule	Se formó después del terremoto del 60
	Lingue	Se formó después del terremoto del 60

PROPUESTA PARA ESTE PROYECTO

Diferenciar principalmente por procesos hidrodinámicos:

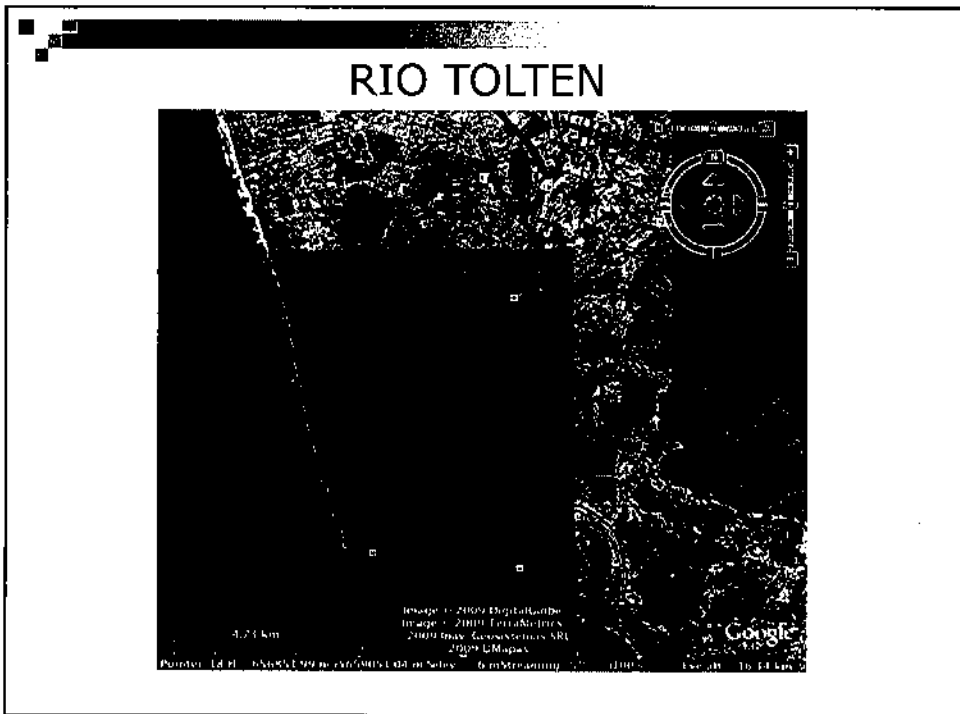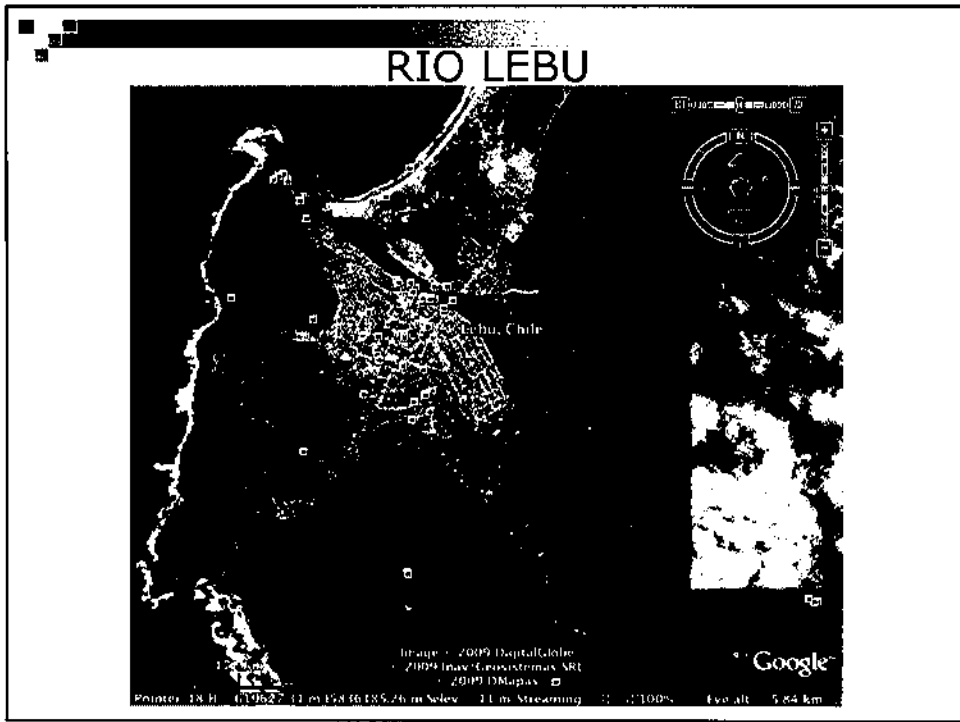ESTRATIFICACION, PROCESOS DE MEZCLA, INTERCAMBIO DE MAREA; PRESENCIA DE BARRA

RIOS CON CUÑA O SIN CUÑA
RIOS CON O SIN BARRA
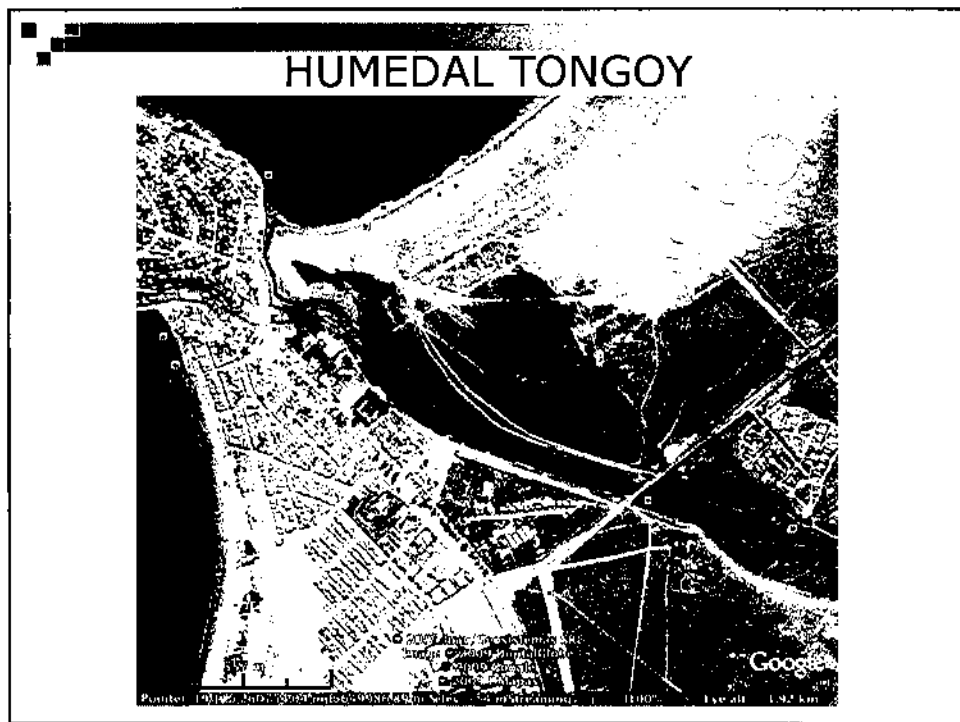SISTEMAS GRANDES O PEQUEÑOS (FIORDOS O SISTEMAS COMPLEJOS V/S RIOS)

SISTEMAS PROPUESTOS:

RIO LEBU
RIO TOLTEN

HUMEDAL TONGOY

RIO LEBU

RIO TOLTEN

HUMEDAL TONGOY

SISTEMAS MAS COMPLEJOS?

DESARROLLO DE METODOLOGIAS

DEFINICION DE ZONA ESTUARIAL

EFECTO DE MAREA:

Variación de nivel o altura de escurrimiento
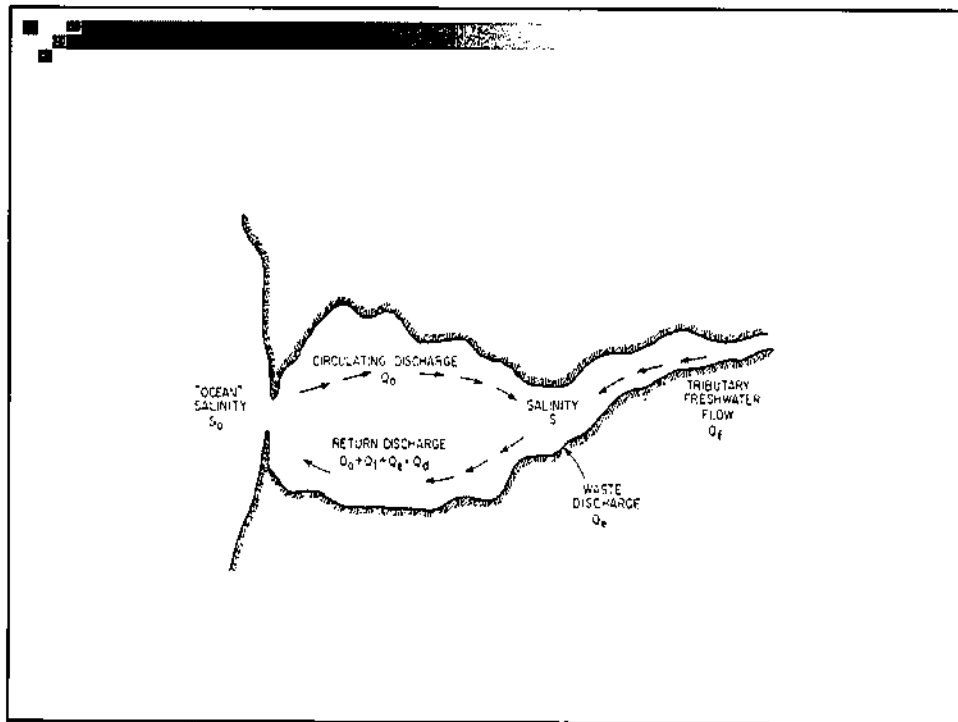
Variación de caudal

INTRUSION SALINA:

Alcance cuña salina

Variación de salinidad

INTERCAMBIO CON EL OCEANO

LONGITUD DE MEZCLA DEL RIO AFLUENTE

CIRCULATING DISCHARGE
Q_0

"OCEAN"
SALINITY
S_0

SALINITY
S

TRIBUTARY
FRESHWATER
FLOW
Q_f

RETURN DISCHARGE
$Q_0 + Q_f + Q_e + Q_d$

WASTE
DISCHARGE
Q_e

DEFINICION DE CAUDAL DE DILUCION

DETERMINACION DE VOLUMEN DISPONIBLE PARA DILUIR
APORTADO POR EL OCEANO

DISTINGUIR CASOS CON ESTRATIFICACION FUERTE DE
LOS DEBILMENTE ESTRATIFICADOS

UTILIZAR MEDICIONES DE SALINIDAD PARA ESTIMAR
LOS VOLUMENES DISPONIBLES (CAPACIDAD DE MEZCLA)
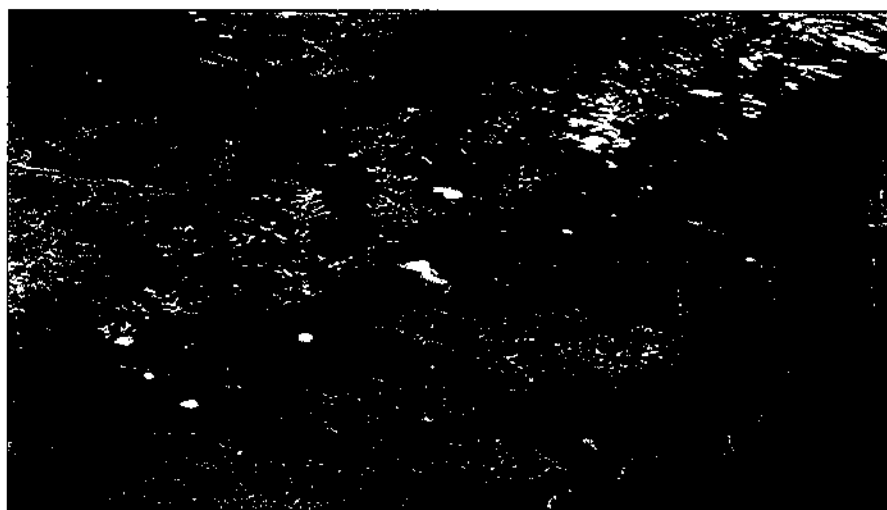
DETERMINACION DE TIEMPOS DE LAVADO

SALMONICULTURA EN LOS LAGOS DEL SUR DE CHILE

ECORREGIÓN VALDIVIANA (35°S - 48°S)

Paula Moreno
Coordinadora Programa Acuicultura
WWF Chile

Área de estudio

Cuencas lacustres de la Ecorregión Valdiviana en cuyos cuerpos de agua se realiza salmonicultura

Visión integral de los impactos a nivel de cuenca

Intervenciones antrópicas

Concesiones lacustres

1991 – 2007:
- Ley General de Pesca y Acuicultura (Ley 18.892)
- Reglamento de Acuicultura (D.S. 290/1993)
- Sistema de Evaluación de Impacto Ambiental (SEIA) (Ley 19300; D.S. 95/2001)
- Norma de Emisión para la Regulación de Contaminantes Asociados a las Descargas de RILes a Aguas Marinas y Continentales Superficiales (D.S. 90/2000)
- Reglamento Ambiental para la Acuicultura (D.S. 320/2001)

No se declaran Áreas Apropiadas para el ejercicio de la Acuicultura (AAA)

![WWF] Distribución espacial

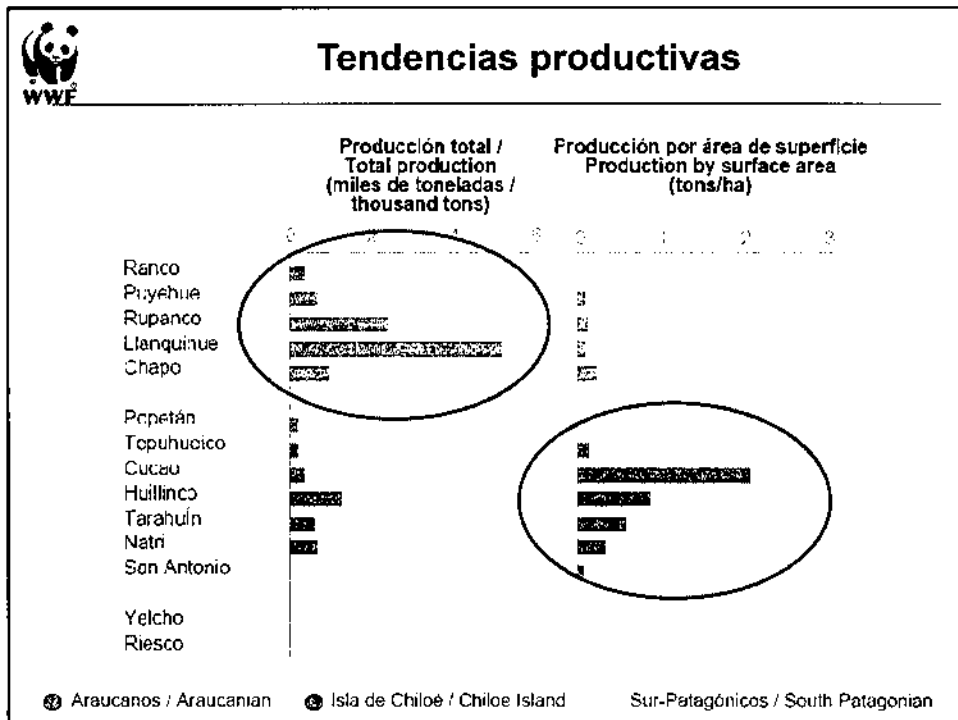| Lagos / Lakes	Concesiones salmonicultoras / Salmon farm concessions	
	Sitios / Sites (N°)	Area (ha)
Araucanos / Araucanian		
Ranco	2	12,5
Puyehue	2	91,
Rupanco	7	100,8
Llanquihue	15	196,8
Chapo	0	31
Subtotal	*32*	*492,2*
Isla de Chiloé / Chiloé Island		
Popetán	1	1,1
Tepuhueico	1	4,9
Cucao	1	1,5
Huillinco	5	02,4
Tarahuín	2	24,6
Natri	3	24,
San Antonio	1	2
Subtotal	*14*	*120,0*
Sur-Patagónicos / South Patagonian		
Yelcho	2	47,4
Riesco	3	15,8
Subtotal	*5*	*65,2*

![WWF] Características morfológicas y limnológicas

Lagos / Lakes	Espejo de agua / Surface Ad (ha)	Cuenca de drenaje / Watershed Ao (ha)	Ao / Ad	Profundidad media / Mean depth (m)	Tiempo renovación / Renewal time (años / years)
Araucanos / Araucanian					
Ranco	44260	396700	9	122,1	5
Puyehue	16500	151000	9,2	76	3,4
Rupanco	23600	99400	4,2	162	8,5
Llanquihue	87000	160500	1,8	182	70
Chapo	4540	31048	6,8	151	5,5
Isla de Chiloé / Chiloé island					
Popetán	160	1328	8,3	8,1	0,2
Tepuhueico	1430	18210	12,7	9	0,2
Cucao	1050	3320	3,1	12	0,1
Huillinco	1910	52980	27,7	20,7	0,2
Tarahuín	770	3820	5	22,2	2,7
Natri	780	4650	6	35	3,5
San Antonio	303	2485	8,2	5,4	0,4
Sur-Patagónicos / South Patagonian					
Yelcho	12000	210127	17,5	135	0,5
Riesco	1470	31538	21,5	66,5	0,6

Tendencias productivas

	Producción total / Total production (miles de toneladas / thousand tons)	Producción por área de superficie Production by surface area (tons/ha)
Ranco		
Puyehue		
Rupanco		
Llanquihue		
Chapo		
Popetán		
Tepuhueico		
Cucao		
Huillinco		
Tarahuín		
Natri		
San Antonio		
Yelcho		
Riesco		

Araucanos / Araucanian   Isla de Chiloé / Chiloe Island   Sur-Patagónicos / South Patagonian

---

Tendencias productivas

Años / Year	Lago / Lake	Río / River	Estuario / Estuary
1998	58	12	21
1999	75	19	33
2000	102	24	39
2001	91	25	61
2002	85	26	67
2003	96	32	167
2004	107	34	140
2005	111	49	133

Millones de smolts

Impactos Ambientales

Biodiversidad y salmonicultura

Esta íctiofauna se caracteriza por presentar pequeños tamaños corporales y ser altamente sensibles a las alteraciones de su hábitat *(Arratia 1983, Vila et al. 1999, Habit 2005; Habit, 2006)*

Originalmente los ecosistemas dulceacuícolas y marino costeros de Chile no exhibían la presencia de especies salmonídeas *(Soto et al., 1997)*

En lagos y ríos de la Ecorregión Valdiviana se han descrito la presencia de 11 especies ícticas nativas y 7 exóticas, de las cuales 5 corresponden a salmonídeas *(Soto et al., 2006)*

Biodiversidad y salmonicultura

La falta de información científica se constituye como uno de los principales problemas tanto para peces como protozoos, crustáceos e incluso mamíferos como la nutria de agua dulce o Huillin *(Habit et al., 2006; Sielfeld & Castilla, 1999; Villalobos, 2006; Woelfl, 2006)*.

El 93% de especies ícticas nativas que ya han sido clasificadas como amenazadas o en estado de vulnerabilidad, ó al 40% que se encuentra en peligro de extinción *(OCDE & CEPAL, 2005; Habit., et al., 2006; Vila et al., 2006)*
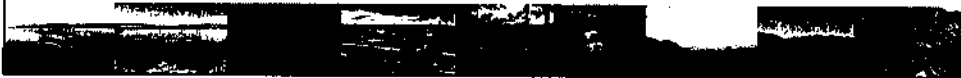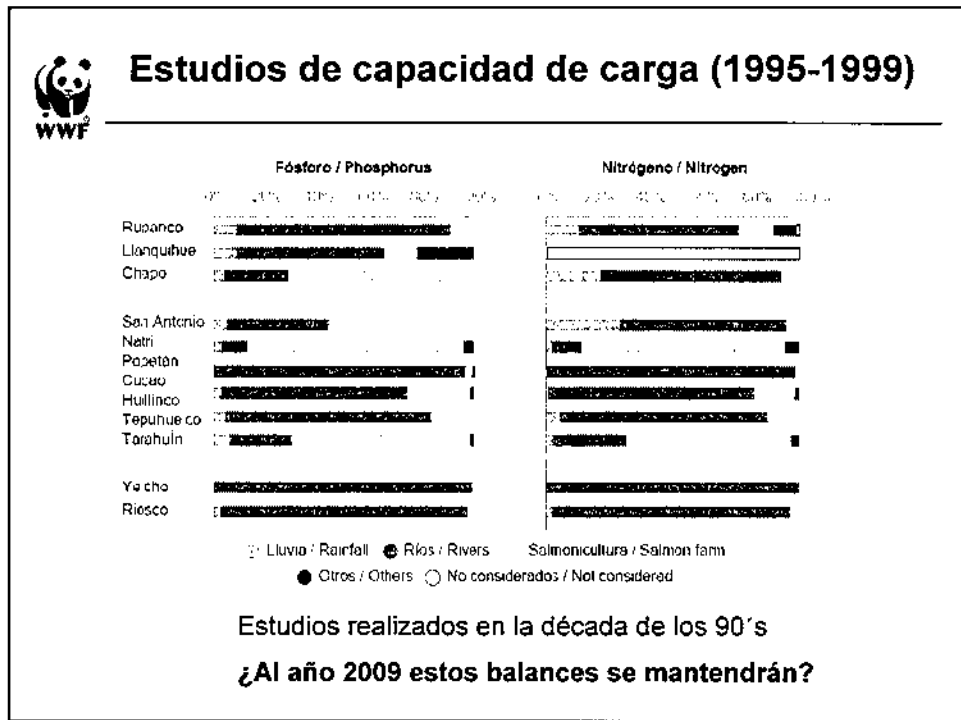
Salmonicultura, fuente puntual de nutrientes

El abastecimiento de nutrientes y su disponibilidad en la masa de agua es un factor que puede explicar las variaciones tróficas de un lago *(Schindler & Fee, 1974)*.

La salmonicultura, es la principal actividad productiva realizada directamente en los cuerpos de agua lacustres

Al conocer las características de sus zonas de cultivo, las tasas de conversión de sus peces y la cantidad de alimento proporcionado, es particularmente la única que tiene un impacto medible sobre la columna de agua y el fondo circundante a sus instalaciones (Soto & Norambuena, 2004)

Estudios de capacidad de carga (1995-1999)

Fósforo / Phosphorus   Nitrógeno / Nitrogen

Rupanco
Llanquihue
Chapo

San Antonio
Natri
Popetán
Cucao
Huillinco
Tepuhueico
Tarahuín

Yelcho
Riesco

Lluvia / Rainfall   Ríos / Rivers   Salmonicultura / Salmon farm
Otros / Others   No considerados / Not considered

Estudios realizados en la década de los 90's

¿Al año 2009 estos balances se mantendrán?

Estudios de capacidad de carga (1995-1999)

Lagos / Lake	Producción / Production (ton/año/year)	Capacidad de carga / Carrying capacity Fósforo / phosphorus (mg/m³/año)		Recomendación / Recommendation
		Crítica / Critical	Medida / Measured	
Araucanos / Araucanian				
Ranco	307,9	*	*	*
Puyehue	587,3	*	*	*
Rupanco	2268,4	784,3	742,4	No incrementar / No increase
Llanquihue	3996,3	241,7	142,87	Sin recomendación / No recommendation
Chapo	732,5	1241	659	< 315 ton/año/year*
Isla de Chiloé / Chiloe Island				
Popetán	124,2	320	4995	No incrementar / No increase
Cucao	150,2	1103,4	34279	No incrementar / No increase
Tepuhueico	193,7	401,9	1216,9	No incrementar / No increase
Huillinco	950,3	924,3	4249	No incrementar / No increase
Tarahuín	506,9	268	857,7	No incrementar / No increase
Natri	408,3	280,8	663	No incrementar / No increase
San Antonio	23,9	149	293	No incrementar / No increase
Sur-Patagónicos / South Patagonian				
Yelcho	82,1	2719	2722	No incrementar / No increase
Riesco	28,8	15541,5	1159,5	Sin recomendación / No recommendation

* No estudiados / Not evaluates

Estudios de capacidad de carga (1995-1999)

Lagos	Recomendación	Aporte (P, %) Salmonicultura	Millones de smolts 1998	2003	2005
Araucanos					
Rupanco	No incrementar	10	10,8	18,1	23,0
Isla de Chiloé					
Popetán	No incrementar	98	0,8	1,3	1,7
Cucao	No incrementar	3	2,2	0,0	0,0
Huillinco	No incrementar	25	11,4	6,9	4,7
Tepuhueico	No incrementar	17	0,7	3,3	2,0
Tarahuin	No incrementar	69	1,0	4,1	4,0
Natri	No incrementar	83	1,6	14,1	11,0
Sur-Patagónicos					
Yelcho	No incrementar	1	0,5	0,9	0,0

Conclusiones del estudio

- El actual uso de los lagos chilenos constituye un pasivo ambiental para las empresas salmoneras

- Los impactos ambientales de este sector productivo pasarán a ser, cada vez más, una preocupación de los mercados mundiales

- No se debe trasladar la producción de smolts desde los lagos a otros ecosistemas acuáticos cuya respuesta a su impacto es pobremente conocida

- Es posible evitar los actuales impactos medioambientales sin mermar la actual producción de smolts

Salmonicultura y DS 90

Situación actual

La contaminación orgánica de los lagos, ríos y aguas marinas no esta siendo controlada efectivamente.

La aplicación del DS 90 a las pisciculturas de flujo abierto se hace cargo sólo de la concentración de P y N pero no de la carga total, ya que estas instalaciones ocupan grandes volúmenes de agua.

¿Qué sucede con los productos químicos usados para el control de enfermedades?

No se aplica el DS 90 a cultivos en balsas jaulas por la definición de efluente.

¿Es posible aplicar la norma de emisión a la salmonicultura?

- Centro de cultivo como fuente emisora
- Se requiere una interpretación apropiada de lo que la LBMA define como efluente.
- El enriquecimiento orgánico de los ríos, lagos y costas generadas por la salmonicultura (fecas y alimento no consumido) **es un hecho**, hay que centrarse en cuál es el objetivo ambiental de la norma:

"prevenir la contaminación de las aguas marinas y continentales superficiales"

Gracias

www.panda.org
www.wwf.cl

**GOBIERNO DE CHILE
CONAMA**

Criterios a considerar para la aplicación de posibles descargas en estuarios

Criterios físicos

- Morfología
  - Caudal
  - Ancho
  - Delta
- Hidrodinámica (influencia marina/cuña salina)
- Geográfico o localización (Chiloé al norte o sur)

Criterios ecológicos

- Conectividad de hábitat
- Áreas de reproducción o alimentación
- Presencia de especies amenazadas, clave y migratorias
- Presencia de áreas protegidas
- Oportunidades de restauración
- Nivel de complejidad del ecosistema y/o resiliencia

Criterios socioeconómicos

- Usos del suelo
- Presencia y cercanía de asentamientos humanos
- Instrumentos de planificación
- Involucramiento local/capacidades
- Oportunidades de monitoreo y GAL

Referencias

- Criteria for Identifying and Prioritizing Habitat Protection and Restoration Projects on the Lower Columbia River and Estuary. Lower Columbia River Estuary Partnership en: http://www.lcrep.org/pdfs/Criteria%202006.pdf
- The New Hampshire Estuaries Project Technical Advisory Committee http://www.nhep.unh.edu/programs/nutrient.htm
- Water quality criteria for marine and estuarine waters of Western Australia http://www.epa.wa.gov.au/docs/2676_bulletin103.pdf
- Biological Criteria, Environmental Health and Estuarine Macrobenthic Community Structure (1993), DM Dauer. Marine Pollution Bulletin, Vol. 26, No. 5. pp. 249-257.

Criterios a considerar para la aplicación de posibles descargas en estuarios

Criterios físicos

- Morfología
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- Biological Criteria, Environmental Health and Estuarine Macrobenthic Community Structure (1993), DM Dauer. Marine Pollution Bulletin, Vol. 26, No. 5. pp. 249-257.

DIRECCIÓN EJECUTIVA
DEPTO CONTROL DE LA CONTAMINACIÓN
ÁREA CONTROL DE LA CONTAMINACIÓN HÍDRICA

GOBIERNODECHILE

COMISION NACIONAL
DEL MEDIO AMBIENTE

LISTA DE ASISTENCIA: REUNIÓN EXTRAORDINARIA COMITÉ OPERATIVO, PROCESO DE REVISIÓN DS90.

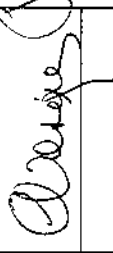| Fecha: | MARTES 07 ABRIL 2009 | Lugar: | CONAMA, PISO 4 |
| Hora inicio: | 10:30 hrs | Hora Fin: | 13:00 hrs |

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1	Article in Press "Beach tar accumulation, transport mechanism, and sources of variability al Coal Oil Point, California"- ScienceDirect. Bernardo R. Broitman; otros.
2	"Recruitment of intertidal invertebrates in the southeast Pacific: Interannual variability and the 1997- 1998. El Niño". Sergio A. Navarrete, Bernardo R. Broitman; otros.
3	"Scales of benthic-pelagic coupling and the intensity of species interactions: From recruitment limitation to top-down control". Sergio A. Navarrete, Bernardo R. Broitman; otros.
4	"Predator- Prey interactions under climate change: the importance of habitat vs body temperature". Bernardo R. Broitman y otros.
5	"Mosaic patterns of thermal stress in the rocky intertidal zone: Implications for climate change". Brian Helmuth; Bernardo R. Broitman y otros

Beach tar accumulation, transport mechanisms, and sources of variability at Coal Oil Point, California

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Abstract

A new field method for tar quantification was used at Coal Oil Point (COP), California to study the mechanisms transporting oil/tar from the nearby COP natural marine hydrocarbon seep field. This method segregates tar pieces into six size classes and assigns them an average mass based on laboratory or direct field measurements. Tar accumulation on the 19,927 m^2 survey area was well resolved spatially by recording tar mass along twelve transects segmented into 4-m^2 blocks and then integrating over the survey area. A seasonal trend was apparent in total tar in which summer accumulations were an order of magnitude higher than winter accumulations. Based on multiple regression analyses between environmental data and tar accumulation, 34% of tar variability is explained by a combination of onshore advection via wind and low swell height inhibiting slick dispersion.
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Keywords: Santa Barbara Channel; Tar; Seeps; Oil slick; Oil advection

1. Introduction

Most concern regarding oil pollution is focused on anthropogenic sources – i.e., oil extraction, transportation, and consumption. However, more than 60% of oil in North American waters and 45% globally come from natural marine hydrocarbon seeps (NRC, 2003). Marine seepage is hydrocarbon (gaseous and/or liquid phase) leakage from subsurface strata into the water column (Hunt, 1996). Among the most visible manifestations of marine oil in the environment is the formation and beach stranding of tar, which is the physically and chemically weathered remnant of an oil slick. Coastal tar accumulation is common on many California beaches due to chronic oil emissions from natural oil seeps in the petroliferous region (Mertz, 1959; Hartman and Hammond, 1981; Leifer et al.,

2006a). Hydrocarbon seeps exist off the coast of California from Santa Monica Bay through the Santa Barbara Channel to Point Conception and in Monterey Bay (Fischer, 1977; Henyey et al., 1977; Lorenson et al., 2002). Despite relevance to the quality of coastal life and its environmental impact, few beach studies regarding tar accumulation from natural seeps have been published.

Previous research has quantified beach tar accumulation as a result of an oil spill or beach stranding of pelagic tar (Iliffe and Knap, 1979; Romero et al., 1981; Golik, 1982; Richardson et al., 1987; Asuquo, 1991; Corbin et al., 1993; Sen Gupta et al., 1993; Gabche et al., 1998; Owens et al., 2002). Although some of these studies had high temporal resolution, spatial resolutions generally were very low and inconsistent. Most studies surveyed a few narrow transects at various beaches over a large stretch of coast or a single line parallel to shore, while others surveyed random transects, potentially introducing bias. Some beach tar studies were conducted following an oil spill and thus, only lasted the duration of high tar/oil stranding. Other studies were conducted in coastal areas or on islands in proximity

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to shipping lanes or ports and recorded relatively low pelagic tar accumulations.

The majority of these studies used similar observational methods, such as recording random tar piece diameters and weight or estimating percent oil/tar cover in an area (Owens et al., 2002). The shoreline cleanup assessment team (SCAT) procedure was developed in order to standardize tar surveys for cleanup agencies (Owens, 1999). This method involves surveying along random transects parallel to shore and averaging the number and size of tar pieces on transects. SCAT procedures provide useful information regarding coastal tar accumulation for the purposes of cleanup, but they do not systematically quantify beach tar with high spatial resolution for the purposes of understanding processes leading to tar accumulation.

Few field studies have addressed the processes by which marine oil reaches the coast. Iliffe and Knap (1979), Shannon et al. (1983), Otero et al. (1987), and Corbin et al. (1993) suggested that much of the variability in the spatial tar distribution was due to the beach location and orientation relative to dominant current and wind patterns. Another potentially important source of variability was the presence and location of shipping lanes. Oil slick models, which largely are based on laboratory results, incorporate many of the physical, chemical, and biological transport and weathering processes that act upon oil at sea (Reed et al., 1999). In general, currents, wind, and waves or swell are the dominant processes in long distance oil slick advection or transport, particularly offshore. Other processes are important in coastal zones, but generally are not incorporated in oil slick models. For example, wave breaking in the surf zone and wave-induced alongshore currents affect shoreline stranding (Reed et al., 1999). Also, tides may be important – Hartman and Hammond (1981) observed that beach tar had a residence time of 1–2 tidal cycles; thus, tides can directly affect measurements of tar mass and estimates of beach tar flux.

This paper describes a new and robust sampling protocol for quantifying beach tar accumulation. We used this method to systematically measure tar accumulation throughout 2005 at Coal Oil Point (COP), California, which is adjacent to one of the largest natural marine hydrocarbon seep fields in the world (Hornafius et al., 1999). The resulting tar accumulation time series was analyzed with respect to environmental parameters that could potentially influence beach tar accumulation. Analysis allowed better understanding of the causes of variability in tar accumulation and identified some of the important processes controlling oil transport in nearby coastal waters to the study site.

1.1. Study area

The study area, COP beach, has the most heavily concentrated tar accumulation along the United States west coast (Mertz, 1959). COP is a south-facing point in the Santa Barbara Channel (SBC) adjacent to the COP seep field (Fig. 1). Oil and gas escape to the ocean from the Miocene Monterey Formation reservoir underlying the SBC. The COP seep field is one of the most prolific (Landes, 1973) and extensively studied marine seepage areas in the world. Studies over the past few decades provide much insight into the temporal and spatial variations in seepage distribution and flux (Allen et al., 1970; Fischer and Stevenson, 1973; Hornafius et al., 1999; Quigley et al., 1999; Leifer and Boles, 2005, 2004; Washburn et al., 2005; Leifer et al., 2006b). The current consensus is a range of 1–$2 \times 10^5 \, m^3 \, CH_4 \, dy^{-1}$ from the COP seep field (Hornafius et al., 1999). Oil emissions were estimated at a minimum of 100 barrels day^{-1}, (Clester et al., 1996; Hornafius et al., 1999), although significant variability exists on a range of time scales.

A few studies have geochemically characterized California beach tar in an effort to identify sources (Hartman and Hammond, 1981; Kvenvolden et al., 2000; Hostettler et al., 2004). Hartman and Hammond (1981) distinguished between various natural seep oil sources of beach tar using carbon and sulfur isotopes and estimated that 55% of Santa Monica beach tar was from the COP seep field, over 250 km to the west. Tar primarily accumulated during the spring, summer, and autumn months. They proposed that during spring and summer COP seep oil exits the SBC to the west and is transported south and east towards Santa Monica Bay by the southerly California Current. They proposed that during winter months the northerly Davidson Current surfaces at the western boundary of the SBC and transports COP seep oil north. Leifer et al. (2006a) looked at physical advection and chemical evolution of oil slicks within the seep field, but did not investigate transport to beaches. In fact, no published studies have identified the transport mechanisms by which COP seep oil/tar reaches
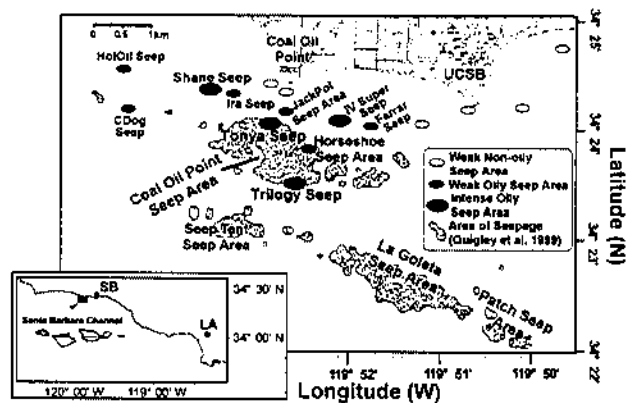

Fig. 1. Overview of the Coal Oil Point seep field, near University of California, Santa Barbara (USCB). Gray regions are areas of high bubble density as detected by sonar returns (Quigley et al., 1999). Informally named oily seeps are noted. Length scales and key on figure. "Weak" and "Intense" are qualitative descriptors for flux. Markers represent seepage areas containing multiple vents, not single vents. Inset shows southern California with study area indicated by small box in the Santa Barbara Channel. SB is Santa Barbara and LA is Los Angeles.

the shore and that influence its spatial or temporal distribution.

Unlike beach tar accumulation studies associated with oil spills or on beaches near heavy ship traffic, which generally have a transient source, natural seepage is a long-term chronic oil spill, albeit with variability in emissions on time scales from tidal (Leifer and Wilson, 2007) to decadal (Boles et al., 2001). Very few studies have investigated seep-related beach tar accumulation, although NOAA – the National Oceanic and Atmospheric Administration – listed this type of research as number one priority in regards to long-term oil weathering research (Mearns and Simecek-Beatty, 2003). A 2-year long tar survey of Santa Barbara County beaches (including COP) found that COP regularly accumulated more tar than any other studied beach by several orders of magnitude. They determined that all tar pieces collected were from the Monterey Formation oil and that concentrations were highest during summer and autumn months (Lorenson et al., 2004).

2. Methods

The experimental approach involved counting tar pieces in six size classes, $S(1-6)$, along a series of north-south transect lines, X_1–X_{12}, perpendicular to the bluffs (Fig. 2). Transect lines were evenly spaced 20-m apart at the bluff with X_6 centered on the point and covered a total area of $19,927\ m^2$. Tar pieces were counted in 2-m square quadrats ($4\text{-}m^2$ area blocks) along each transect line, extending from the bluff, Y_0, to the water line Y_n. To ensure repeatability of the location of transect lines, rebar was hammered into the sand at the base of the bluffs. The rebar defined Y_0, the top of each transect.

Tar mass was calculated from the tar counts using a functional relationship between tar size and mass. Counted tar mass was integrated over the survey area to yield total accumulated tar mass, M, which accounted for the irregular grid shape. In order to understand how environmental

factors modify beach tar accumulation, the time series of total tar mass throughout the study, $M(t)$ where t is time, was related to oceanographic and meteorological parameters, including swell, currents, wind, and sea temperatures.

2.1. Tar quantification

Beach tar size classes were based on their surface area, specifically the approximate diameter of the longest surface dimension (Table 1; Fig. 2a). Typically, the surface cross-sections of tar pieces were circular to elliptical, allowing size classification within a set range of diameters. $S(1-5)$ had defined surface areas, while $S(6)$ was a catch-all class for tar pieces larger than $S(5)$.

To convert tar size counts into tar size mass, m_s, 100 representative tar pieces for $S(1-4)$ were collected and the mass of each was measured. Each tar piece was collected on aluminum foil and weighed on a digital scale. Then, each tar piece was dissolved through filter paper with dichloromethane leaving sand grains and other debris, which had been aggregated into the tar, stranded on the filter paper. The sand and debris were placed back on the original aluminum foil, weighed, and subtracted from the initial mass measurement. The average tar mass for $S(1-4)$, $\langle m_{1-4}\rangle$, allowed calculation of total tar mass observed for those size classes (Table 1).

$S(5)$ and $S(6)$ were treated differently. In the field, the three dimensions of each tar piece were recorded (length, width, and thickness) and the tar mass calculated based on a box volume model of tar shape and an assumed tar density, ρ_t, of $1.00\ g\ cm^{-3}$. Beach tar densities must be within a narrow range, between that of COP seep oil (0.9861–$0.9953\ g\ cm^{-3}$; Jokuty et al., 1999) and seawater ($1.025\ g\ cm^{-3}$), else the asphalt would sink and thus not float to the beach. As a result, actual tar densities should be within 1–2% of $1.00\ g\ cm^{-3}$, which was far less than the typical observed variability in $M(t)$. The average mass for $S(5)$ was calculated from the mass of all $S(5)$ tar pieces observed in the field (Table 1). The average mass of $S(6)$
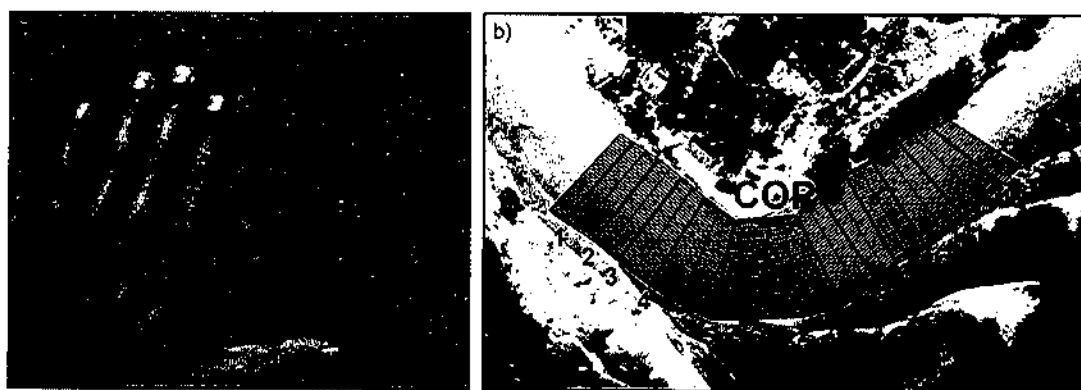

Fig. 2. (a) Tar balls were segregated into six size classes and counted along (b) twelve transects around Coal Oil Point (COP). Thick lines perpendicular to shore are transect centers (X_{1-12}). These lines parallel to those are transecting boundaries. Thin lines parallel to shore are the boundaries of transect segments (34 segments for each transect, Y_{1-34}).

Table 1
Properties of tar ball size classes

Size class	D (cm)	⟨m_s⟩ (g)	⟨h⟩ (cm)	⟨r⟩ (cm)	⟨k⟩ (cm)	Count (%)	Mass (%)
S(1)	0.25	0.006 ± 0.004	0.122	0.125	0.182	53.38	4.27
S(2)	0.50	0.022 ± 0.011	0.112	0.250	0.280	33.23	9.75
S(3)	1.00	0.073 ± 0.037	0.093	0.500	0.418	9.60	9.35
S(4)	2.00	0.169 ± 0.096	0.054	1.000	0.553	3.05	6.87
S(5)	3.00	5.960 ± 7.444	0.405	1.500	1.327	0.54	21.31
S(6)	>4.00	25.82 ± 50.96	0.533	>2.00	2.220	0.21	48.45

S: size class; D: the approximate diameter; m_s: tar ball mass per size class; h: thickness; r: radius; k: characteristic length; ⟨⟩ denotes average.

was calculated in the same manner as S(5), but is not a meaningful value because S(6) does not have a defined size range.

Prior to 11 April 2005, data were collected only for transects X_{1-10}. A consistent peak in mass was noted at the eastern edge of the study area, X_{10}. Consequently, two eastern transects, $X_{11,12}$, were added to the study area to resolve the observed peak. The study area size was chosen to allow survey completion in less than half a tidal cycle (~3 h). For surveys prior to 11 April 2005, tar counts for transects $X_{11,12}$ were extrapolated based on the ratio of tar counts for those transects to the other 10 transects on surveys subsequent to 11 April 2005. Extrapolation allowed comparison of data before and after addition of the two transects.

2.2. Survey area integration

In order to calculate M, total tar mass throughout the study area, we integrated tar mass in each quadrat over the full survey area, accounting for the irregular geometry around Coal Oil Point. The conversion from a Cartesian coordinate system (X is transect, Y is quadrat) to a geographical map was based on the Global Positioning System (GPS) locations of the bluff and waterline ends of each transect line (Fig. 2b). Each transect extended 68 m from the bluff to the defined waterline. Data for each transect was considered representative of the beach spanning halfway between the two adjacent transects. Each transect was subdivided into 2-m segments along the Y-axis forming

34 segments, $Y_1 - Y_{34}$. The width of each segment was the average of the distance to each adjacent transect. The area of each segment was calculated in square decimal-minute from half the determinant of the two triangles that form the rectangular segments and then converted into meter-squared using the meter distance between a minute latitude and minute longitude at 34°N, 119°W.

2.3. Environmental forcing analysis

To identify transport processes related to variations in tar accumulation, several environmental data were acquired for the study period (see Table 2). Parameters hypothesized as potential environmental forcing factors were analyzed individually by comparing their temporal trends with that of M(t) and calculating Pearson correlation coefficients (Sokal and Rohlf, 1995). These factors included the east-west component and north-south component of surface currents (as measured by CODAR – Coastal Ocean Dynamics Application Radar) and winds, significant swell height and direction, sea bottom (SBT) and sea surface temperatures (SST).

To examine patterns of association over a range of temporal scales, we also conducted cross-correlations by lagging the environmental records every 2 h and up to 24 h prior to the survey time. Lagged correlations were performed on raw environmental data as preliminary analyses showed a lack of correlation between tar accumulation and data filtered over 12, 18, and 24 h with inconclusive results for 6-hour filtered data. A Bonferroni correction (Sokal

Table 2
Environmental data sources

Factor	Source	Location (34°, 119°)	Dist. (km)	Direction	Sampling time (min)
Wind (http://www.sbcapcd.org/Default.htm)	SBCAPCD	24'55"N, 52'43"W	0.9	NW	5
Swell/SST (http://cdip.ucsd.edu/)	CDIP (Buoy #107)	20'6"N, 8'12"W	10	SE	30
SBT (http://sbc.lternet.edu/)	SB LTER Naples ADCP (16 m)	25'25"N, 57'1"W	7	W	20
Currents (http://www.oceancurrentmaps.net/)	UCSB IOG (CODAR)	23'45"N, 53'14"W	1.5	SSW	60

SBCAPCD: Santa Barbara county air pollution control district; SST: sea surface temperature; CDIP: coastal data information program; SBT: sea bottom temperature; SB LTER: Santa Barbara long term ecological research; UCSB: University California, Santa Barbara; IOG: interdisciplinary oceanography group; CODAR: coastal ocean dynamic application radar; Dist: distance from Coal Oil Point; Direction: from Coal Oil Point.

and Rohlf, 1995) was used to adjust the significance level ($x = 0.05$) in multiple comparisons. Finally, we combined the observed maximal lagged correlations between individual environmental variables and tar mass in a multiple linear regression model in order to propose a mechanistic model of environmental forcing of tar to COP. Correlation and regression analyses were performed on log($M(t)$).

3. Results

3.1. Tar size characteristics and distribution

The average mass, $\langle m_s \rangle$, and variability in $\langle m_s \rangle$ increased with tar size (Table 1). Because tar size segregation used only surface area, tar thickness, h, was a derived parameter. For $S(1–4)$, h was estimated using the volume, V, equation of an ideal cylinder ($V = f\pi r^2 h$), where f is the fraction to which the surface area is equivalent and r is radius. In this case,

$$h = V/f\pi r^2 = m/\rho_t f\pi r^2, \qquad (1)$$

where $m = \langle m_s \rangle$ when $\rho_t = 1.00 \text{ g cm}^{-3}$. A comparison of h to r shows that as tar pieces increase in surface area, they become thinner (Table 1). This method of determining h was unnecessary for $S(5)$ and $S(6)$ where h was directly measured. An average h was computed from the individual $S(5)$ and $S(6)$ thickness measurements and are significantly higher than h for $S(1–4)$ (Table 1).

A characteristic length, k, also was calculated for the size classes, where k is defined as $V^{(1/3)}$ and $V = \langle m_s \rangle/\rho_t$. k is the dimension for an idealized cubic tar piece and provides a single dimension for each size class. Mean k for $S(5)$ and $S(6)$ was calculated from individual values of k based on the measured tar piece dimensions. A linear fit of k to r showed that tar thickness did not increase in proportion with surface area ($k = 1.0221r - 0.0856$, $r^2 = 0.9169$) – i.e., tar piece surface area increased with size class at a faster rate than tar thickness. Our defined tar size classes, $S(1–5)$, included over 99% of the tar pieces observed and over 51% of tar mass observed (Table 1). $S(6)$ tar provided the remainder of mass observed but were much more rare (0.21% of observed tar).

3.2. Observed tar accumulation

COP tar accumulation was surveyed on 57 days from February through December 2005 (Fig. 3a) with 17, 14, 9, and 17 days during winter, spring, summer, and autumn, respectively. Zero tar was observed on only two winter days (24 February and 8 March). Non-zero values of M ranged from 0.10 kg (4 November) to 39.11 kg (27 February). For the entire study, mean M (steady state tar accumulation) was 4.40 kg.

Except for 27 February 2005, which for several reasons was unique (discussed in Section 4.2), tar accumulation data showed an overall seasonal cycle with M doubling from winter to spring and then roughly doubling again into
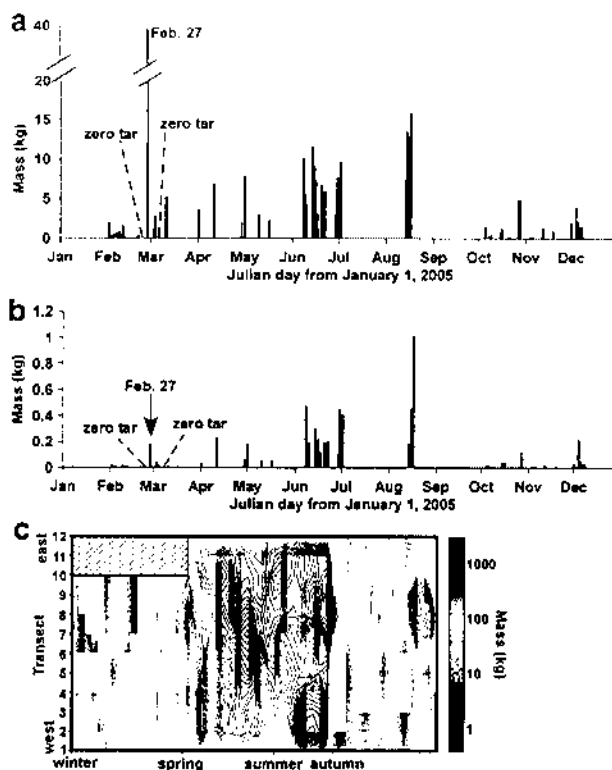

Fig. 3. (a) Total tar mass on 57 days during 2005. (b) Tar mass observed in four smallest size classes. (c) Total tar mass with respect to transect and survey (season transition noted below figure). Contour mass values indicated by color bar at right. Shaded region had no data; white areas represent zero tar accumulation.

summer, followed by a sharp decrease in autumn to M values comparable to winter (Fig. 3a). Further, the variation between seasons was much larger than the intra-season variability. Mean summer M was about an order of magnitude larger than mean winter M (excluding 27 February 2005; Table 3). Mean tar coverage for the study area varied from 0.052 g m^{-2} in winter (excluding 27 February) to 0.465 g m^{-2} in summer (Table 3). With 27 February, winter tar coverage was greater than autumn, but still lower than spring and summer.

The inter-seasonal variability is readily apparent in the spatial tar accumulation distribution of $M(X,t)$ or mass per transect per day (Fig. 3c). Sharp transitions are clear across the entire survey area at the winter/spring and summer/autumn boundaries. Another notable difference is the many days during winter and autumn in which $M(X,t) = 0$ for some transects (white indicates zero tar in Fig. 3c). In contrast, $M(X,t)$ was always greater than zero during spring and summer surveys. Generally, transects during spring and summer had more than 500 g of tar, while winter transects typically had less than 50 g. Over half the autumn transects contained less than 50 g of tar, but a few transects had between 100 and 500 g and there were fewer tar-free transects during autumn compared to winter.

Table 3
Summary of seasonal tar accumulation

	Spring	Winter[a]	Winter[b]	Summer	Autumn
Days surveyed	14	17	16	9	17
(M) (kg)	5.97 ± 3.05	3.27 ± 9.33	1.03 ± 1.38	9.27 ± 4.22	1.66 ± 1.54
Mean coverage $(g\,m^{-2})$	0.300	0.164	0.052	0.465	0.083
(M_{1-5}) (kg)	3.20	0.521	0.346	6.20	1.04
(M_{1-4}) (kg)	2.02	0.209	0.102	4.00	0.467

(M): Mean tar accumulation (subscripts are tar size classes).
[a] With 27 February.
[b] Without 27 February.

3.3. Environmental forcing of tar accumulation

Oceanographic (surface currents, swell height and direction, sea surface and sea bottom temperatures) and meteorological (wind direction and speed) factors can affect M. These factors were compared to $M(t)$ with particular attention to seasonal variations.

Although u_w, the east-west component of the wind, was more or less constant throughout the year, v_w, the north-south component of the wind, showed a seasonal pattern (Fig. 4a). v_w was often positive (to the north) during spring and summer and negative (to the south) during autumn and winter.

Surface current speeds from the CODAR grid location closest to the COP seep field ranged widely, from less than
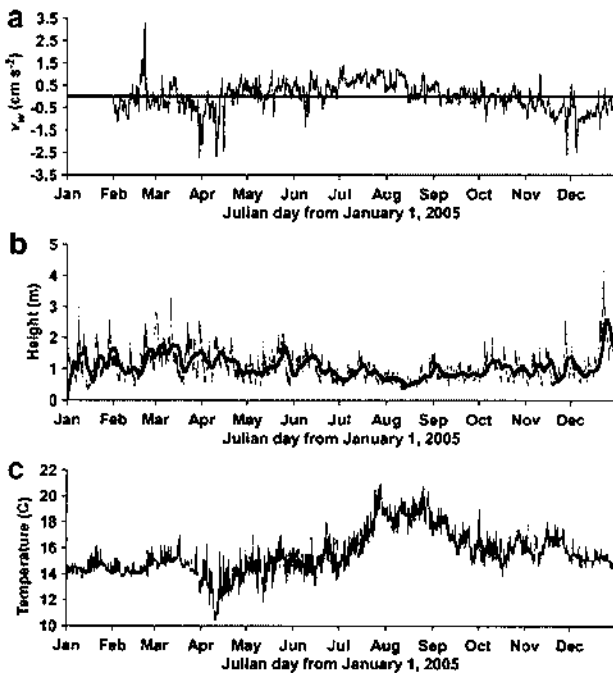
Fig. 4. (a) Daily mean of 10 m north-south wind component, v_w for 2005. Horizontal line at $v_w = 0$ marks boundary between winds to the north (positive) and winds to the south (negative). (b) Significant swell height in meters for 2005. Light gray and black lines are 30 min and 5-day resolutions, respectively. (c) Sea surface temperature (30 min resolution) during 2005.

1 to 60 cm s^{-1}, and the direction was to the WNW over 50% of the year. There was no apparent seasonal trend in u_c, the east-west current component, or v_c, the north-south current component.

Swell height typically was less than 1 m during late spring, summer and early fall and ranged from 1 to 2 m during late fall and winter (Fig. 4b). Thus, swell height trended inversely to $M(t)$. Swell direction was from the west more than 90% of the year.

The SST time series (Fig. 4c) appeared to follow $M(t)$, except for a sudden decrease and subsequent increase of temperature in April. SBT, recorded at 16 m of an 18-m deep water column, were similar to SST, including the mid-April decrease. SBT for the last 2 months of 2005 were missing from the dataset.

We found several environmental factors correlated with $M(t)$. Swell height was inversely related to $M(t)$ with no temporal lag ($r = -0.40$, $p = 0.002$). v_w showed a maximal positive correlation to $M(t)$ with a time lag of 14 h ($r = 0.35$, $p = 0.009$). The maximal lagged correlation between u_w and $M(t)$ was a positive one with a time lag of 18 h ($r = 0.35$, $p = 0.007$). A significant correlation was found between $M(t)$ and u_c at a time lag of 12 h ($r = 0.34$, $p = 0.009$). SBT was negatively and significantly correlated with $M(t)$ at all time lags ($r = 0.44$, $p = 0.001$). No significant correlation was found between $M(t)$ and v_c or SST for any time lag ($p > 0.05$).

We used swell height at zero lag, u_w with an 18-hour lag, and v_w with a 14 h lag in a multiple linear regression model. We selected these variables because they were orthogonal at those time lags – i.e., the variables were not correlated to each other. We found that u_c was significantly correlated with u_w and swell height. As CODAR measurements in the area have limited onshore resolution, we excluded them from the multiple regression model. In the case of SBT, it was significantly correlated with v_w and the record lacked two months of data, thus we also excluded SBT from the regression model. The multiple regression model with the three lagged, orthogonal and unfiltered environmental variables was highly significant ($R^2 = 0.34$, $p < 0.0001$, $F = 8.94$, d.f.e. $= 53$) and all regression coefficients were significant (for swell height, u-wind, and v-wind, $p = 0.006$, 0.0005, and 0.004, respectively).

4. Discussion

4.1. Tar size characterization

Estimating thickness, h, by the cylinder volume equation for $S(1-4)$ predicted a decreasing h with increasing surface area, which clearly disagreed with visual observations. The discrepancy probably lay in the assumption that tar piece cross-sections were circular ($f = 1$), which clearly was seldom true. Elliptical cross-sections were very common, especially among $S(3)$ and $S(4)$ tar pieces. h for $S(5)$ and $S(6)$ were measured directly and therefore fairly accurate.

The mass of $S(5)$ and $S(6)$, however, likely was overestimated by assuming tar pieces were best described by a box instead of a cylinder. For a circular cross-section tar piece, the box volume equation overestimates the cylinder volume value by 27%. Based on the contributions of $S(5)$ and $S(6)$ to the total mass (Table 1), this could have resulted in an upper limit overestimate of M by 6% and 13.5%, respectively. For most surveys, the overestimation likely was less because the true shape of $S(5)$ and $S(6)$ tar was in between these shapes. For the typical unequal length and width, the box volume model generally was more accurate than the cylindrical volume model.

Analysis of k showed that h increased with size class, but not in proportion to surface area. Visual tar observations during surveys confirmed this conclusion; h varied little between $S(1-6)$. This suggests that some physical process(es) inhibited thickening of tar pieces relative to surface area growth. Sun exposure is one possible process causing this. As the sun warms tar, whether on the sea surface or the beach, it becomes less viscous and tends to spread.

Overall, our tar size characterization method provided highly accurate mass estimates and covered the size range of tar pieces present on COP, such that each class contained a statistically significant number of tar pieces and the presence or absence of a $S(6)$ tar piece did not measurably affect total tar mass. Thus, this approach addressed a significant problem with lower spatial resolution surveys wherein random variability in the largest tar pieces affects the estimate of total beach tar. Moreover, a comparison of tar accumulation with respect to transect showed similar trends with and without $S(6)$ tar pieces.

4.2. Temporal tar variation

The observed seasonal beach tar trend at COP (higher in spring and summer) is similar to variations found in other studies (Hartman and Hammond, 1981; Lorenson et al., 2004). Importantly, this temporal variation was not solely determined by the mass contributions from the largest size classes, $S(5-6)$, where the statistics can be poor. The same seasonal trend is apparent in M_{1-4}, tar accumulation for $S(1-4)$ pieces (Fig. 3b), as well as in $\langle M_{1-5} \rangle$ (Table 3). February 27th also was exceptional in terms of winter $\langle M_{1-4} \rangle$ (Fig. 3b).

During the study, we estimated the tar residence time at between one and two tidal cycles depending on the phase of the lunar tidal cycle. Thus "bluff tar" could be counted multiple times on consecutive day surveys. Bluff tar was tar stranded at the top of the beach near the bluff following the highest high tide of a diurnal cycle. However, removal of bluff tar from the upper 8 m of each transect within the dataset reduced $M(t)$ by <10%, and $M(t)$ absent bluff tar showed the same seasonal patterns. Therefore, we concluded that bluff tar did not significantly affect the conclusions of this study.

M for 27 February was unique for several reasons. Not only was it the day of highest M during 2005, it also occurred during the season with the lowest $\langle M \rangle$ (Table 3). In fact, 27 February significantly skewed the mean winter mass by a factor of three. Inspection of the raw data showed that the exceptionally high M observed that day was real. We interpret this as an indication that the processes responsible for tar mass accumulation on 27 February were unique compared to those responsible for typical accumulation throughout the rest of the winter and possibly the entire year.

4.3. Environmental forcing of tar accumulation

The correlation and multiple regression analyses do not necessarily explain the seasonal variation in $M(t)$, but rather point out a set of environmental conditions that promotes tar accumulation at COP any time of the year. The analysis indicated that winds to the east 18 h prior to sampling, followed by winds to the north 4 h later (14 h lag), were conducive to high beach tar accumulation if the swell height was small at the time of sampling. As lagged correlations were performed every two h, the intervals provide a conservative approximation of the temporal window when environmental conditions may have promoted tar accumulation.

In addition, u_w was significantly correlated to $M(t)$ at other time lags, and thus winds to the east were important from 9 to 19 h prior to sampling. This time range is expected because environmental forcing is modulated by the parameter integrated over the requisite oil/tar transport time from the seep source to COP. Further, many environmental variables show strong diurnal and/or tidal cycles, such as winds and currents, respectively. Therefore, diurnal factors likely played a role in COP oil/tar transport.

Based on the multiple regression model, the set of conditions found that explains 34% of tar accumulation variability at COP during our study are consistent with the oceanographic setting of the northern SBC and orientation of COP relative to the oily seeps of the COP field. The majority of oily seeps lie between 0.5 and 3 km to the south of COP (Fig. 1). Other oily seeps are located further offshore to the southeast.

Surface currents act as a dominant oil advection mechanism, but tend to be more important in open water than in coastal environments (Reed et al., 1999). Generally,

currents off COP flow to the west completing the cyclonic gyre common to the SBC (Harms and Winant, 1998). Surface water trajectories from CODAR showed that during much of 2005 currents were to the WNW. Thus, when winds are light or out of the east, oil slicks originating from the seep field tend to travel west of COP (Fig. 5a).

The literature suggests that oil is advected at 3.5% of the 10-m wind speed plus the surface current velocity. Higher wind speeds cause wave breaking, which disperses oil slicks (Reed et al., 1999). In the coastal zone near COP, where winds and currents often are not aligned, the role of wind may be more significant than suggested. The multiple regression model suggests the following processes (as illustrated in Fig. 5 by a simplified schematic) are favorable for tar accumulation and occur more commonly in summer. First, currents advect oil westward and then a wind to the east directs the slick back towards COP (Fig. 5b) with subsequent winds to the north helping advect the slick onshore (Fig. 5c). Winds at COP generally were onshore (to the north) during spring and summer, which would increase beach tar accumulation, while the frequent offshore winds during winter and autumn would decrease tar accumulation (Fig. 4a).

Finally, intense surf zone activity affects beach tar in two manners. First, it disperses oil slicks into the water column, thus less oil/tar reaches the beach. Second, alongshore current induced by large swell would reduce the residence time of tar on the beach. Thus, when swell height is small, energy in the surf zone will be minimal and slicks will disperse less, while also increasing beach residence time. Swell height generally was smaller during spring and summer implying a weaker alongshore current and less surf zone activity.

These three conditions helped explain in part why tar accumulates so heavily during one season and not much during another. However, there was significant accumulation variation within a season. This variability is in part due to changes in the magnitude and direction of winds and currents. As illustrated in Fig. 5, even small changes

in u or v will change the angle that an oil slick travels, and thus the slick's impact upon the beach when it makes landfall. Further, certain acute angles would deposit more tar on one side of the point than the other, a close to perpendicular angle would deposit tar evenly along a wider swath of beach, and still at other angles, most of the tar would miss the survey area.

Another factor that is likely responsible for some of the accumulation is the tidal cycle. The three conditions and lag times selected for the multiple regression model leave $M(t)$ unexplained in terms of environmental conditions for ~12 h prior to sampling. During the 12 h prior to sampling, the beach experiences a complete cycle of one high and low tide. Observations showed that a flooding tide pushes tar further up the beach and depending on how much tar was left from the ebbing tide prior, tar will be present in the swash zone and perhaps at the top of the beach. An ebbing tide tends to remove some tar from the beach, but an onshore wind and/or a weak alongshore current will help strand tar on the beach as the tide is falling. During both tidal phases, some tar is most likely removed from the beach to open water. Although it seems intuitive that flooding tides bring in tar and ebbing tides remove it, the exact mechanism behind tar deposition and removal with respect to tides remains unclear.

Finally, the variability not explained by the multiple regression model and the observed intra-seasonal variability likely are due to source variability (discussed below), physical and chemical weathering processes, and additional oil transport processes (such as Langmuir circulation, current shears, etc.). These additional factors can change the volume of an oil slick significantly and thus the amount of tar that washes ashore. Mechanistically, some oil weathering processes (i.e., spreading and evaporation) are temperature dependant (Reed et al., 1999); thus, SST likely alters weathering rates. Oil slick dispersion due to the thinning of a slick, as a result of warmer temperatures increasing the rate of spreading and evaporation, could ultimately
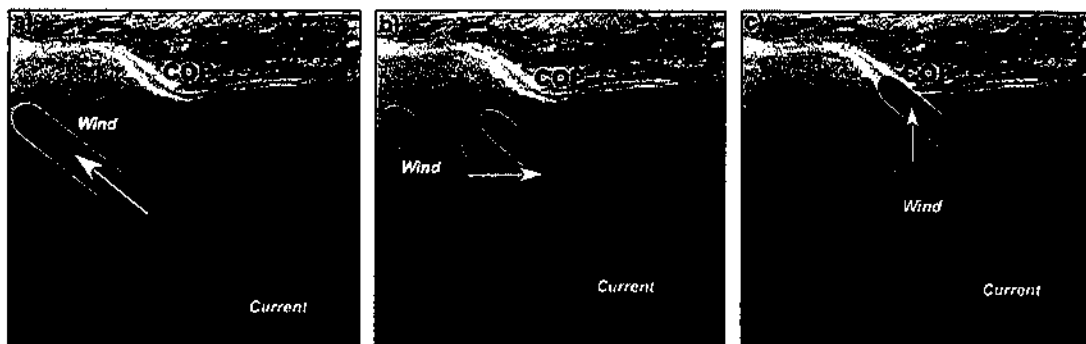

Fig. 5. Simplified schematic superimposed on aerial image of Coal Point showing sequence of conditions favorable for tar accumulation. Black arrow lengths represent surface speed and direction due to winds and currents. White arrows show oil slick transport direction. Black and gray ovals represent oil slick's current and former position, respectively. (a) Initially, currents near Coal Point (COP) transport oil slicks originating from marine hydrocarbon seeps (e.g., location 'X') northwest for conditions of light wind. (b) Winds to the East then transport the slick back towards COP. Absent a wind to the north component (c) the slick may miss COP.

decrease beach tar accumulation (i.e., we would expect SST to be inversely related to tar accumulation).

4.4. Source strength variations

In addition to environmental factors, some of the variability in M likely arises from source emission variability. It is known that seep gas emissions vary over a range of time scales, from second to decadal (Boles et al., 2001; Leifer and Boles, 2005). Few studies have looked at oil emissions; however, Leifer and Wilson (2007) showed a strong tidal influence on the oil emission from a seep with higher emissions during lower water levels. It is unknown if there is a seasonal variation in seep field oil emissions. One potential mechanism for a seasonal emission variation is via temperature-dependent oil viscosity changes in the shallow sediment near the seabed as a result of SBT changes. Oil viscosity is inversely correlated with temperature; therefore, high sea bottom temperatures in summer may result in greater oil emissions, and thus higher M. Our analyses, however, showed a significant negative correlation between SBT and $M(t)$. This cannot be explained physically and may be an artifact of an incomplete dataset. Other factors that also could lead to variability in emissions include aquifer pressure and earth tides, as well as geological factors related to oil and gas migration within the subsurface oil reservoir and along faults and fractures to the seabed.

4.5. Implications of studies on tar from natural marine seeps

Locally, the study of COP tar accumulation is important to the public whom regularly use COP beaches and to the Coal Oil Point Reserve Snowy Plover Program, whom monitors a dense nesting site for the threatened Western Snowy Plover, *Charadrius alexandrinus* (Lafferty, 2001). Our study has found a significant seasonal variation in COP beach tar with ten times more tar in summer than in winter. COP beaches are heavily used in summer and the nesting season for Snowy Plovers is March through September (Lafferty, 2001). Thus, better understanding of seasonal trends and causes of high tar accumulation could play a role in management plans for the endangered Snowy Plover. Further, absent an understanding of seasonal trends in tar accumulation near COP, an anthropogenic oil spill (from nearby shipping lanes or oil platforms) could be masked by the high summer tar deposits. This study has thus provided a method and a background value that can help distinguish between natural and anthropogenic beach tar accumulation at COP.

The complex oceanographic parameters influencing oil/tar transport in the coastal zone are lacking in most oil spill modeling programs. Our study used a natural and continuous oil spill source in coastal waters and natural beach tar accumulation to identify the coastal oceanographic parameters important for oil/tar transport and beach stranding. This type of study could not only help oil spill modelers with coastal parameters, but also inform oceanographers about advective processes in the coastal zone.

5. Conclusions

This paper describes a new and robust sampling method to quantify beach tar accumulation at one of the most heavily tarred beaches in North America. We have highly resolved beach tar mass repeatedly at COP using a tar size segregation method that encompasses the tar piece size range found in that area. Our method is standardized to the size ranges found at COP on designated transects and was designed to be repeated objectively by different surveyors. Our study found a seasonal variation in beach tar accumulation with an order of magnitude more tar accumulating on COP beaches during summer than during winter. The collection of 57 tar mass data points was sufficient to analyze tar accumulation with respect to environmental factors, while the dense sampling grid and survey area integration assured that tar at COP was well quantified and not dependant on a few very large tar pieces.

Although natural seeps introduce complexities, their long-term chronic nature and constrained geographic location provides advantages, particularly for long-term studies, for identifying important environmental variables to tar accumulation. The multiple regression analysis indicated that winds and swell are important factors influencing tar accumulation at COP. The remaining variation may be explained by other environmental factors not addressed in our study or in the stochastic nature of oil seep emissions.

Table of nomenclature

Variable	Units	Definition
D	cm	Diameter of tar piece surface area
f	n/a	Fraction of a circle to which tar piece surface area is equivalent
h	cm	Tar piece thickness
k	cm	Characteristic length of tar piece
M	kg	Total tar mass in survey area
m	g	Mass of individual tar pieces
r	cm	Radius of tar piece surface area
S	n/a	Tar piece size class
t	day	Time
u_c	cm s^{-1}	East-west surface current component
u_w	cm s^{-1}	East-west wind component
V	cm^3	Volume
v_c	cm s^{-1}	North-south surface current component
v_w	cm s^{-1}	North-south wind component
X	n/a	Transect
Y	n/a	Quadrat along transect
ρ_t	g cm^{-3}	Tar density

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Recruitment of intertidal invertebrates in the southeast Pacific: Interannual variability and the 1997–1998 El Niño

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Abstract

We evaluated interannual variability and the effect of the 1997–1998 El Niño event on recruitment of intertidal mussels and barnacles along the coast of central Chile in the southeast Pacific. Monthly monitoring of recruitment at 11 sites spread over 900 km (29–34°S) during the 1997–1998 El Niño and over the same months in 1998–1999 and 1999–2000 allowed us to assess geographic patterns in interannual recruitment variation. The geographically most consistent interannual trend was observed for the mussel *Perumytilus purpuratus,* which showed overall lower recruitment rates during the 1997–1998 El Niño year. However, the magnitude of the effect at any given site was small. Interannual variation in recruitment rates of the other two intertidal mussel species, as well as two chthamaloid barnacles, were not consistent across the region, and overall, few sites exhibited significant differences among years. Differences between two and three orders of magnitude in mean annual recruitment of mussels and barnacles were observed among sites, yet the relative ranking of sites was fairly similar among years for most species. Contrary to the large positive effect that the 1997–1998 El Niño had on barnacle recruitment along the coast of central and northern California, our results show that recruitment of dominant intertidal barnacles along central Chile were not significantly altered by this strong oceanographic event. Lack of consistent trends among sites emphasizes the need to study several sites when looking at large-scale oceanographic anomalies and shows that El Niño effects on interannual recruitment variation are not predictable.

Over the past few decades, benthic marine ecology has made great advances in understanding the dynamics of species interactions and their consequences for the rest of the community. There is now general consensus, however, that further development will only be achieved by improving our understanding of the factors that produce variability in the settlement and recruitment of benthic species (Gaines and Roughgarden 1985). The specific processes and mechanisms by which larvae of benthic species return to the adult habitat after their pelagic life are still scarcely understood and, for the most part, unexplored in all but a few places in the world. Because larvae of invertebrates are small and cannot swim long distances, it is generally accepted that physical processes are largely responsible for larval transport and settlement events on the shore (e.g., Roughgarden et al. 1988; Shanks 1995). Large variability in recruitment is therefore

expected to occur over broad temporal and spatial scales, and association between recruitment variability and physical processes has become a central focus of research (e.g., Shanks 1995; Wing et al. 1995). One aspect of this research centers on identifying the specific mechanisms responsible for larval transport and subsequent settlement events on the shore (e.g., Wing et al. 1995). A complementary research program focuses on evaluating the effects of variability in oceanographic processes on recruitment to benthic populations over longer periods of time, which can have direct consequences on population and community dynamics (e.g., Cury and Roy 1989; Connolly and Roughgarden 1999).

One of the main factors causing large interannual variation in oceanographic conditions is the El Niño–Southern Oscillation (ENSO), which is considered to be the major oceanographic and climate anomaly in the Pacific Ocean (Philander 1989). During ENSO events, important climatic and hydrographic changes occur in the Pacific ocean, such as changes in sea level, surface temperature, the strength and general pattern of circulation, the intensity of equatorward winds, and the availability of nutrients and phytoplankton productivity (Philander 1989). Therefore, it is expected that El Niño would cause major and clearly detectable changes in patterns of recruitment of benthic and pelagic invertebrates and fish. Indeed, several studies have attributed increased or decreased recruitment of different species to El Niño (Paine 1986; Ebert et al. 1994; Moreno et al. 1998; Davis 2000). However, the strength of the evidence for El Niño effects on recruitment is limited by the temporal and spatial scope of the studies; most studies are short in duration and limited to one or a few sites. Because the environmental change produced by El Niño is expected to have geographically broad effects, sites spread over tens to hun-

dreds of kilometers must show similar responses, and the magnitude of the effect must be larger than the background year-to-year recruitment variation (Connolly and Roughgarden 1999). Regardless of the specific mechanisms by which El Niño could increase, decrease, or prevent specific settlement events of some species (Lundquist et al. 2000), demonstration of overall enhancement or reduction of recruitment during El Niño is important, for it suggests that the effects of this large-scale anomaly are essentially predictable.

In a recent study, Connolly and Roughgarden (1999) showed that the strong 1997–1998 El Niño had positive effects on barnacle recruitment across nine sites spread over 750 km along the coast of California. The similarity of the interannual change across sites, as well as the magnitude of the change, strongly suggested that observed recruitment variation was due to El Niño. Connolly and Roughgarden (1999) attributed the increased barnacle recruitment to the general depression of upwelling intensity during El Niño (Ramp et al. 1997). Indeed, an important cross-shelf transport process on the coast of California is the shoreward movement of larvae in upwelling fronts during relaxation of equatorward winds (e.g., Wing et al. 1995; Morgan et al. 2000). Increased frequency of relaxation events during El Niño should then lead to increased recruitment, rendering the effects of El Niño on barnacle recruitment predictable at the regional level.

Here, we evaluated the magnitude of interannual variability and the generality of El Niño effects on recruitment of mussels and barnacles on the much less studied Pacific coast of South America. As in the northern hemisphere, the region is characterized by an offshore equatorward current (Humboldt Current) and the presence of coastal upwelling, where the more saline sub-superficial water, rich in nutrients, is upwelled to the surface, particularly in spring and summer months when equatorward winds are stronger (Kelly and Blanco 1984; Strub et al. 1998). Similar to California, onshore movement of upwelling fronts following wind relaxation has been documented in central southern Chile (Peterson et al. 1988). The negative effects of El Niño on primary and secondary productivity have been well documented in the past (Avaría and Muñoz 1987), but information about its effects on nearshore currents are scarce. Observations in northern Chile (ca. 20°S) show that the 1997–1998 El Niño was first detected as a pulse of warm water in March 1997, with peaks in surface temperature and sea level in May and September of the same year (Thomas et al. 2001; Ulloa et al. 2001). The thermocline was depressed down from the normal 40–60 m to 150–200 m deep, and strong poleward flow was measured in the first 100 m (Blanco et al. 2001; Thomas et al. 2001). A sharp decrease in nearshore chlorophyll *a* concentration was evident during El Niño warming (González et al. 1998; Thomas et al. 2001). As with previous El Niño events, a period of colder than normal conditions, or La Niña, followed the strong 1997–1998 El Niño event, but the intensity of La Niña was weak to moderate (Wolter 2001).

The only connection between El Niño and invertebrate recruitment in temperate latitudes along the coast of Chile has been made at one site near 40°S. There, strong El Niño

events and the associated predominance of poleward winds were linked to failure in intertidal recruitment of the muricid gastropod *Concholepas concholepas* (Moreno et al. 1993, 1998). General patterns of intertidal mussel and barnacle recruitment have been documented at a few sites in central and northern Chile (Navarrete and Castilla 1990; Camus and Lagos 1994), but we have no information about the effects of upwelling–relaxation or other transport processes on recruitment events. Because larvae of mussels and barnacles are planktotrophic, spend considerable time in the water column, and settle predominantly during spring and summer, they can all be affected by the general decrease in phytoplankton biomass, increased surface temperature, and changes in nearshore currents that presumably occur during El Niño events.

Materials and methods

In April 1997, we initiated monthly monitoring of recruitment of intertidal mussels and barnacles at 11 sites along the coast of central Chile covering 900 km of coastline (Fig. 1). Three sites were spread over ~1 km of coast toward the center of the region (ECIM-Norte, ECIM-Sur, Las Cruces; Fig. 1). Recruitment of barnacles was quantified on 10 × 10 cm Plexiglas® plates covered with Safety-Walk (3M®), a nonslip surface that provides substratum heterogeneity and ensures homogeneity of conditions across plates and sites (Menge et al. 1994). Five barnacle recruitment plates were deployed over a 20–50 m transect at the upper intertidal zone of wave-exposed benches at each study site. In 1997 we missed several months of barnacle recruitment at Quintay because of lost plates. Therefore, this site was not included in analysis of barnacle recruitment. Recruitment of mussels was quantified on 7-cm-diameter scrub pads (Tuffy®), which emulate the complex microhabitat preferred by mussel larvae (Navarrete and Castilla 1990; Menge et al. 1994). Five Tuffy pads were deployed in the mid intertidal zone of the same benches with barnacle plates. Plates and pads were replaced every 25 to 70 d, depending mostly on weather conditions and accessibility to the sites, then brought to the laboratory and examined under dissecting scopes. In other studies (S. Navarrete unpubl. data), we have determined that five collectors per site do not capture the full within-site variability, but they represent well the geographic trends and ranking of sites across the region.

Two common species of chthamaloid barnacles are found in the upper intertidal zone at roughly similar abundances: *Jehlius cirratus* and *Notochthamalus scabrosus*. They both recruit and survive on the monitoring plates, but they cannot safely be separated into species at small postmetamorphic size (set). Thus, we pooled both species of barnacles in analyses. Other barnacle species rarely settle in the upper intertidal zone and they can be identified easily. All three mussel species typically found in the intertidal zone of central Chile—*Perumytilus purpuratus, Semimytilus algosus,* and *Brachidontes granulata*—were observed in Tuffy pads and identified to species level. On several occasions, all mussels in the Tuffy pads were measured under the scope to evaluate the potential for secondary settlement (Hunt and Scheibling
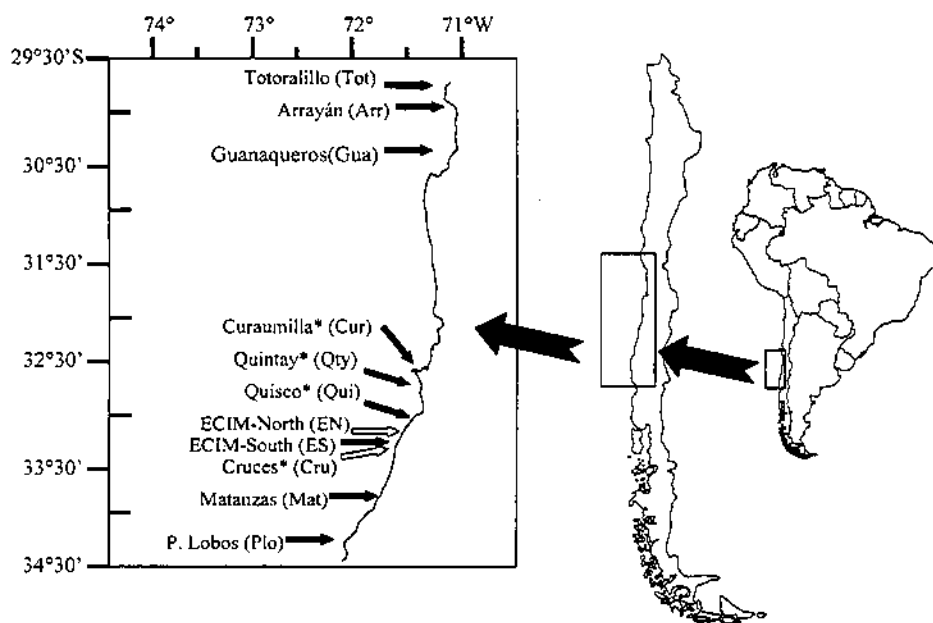
Fig. 1. Map of central Chile showing geographic position of study sites. Solid arrows indicate sites where temperature loggers were placed, and a star next to the site name indicates the temperature records used in calculation of SST for 33°S. Abbreviations of site names in parenthesis as used in tables.

1998). In all cases, judging by spat size and shape, we estimated that most settlers (>90%) corresponded to individuals settling directly from the plankton over the past few days to weeks (Ramorino and Campos 1979).

Larval duration and timing in the water column are important to determine susceptibility to El Niño. The larval phase of the mussel species varies from 17 to 20 d in the case of *P. purpuratus* to >40 d in the case of *B. granulata* (Campos and Ramorino 1979; Ramorino and Campos 1979). Settlement occurs throughout the year in all species, with major peaks in summer (December–February) and fall (March–May) months in the case of *P. purpuratus* and *B. granulata* and summer and, secondarily, winter months (June–August) in the case of *S. algosus* (this study). Larvae of the two chthamaloid barnacles reach competent cyprid stage between 20 and 31 d from release (Venegas et al. 2000). Settlement of barnacles is more discrete than that of mussels, occurring as one or a few pulses between spring and summer months.

At all sites, recruitment time series encompassed the period during the 1997–1998 El Niño and the following 2 yr, when the warming event was no longer detectable along the central coast of Chile and nearly neutral conditions prevailed (see below). To evaluate the hypothesis of El Niño effects versus "normal" interannual variability, we compared recruitment rates between July 1997 and May 1998 (1997–1998) versus those between July 1998 and May 1999 (1998–1999) and between July 1999 and May 2000 (1999–2000). The period was determined according to data from González et al. (1998) and Blanco et al. (2001) for northern Chile and by in situ temperature loggers in central Chile (*see also* the

National Oceanic and Atmospheric Administration (NOAA) altimeter and global coverage satellite observations, http://www.cdc.noaa.gov/~kew/MEI/mei.html). Surface conditions in the central eastern Pacific between 1998 and 2000 have been characterized as slightly cooler than normal (La Niña; Davis 2000; Wolter 2001), but the effect was weak in central Chile (Fig. 2). Therefore, the 2 yr following El Niño can be considered as nearly neutral or as weak La Niña conditions (Blanco et al. 2001, Thomas et al. 2001).

In situ temperature loggers ("tidbits," StowAway®) were deployed 1–2 m deep at nine sites along the region (Fig. 1). Here, we present means of surface temperature from four sites centered 1° around 33°S for which we have data for the 1997–2000 period. Monthly upwelling indices (offshore Ekman transport, OET) spanning the latitudes of the present study (30°S, 73°W; 33°S, 74°W; and 36°S, 74°W) from 1997 to 2000 were provided by Pacific Fisheries Environmental Laboratories, a division of the NOAA National Marine Fisheries Service, and are publicly available (http://www.pfeg.noaa.gov). These indices are calculated on quadrants of 3° × 3° of latitude by longitude based on average wind fields and the Coriolis parameter for that latitude. Therefore, they did not provide site-specific information about upwelling intensity but were used to determine temporal trends. The OET index varies latitudinally, but temporal trends were closely similar within the study region between 33 and 36°S (*see Results*). As estimates of the strength of El Niño (and La Niña), monthly values of the Southern Oscillation index (SOI) and the multivariate ENSO index (MEI) were obtained from the Bureau of Meteorology, Australia (http://www.bom.gov.au/climate/current/soi2.shtml) and the Climate Diagnostic Center of NOAA (http://www.cdc.noaa.
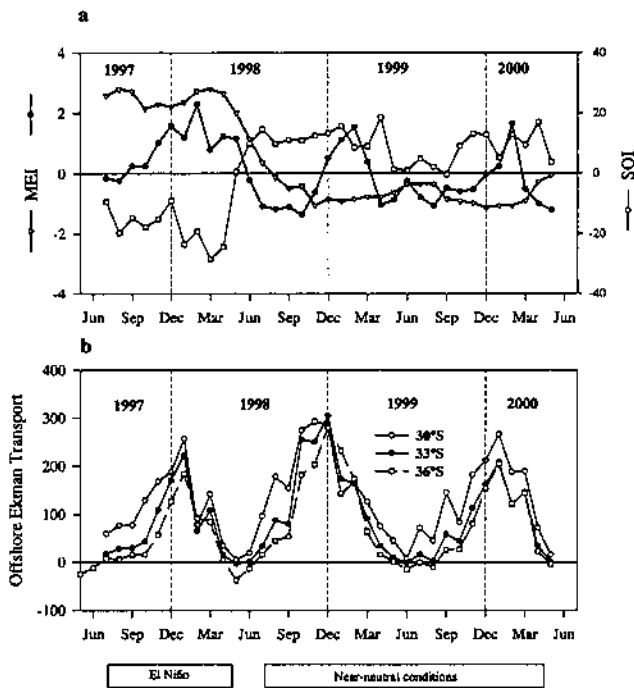
Fig. 2. (a) Surface temperature anomaly at 33°S, Southern Oscillation index (SOI) and multivariate ENSO index (MEI) for the period of the study. (b) Upwelling indices (offshore Ekman transport, OET) at 74°W and 30, 33, and 36°S for the period of the study.

Table 1. (A) Yearly mean (±SE) upwelling indices (offshore Ekman transport, m³ s⁻¹ per 100 m coastline) for quadrants of 3° × 3° of latitude by longitude along central Chile. (B) Results of two-way ANOVA comparing upwelling indices among latitudes and years. Boldface indicates significant differences at $\alpha = 0.05$. df, degrees of freedom; MS, mean square.

(A)	Year		
Latitude (°S)	1997	1998	1999
30	100.6(±18.2)	151.2(±30.9)	108.2(±18.2)
33	71.2(±18.7)	118.1(±31.8)	72.2(±19.2)
36	49.1(±18.4)	91.2(±28.7)	62.3(±23.5)

(B) Source of variation	df	MS	F	P
Year	2	22,578.8	3.34	**0.0395**
Latitude	2	25,287.1	3.74	**0.0271**
Year × Latitude	4	276.55	0.04	0.9968
Residual	99	6,759.4		

gov/~kew/MEI/mei.html), respectively. The SOI index is calculated as the sea level pressure differential between Tahiti (150°W) and Darwin, east Australia (150°E). It represents the general state of the tropical Pacific and does not vary latitudinally. A negative SOI value, which occurs during El Niño events, reflects lower pressure over Tahiti and the movement of warm west Pacific waters to the eastern Pacific. The MEI index corresponds to the rotated first axis of a principal components analysis (PCA) ordination of six main state variables over the tropical Pacific: sea level pressure, zonal and meridional components of surface winds, SST, surface air temperature, and cloudiness (Wolter 2001). The MEI index does not vary with latitude.

Two different statistical analyses were conducted to evaluate the hypothesis of El Niño effects on recruitment. First, monthly recruitment means for each period were compared using a two-way analysis of variance with Year and Site as fixed and random factors, respectively. The means of five plates or Tuffy pads for each month were used as replicates (Connolly and Roughgarden 1999; Lundquist et al. 2000). When a significant Site × Year interaction was found, Tukey's multiple comparison tests were used to determine the direction of among-year differences in each site. These analyses included only sites where nonzero recruitment was observed in all years, which allowed us to compare results with data presented by Connolly and Roughgarden (1999) for intertidal barnacles in California. Second, we calculated Pearson correlations between monthly recruitment of each spe-

cies and the values of OET, MEI, and SOI for each study site. Correlation analyses used the entire time series of recruitment from July 1997 through April 2000.

Results

Hydrography—The sea surface temperature anomaly at 33°S, calculated as the average temperature at four sites around 33°S minus the overall mean for the period 1997–2000, showed clear warming between July 1997 and April–May 1998, corresponding well with the period of negative SOI and high (>1.6) MEI values (Fig. 2a). Indeed, SST at 33°S was negatively correlated to SOI ($r = -0.48$, $P = 0.0034$) and positively correlated to MEI ($r = 0.45$, $P = 0.0063$). Maximum El Niño warming was observed between November and December 1997 and then again between April and May 1998 when water temperature was between 1.0 and 1.6°C above that observed on the same months the following 2 yr (Fig. 2a). After May 1998, monthly water temperature was similar to the following 2 yr (within 1°C), with slightly colder values in 1999–2000 than the previous year, suggesting only a mild effect of La Niña conditions on surface water temperature at this latitude. Upwelling indices at 33°S (estimated OET toward the center of the study region) showed maximum values in austral spring and summer months, reaching nearly neutral or slightly downwelling conditions in winter months (Fig. 2b). Significant differences in upwelling indices were observed among years (Table 1). Upwelling indices in 1998–1999 were significantly higher than those in 1997–1998, whereas values in 1997–1998 were similar to those in 1999–2000 (a posteriori Tukey tests, Fig. 2b). The same temporal trend in OET was observed at 30, 33, and 36°S (Fig. 2b), with a weak but significant latitudinal trend to increasing mean upwelling indices to lower latitudes, a geographic trend that was consistent among years (Table 1). Mean upwelling indices were roughly comparable in magnitude to those reported for the coast of California (Connolly and Roughgarden 1999). Thus, it appears that upwelling of water did occur during El Niño in the austral
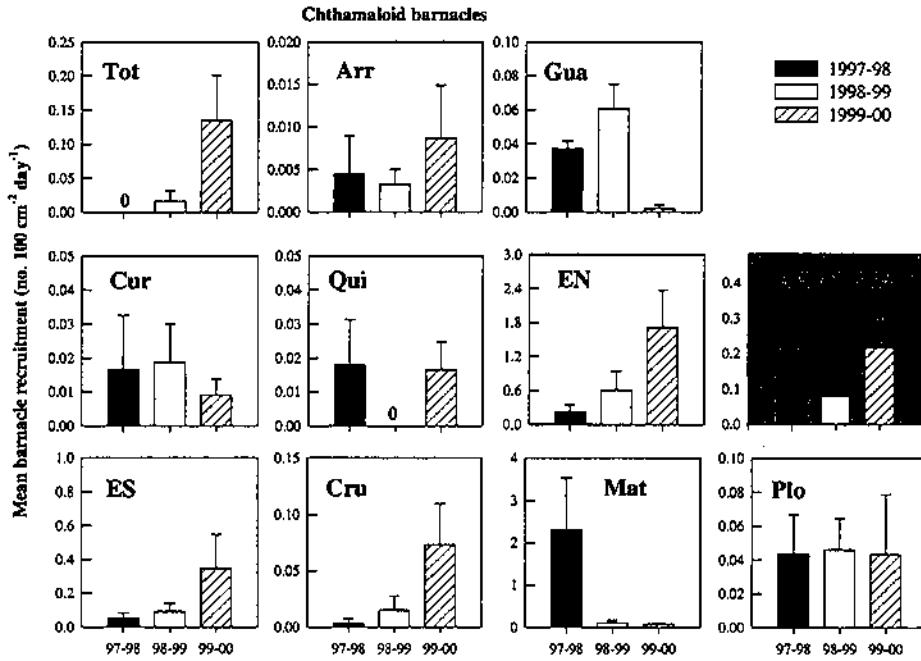
Fig. 3. Mean (±SE) yearly barnacle recruitment rates at study sites for 1997–1998, 1998–1999, and 1999–2000. Sites are ordered north to south going from left to right and top to bottom panels. Note the different *y*-axis scales among panels used to highlight among-year differences within each site. The shaded panel on the right corresponds to yearly averages (±SE) across all sites, including those with zero recruitment. Site abbreviations as in Fig. 1.

spring–summer 1997–1998, but the temperature of upwelled water was warmer than in normal years (González et al. 1998; Blanco et al. 2001).

Recruitment—Across the study region and in all years, mean barnacle recruitment rates varied by almost two orders of magnitude among sites (Fig. 3). The magnitude and the direction of among-year differences varied across sites, however, and a two-way analysis of variance showed a significant Site × Year interaction (Table 2). Multiple contrasts for each site showed significant among-year differences at only 3 of the 11 sites, and only one site, Matanzas, showed significantly higher recruitment during El Niño than the 2 yr after (Table 2). Moreover, there was no detectable latitudinal trend in the direction nor in the magnitude of the interannual differences. Despite the significant differences in the pattern of interannual variability across sites, the ranking of sites was generally maintained between successive years; that is, sites with high barnacle recruitment one year had high recruitment the following year (Table 3). This order broke, however, when comparing recruitment rates between 1997–1998 and those in 1999–2000, the two seasons with similar upwelling indices (Fig. 2b).

Recruitment rates of the mussels *P. purpuratus* and *S. algosus* varied by more than three orders of magnitude across sites, with generally higher rates toward southern sites within the region (except Totoralillo for *S. algosus*) (Figs. 4, 5). Both the magnitude and direction of interannual variation changed between species and sites. The most geographically

consistent pattern was observed in *P. purpuratus*, for which recruitment rates were generally higher in 1998–1999 or 1999–2000 than during the 1997–1998 El Niño year at 9 of the 11 sites (Fig. 4), rendering a significant year effect and a nonsignificant Year × Site interaction (Table 4). A Tukey's multiple comparison test showed that, on average across all sites, recruitment rates were significantly lower during 1997–1998 than the 2 yr after. However, multiple comparisons showed that only three sites presented significant among-year differences in recruitment (experimentwise α = 0.05). In contrast to *P. purpuratus*, the pattern of interannual variation in recruitment rates of *S. algosus* varied significantly across sites (Fig. 5), rendering a significant Site × Year interaction and highly significant main effects of Site (Table 4). Multiple contrasts for each site showed significantly higher recruitment rates during 1997–1998 and 1999–2000 than 1998–1999 at one site, Guanaqueros, but significantly lower rates in 1997–1998 and 1999–2000 than 1998–1999 at El Quisco. Recruitment rates at ECIM-Sur and Punta Lobos were greatest during 1999–2000 (Table 4).

In agreement with the relative abundances of adults in the field (Broitman et al. 2001), recruitment rates of *B. granulata* were 10 to 100 times lower than those of *P. purpuratus* and *S. algosus* across the region. Interannual variation in recruitment rates of *B. granulata* also changed across sites (Fig. 6; Table 4), producing a significant Site × Year interaction term and highly significant main effects of Site. Multiple comparisons showed that interannual differences were statisti-

Table 2. (A) Two-way ANOVA comparing barnacle recruitment rates across sites and among years (1997–1998, 1998–1999, 1999–2000). Year was considered as fixed and Site as a random factor. Only the eight sites where recruitment was observed on each year were considered in this analysis. Boldface indicates significant effect at $\alpha = 0.05$. (B) Direction of statistically significant interannual change in mean barnacle recruitment according to Tukey's multiple comparison tests. 97, period 1997–1998; 98, 1998–1999; and 99, 1999–2000 (experimentwise error rate $\alpha = 0.05$). Abbreviations for sites as used in figures and tables. ns, non significant differences among years; nd, no data available; ni, not included in statistical analyses because there was no recruitment for an entire period; df, degrees of freedom.

(A)

Source of variation	df	MS	F	P
Site	7	0.085	7.53	**0.0001**
Year	2	0.014	0.37	0.6963
Site × Year	14	0.041	3.68	**0.0001**
Residual	263	0.011		

(B)

Site	Direction
Totoralillo (Tot)	ni
Arrayán (Arr)	ns
Guanaqueros (Gua)	99<97=98
Curaumilla (Cur)	ns
Quintay (Qty)	nd
El Quisco (Qui)	ni
ECIM Norte (EN)	99>97
ECIM Sur (ES)	ns
Las Cruces (Cru)	ns
Matanzas (Mat)	97>98=99
Punta Lobos (Plo)	ns

cally significant at only three sites, with no consistent interannual variability among these sites (Table 4).

Despite differences in the direction of interannual changes in mussel recruitment rates across the region, the pattern of among-site differences tended to be preserved from one year to the next, including the 1997–1998 El Niño year. The temporally most robust among-site differences were observed in *P. purpuratus*, for which the ranking of sites (and overall rates) was tightly maintained ($r > 0.86$) from year to year (Table 3). The most variable pattern of among-site differences was that of *B. granulata*, in which a similar pattern of recruitment across sites was observed between 1997–1998 and 1999–2000 but was different when comparing other years (Table 3). Moreover, there was no detectable latitudinal trend in the direction nor the magnitude of interannual differences for any of the mussel species.

Among-site variability in recruitment of mussel and barnacle species was larger than among-year variation, as revealed by coefficients of variation calculated across the 3 yr and among all study sites (Table 5). The same trend was observed in all species, but it was particularly striking for barnacles and *P. purpuratus*, for which recruitment rates were on average between 2 and 2.5 times more variable among sites than among years. A complete analysis of spatial and temporal variation in recruitment time series will be presented elsewhere.

Table 3. Pearson correlation coefficients and significance (in parentheses) comparing mean recruitment rates per site from year to year. Significantly positive correlation indicates maintenance of among-sites pattern. Boldface figures indicate significant correlations at $\alpha = 0.05$.

	1997–1998 vs. 1998–1999	1998–1999 vs. 1999–2000	1997–1998 vs. 1999–2000
Chthamaloid barnacles	0.71 (**0.0067**)	0.77 (**0.0019**)	0.46 (0.1366)
Perumytilus purpuratus	0.87 (**0.0011**)	0.93 (**0.0001**)	0.96 (**0.0001**)
Semimytilus algosus	0.75 (**0.0131**)	0.86 (**0.0014**)	0.60 (0.0691)
Brachidontes granulata	0.17 (0.6401)	−0.24 (0.5054)	0.71 (**0.0221**)

The patterns of interannual variability described above for mussels and barnacles were not affected by the specific months included in the analyses. That is, similar trends (or lack thereof) were observed when using our functional classification of years following the months of El Niño anomaly in central Chile or whether the calendar year was used. Also, selecting only the 4 months of maximum El Niño effect, October–January, did not alter the conclusions.

Recruitment and ENSO indices—To look at the potential association between El Niño and OET indices versus recruitment of barnacles and mussels across the entire region, we rescaled recruitment at each site as the percentage of the maximum recruitment observed throughout the time series at that site. When expressing recruitment in this manner and pooling all sites together, we found no pattern of association between El Niño or upwelling indices and barnacle recruitment (Fig. 7a). For instance, the maximum barnacle recruitment ever registered at some sites was observed during months of intense El Niño (e.g., negative SOI values), but at many other sites, maximum recruitment was observed in periods of nearly normal or La Niña conditions (Fig. 7a). Examining the association between recruitment and El Niño indices for each site using the entire time series of barnacle recruitment (April 1997–May 2000), recruitment rates appeared weakly but significantly correlated to the intensity of El Niño/La Niña expressed by the MEI index only at two close sites (ECIM-Norte: $r = -0.36$, $P = 0.0293$; ECIM-Sur: $r = -0.35$, $P = 0.0343$), but a Bonferroni correction for multiple comparisons (corrected $\alpha = 0.005$) rendered these correlations nonsignificant. No other correlation with MEI, SOI, or OET was observed.

No associations with El Niño or OET indices were observed in recruitment of *S. algosus* or *B. granulata* when pooling all sites across the region (Fig. 7c,d). Separate correlations between recruitment of these mussel species and SOI and MEI indices for each site evidenced significant association at six sites, but the direction of change (positive or negative with respect to El Niño intensity) was not consistent among them. Only one, a negative correlation with MEI values at ECIM Sur (ES) remained significant after Bonferroni correction.
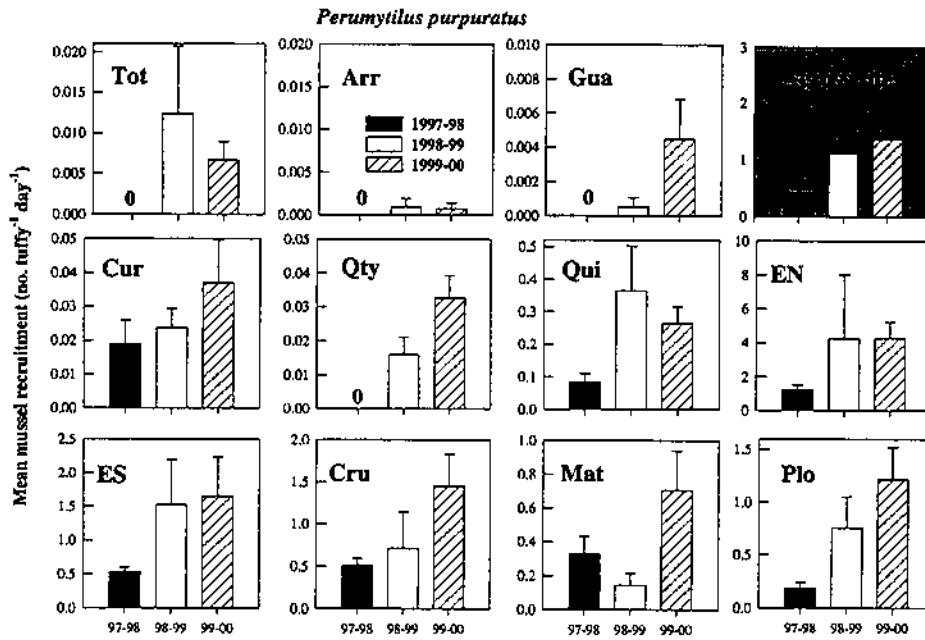
Fig. 4. Mean (± 1 SE) yearly recruitment rates of the mussel *Perumytilus purpuratus* at study sites for 1997–1998, 1998–1999, and 1999–2000. Sites are ordered north to south going from left to right and top to bottom panels. Note the different *y*-axis scales among panels used to highlight among-year differences within each site. The shaded panel on the top right corresponds to yearly averages (±SE) across all sites, including those with zero recruitment. Site abbreviations as in Fig. 1.

In contrast to barnacle and other mussel species, the depression caused by El Niño on *P. purpuratus* recruitment across all sites in the study region was apparent both with SOI and MEI indices (Fig. 7b). During months of intense El Niño, no site exhibited more than 60% of the maximum recruitment observed under either normal or La Niña conditions. Correlations between monthly mussel recruitment and monthly values of SOI, MEI, and OET for each site

Table 4. (A) Two-way ANOVA comparing mussel recruitment rates across sites and among years (log-transformed data). A separate analysis was conducted for each species. (B) Direction of interannual change at each study site from Tukey's multiple comparison tests (experimentwise error rate α = 0.05). Only sites with nonzero recruitment were considered. Abbreviations as in Table 2.

(A) Source	*Perumytilus*				*Semimytilus*				*Brachidontes*			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
Site	6	0.446	13.2	0.0001	9	0.377	25.8	0.0001	8	0.0009	4.6	0.0001
Year	2	0.374	9.4	0.0035	2	0.094	1.9	0.1687	62	0.0009	1.8	0.1907
Site × Year	14	0.040	1.2	0.2970	18	0.054	3.7	0.0001	16	0.0005	2.3	0.0031
Residual	178	0.034			240	0.014			208	0.0002		

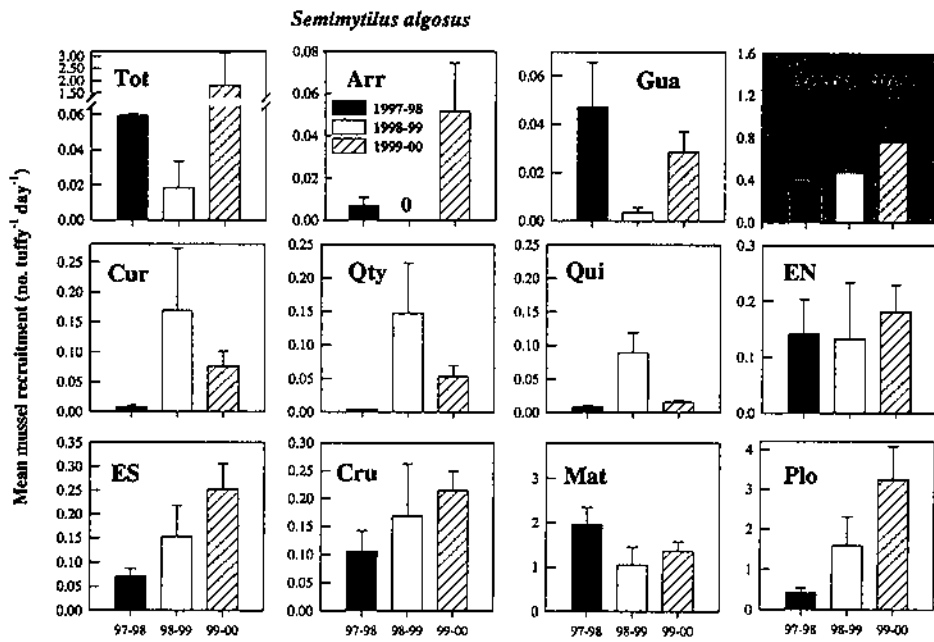| (B) Site	Direction	Direction	Direction
Tot	ni	ns	ns
Arr	ni	ni	ni
Guan	ni	97=99>98	99>98=97
Cur	ns	ns	ns
Qty	ni	ns	ni
Qui	98=99>97	98>97=99	ns
EN	98=99>97	ns	ns
ES	ns	99>97=98	97=99>98
Cru	ns	ns	97=99>98
Mat	ns	ns	ns
Plo	98=99>97	99>97=98	ns

Semimytilus algosus

Fig. 5. Mean (±1 SE) yearly recruitment rates of the mussel *Semimytilus algosus* at study sites for 1997–1998, 1998–1999, and 1999–2000. Sites are ordered north to south going from left to right and top to bottom panels. Note the different *y*-axis scales among panels used to highlight among-year differences within each site. The shaded panel on the top right corresponds to yearly averages (±SE) across all sites, including those with zero recruitment. Site abbreviations as in Fig. 1.

Brachidontes granulata

Fig. 6. Mean (±1 SE) yearly recruitment rates of the mussel *Brachidontes granulata* at study sites for 1997–1998, 1998–1999, and 1999–2000. Sites are ordered north to south going from left to right and top to bottom panels. Note the different *y*-axis scales among panels used to highlight among-year differences within each site. The shaded panel on the top right corresponds to yearly averages (±SE) across all sites, including those with zero recruitment. Site abbreviations as in Fig. 1.
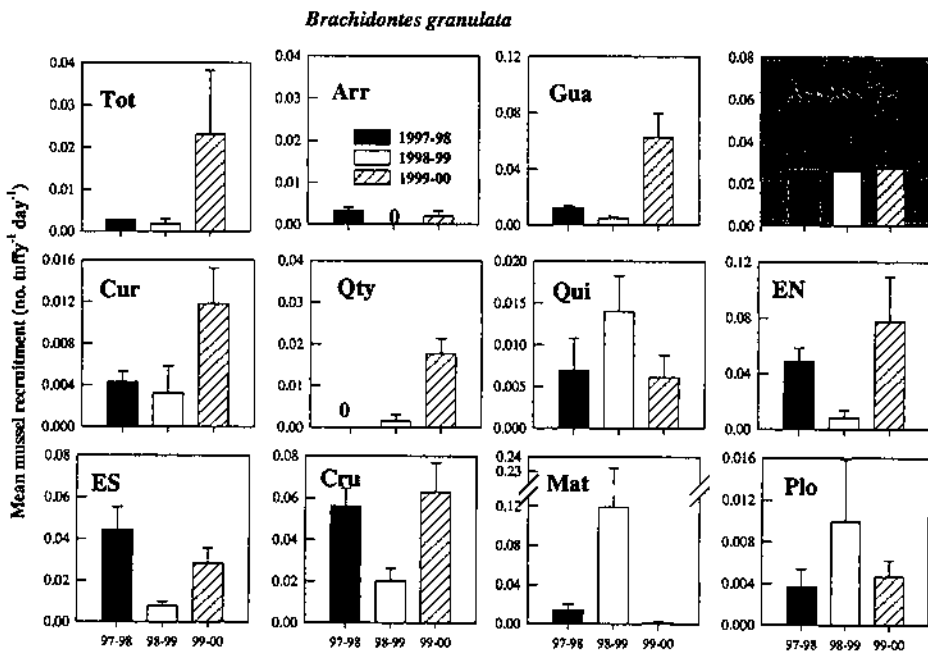
Table 5. Average among-site and among-year coefficients of variation (mean C.V.) and 95% confidence intervals (95% C.I.) for barnacle and mussel recruitment.

Species	Among-site		Among-year	
	Mean C.V.	95% C.I.	Mean C.V.	95% C.I.
Chthamaloid barnacles	223.19	196.72	87.08	63.18
Perumytilus purpuratus	157.50	91.97	75.71	41.98
Semimytilus algosus	180.92	180.62	84.67	63.02
Brachidontes granulata	139.35	250.08	92.08	51.87

were also more consistent for *P. purpuratus* than for any other species. At two sites, recruitment of *P. purpuratus* appeared significantly and positively associated to SOI values (Punta Lobos: $r = 0.43$, $P = 0.0093$; Quisco: $r = 0.48$, $P = 0.0023$) and at four sites negatively associated to MEI (Las Cruces: $r = -0.33$, $P = 0.0441$; ES: $r = -0.38$, $P = 0.0187$; Punta Lobos: $r = -0.55$, $P = 0.0006$; Quisco: $r = -0.48$, $P = 0.0025$), suggesting lower recruitment when El Niño conditions intensify. Three of these correlations were significant after Bonferroni correction (corrected $\alpha = 0.005$).

Discussion

Along the coast of central and northern California, Connolly and Roughgarden (1999) and others (Roughgarden et al. 1988; Ebert et al. 1994) have shown consistent patterns of interannual variation in barnacle and sea urchin recruitment produced, apparently, by El Niño events (Ebert et al. 1994; Connolly and Roughgarden 1999; see also Roughgarden et al. 1988). Our results along the coast of central Chile show that recruitment rates of two barnacles and two intertidal mussel species were not significantly altered by the strong 1997–1998 El Niño or by the weak La Niña conditions that ensued. Recruitment of the competitively dominant intertidal mussel, *P. purpuratus*, exhibited significantly lower recruitment across the region in the 1997–1998 El Niño than during the same months the following 2 yr. We interpret this result as a weak, but significantly negative, effect of El Niño on recruitment of this species. However, when examining individual sites, significant interannual changes were observed at only three of seven sites, and although no recruitment of *P. purpuratus* was observed in the three northernmost sites in 1997–1998, recruitment rates at these sites in subsequent years were among the lowest recorded for the study region. Therefore, it appears that El Niño did reduce average recruitment rates of *P. purpuratus* across the entire study region (Fig. 7b).

The main goal of this study was to evaluate whether an El Niño event produced a clear, and therefore geographically and temporally predictable, signal in recruitment to benthic populations. From this point of view, mean or total recruitment measured over the entire recruitment season of the species, as in this study, will be the most sensitive variable determining dynamics of adult populations and communities (Sutherland 1990). As indicated earlier, our calculations of mean recruitment encompassed the recruitment season of the species, thus representing well the total recruitment for that

year. The relatively low frequency (ca. monthly) of our recruitment time series compromises our ability to resolve potential El Niño effects on individual settlement events. However, if such effects occurred, our results showed that depression or enhancement of settlement events did not produce differences in recruitment at the end of the month in all species studied, except *P. purpuratus* (Fig. 7). It must be noted that monthly recruitment rates might not represent well the addition of all settlement events occurring in the time elapsed between successive samplings (replacement of collectors), which probably also varies from species to species because of differences in rates of mortality and gregarious settlement. However, given the roughly similar sampling times throughout the study period (1997–2000) and the consistency of the settlement substrata across sites and years, it seems unlikely that these effects could substantially alter the results presented here.

Because one of the strongest and more general effects of El Niño in the southeastern Pacific is the reduction of phytoplankton biomass (Avaría and Muñoz 1987; Thomas et al. 2001), a distinct possibility is that low food availability produced unusually high larval mortality of *P. purpuratus*, which in turn led to overall lower recruitment rates across the region. Indeed, experiments conducted at five sites within the same study region showed that the 1997–1998 El Niño had significantly negative effects on growth rates of intertidal adults of this mussel species (Finke, Navarrete, and Venegas unpubl. data). Available data are insufficient to determine whether cross-shelf larval transport of *P. purpuratus* was altered by El Niño. However, lack of correlation between monthly recruitment rates and either SST or upwelling indices (OET) at any of the 11 sites studied suggests that the upwelling–relaxation model (e.g., Wing et al. 1995; Connolly and Roughgarden 1999) does not strongly determine recruitment of this species in central Chile. Higher frequency data and in situ measures of wind stress are needed to evaluate this proposition.

Less coherent patterns of interannual variation were observed in the other two intertidal mussel species, for which the direction of the few significant interannual changes varied across sites. This suggests that the processes determining year-to-year variation in recruitment of these species are site-specific and not geographically coupled by the temporal changes in larger scale oceanographic processes, such as El Niño.

Clearly, different patterns were found in the effects of El Niño on intertidal barnacle recruitment in central Chile and in those observed in central and northern California (Roughgarden et al. 1988; Connolly and Roughgarden 1998). Using basically the same methodology to that used here, and with a geographically similar scope and intensity, Connolly and Roughgarden (1999) showed that the 1997–1998 El Niño produced increased barnacle recruitment across northern and central California. The mechanism producing such changes seems to be related to the weakening of upwelling-favorable winds during El Niño, which have been shown to increase the frequency of recruitment pulses of barnacle and other invertebrates (e.g., Wing et al. 1995; Morgan et al. 2000). No such barnacle recruitment pattern was observed in central Chile. Upwelling indices for the study region were lower in
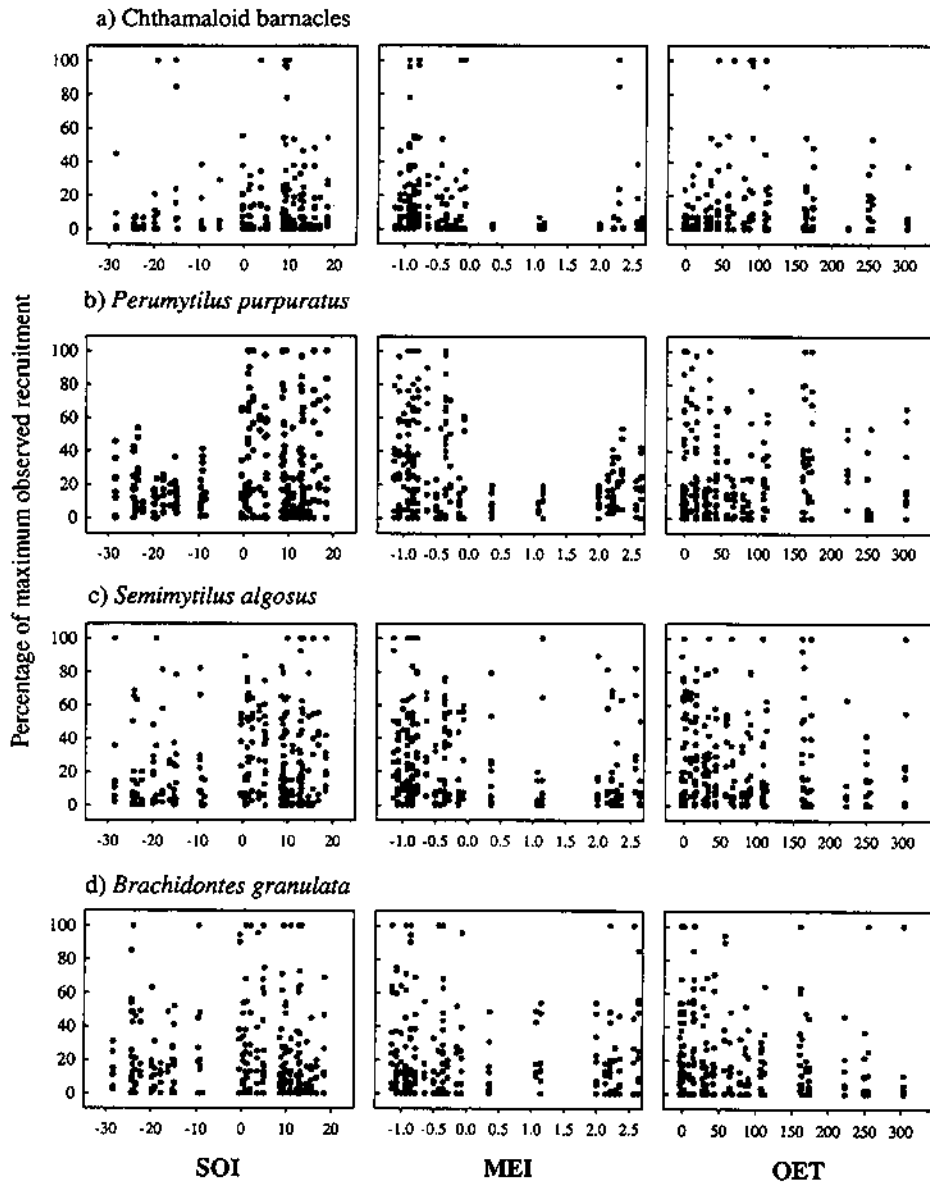
Fig. 7. Scatter plots of monthly recruitment, expressed as the percentage (%) of the maximum recruitment observed at a given site over the course of the study, versus Southern Oscillation index (SOI), multivariate ENSO index (MEI), and offshore Ekman transport (OET) at 33°S. (a) Chthamaloid barnacles, (b) *Perumytilus purpuratus*, (c) *Semimytilus algosus*, and (d) *Brachidontes granulata*. All sites were pooled to evaluate trends across the region.

1997 than 1998, but similar to those in 1999 and wind stress in northern Chile (ca. 20°S) was not strongly reduced during the 1997–1998 El Niño (Blanco et al. 2001). Thus, it is not clear that El Niño significantly reduces wind forcing and therefore increases the frequency of upwelling–relaxation events along the coast of Chile. Significant among-year differences in upwelling indices did occur (higher OET values in 1998), but unlike the pattern shown by Lundquist et al. (2000) for cancrid crab settlement, these differences were not clearly associated with El Niño and did not lead to

among-year differences in barnacle recruitment. Moreover, lack of consistent trends between recruitment and OET or SST suggests that barnacle settlement does not follow the upwelling–relaxation model in a simple manner. Daily settlement data at one site in central Chile (Las Cruces) also failed to show correlations between settlement and locally measured wind stress/relaxation and temperature (R. Venegas and S. Navarrete unpubl. data). As suggested by Ebert et al. (1994) for southern California, differences in mesoscale alongshore circulation patterns among sites could

swamp the regional signal of El Niño. Recent studies by Lundquist et al. (2000) conducted at one site in central California, but at higher sampling frequency, also suggest that the upwelling–relaxation model and its interaction with El Niño can be much more complex and less predictable than originally envisioned on the coast of California. Another interesting difference between our study and that of Connolly and Roughgarden (1999) is the generally lower interannual variability observed in Chile in comparison to among-site variation (Table 5). This pattern suggests marked spatial differences in transport or retention processes along what appears to be a fairly homogeneous coastline in central Chile. These spatial differences are persistent over time, highlighting the importance of coastal geomorphology. Much more research is needed to determine the processes responsible for regional and interhemispheric differences.

Our results suggest the existence of regional differences in the way large-scale oceanographic anomalies interact with local processes to determine patterns of recruitment of benthic species. In general, the effects of El Niño on recruitment of intertidal species, if any, were not consistent across sites and therefore are unpredictable. The broad similarities of the physical environment along the Pacific coast of both hemispheres (Longhurst 1998) makes such differences particularly intriguing and they deserve further investigation. As more biological and physical data become available, particularly in the southern hemisphere, we will be able to understand the mechanisms behind such differences and regularities.

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Scales of benthic–pelagic coupling and the intensity of species interactions: From recruitment limitation to top-down control

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Large and usually unpredictable variation in species interaction strength has been a major roadblock to applying local experimental results to large-scale management and conservation issues. Recent studies explicitly considering benthic-pelagic coupling are starting to shed light on, and find regularities in, the causes of such large-scale variation in coastal ecosystems. Here, we evaluate the effects of variation in wind-driven upwelling on community regulation along 900 km of coastline of the southeastern Pacific, between 29°S and 35°S during 72 months. Variability in the intensity of upwelling occurring over tens of km produced predictable variation in recruitment of intertidal mussels, but not barnacles, and did not affect patterns of community structure. In contrast, sharp discontinuities in upwelling regimes produced abrupt and persistent breaks in the dynamics of benthic and pelagic communities over hundreds of km (regional) scales. Rates of mussel and barnacle recruitment changed sharply at ~32°-33°S, determining a geographic break in adult abundance of these competitively dominant species. Analysis of satellite images demonstrates that regional-scale discontinuities in oceanographic regimes can couple benthic and pelagic systems, as evidenced by coincident breaks in dynamics and concentration of offshore surface chlorophyll-a. Field experiments showed that the paradigm of top-down control of intertidal benthic communities holds only south of the discontinuity. To the north, populations seem recruitment-limited, and predators have negligible effects, despite attaining similarly high abundances and potential predation effects across the region. Thus, geographically discontinuous oceanographic regimes set bounds to the strength of species interactions and define distinct regions for the design and implementation of sustainable management and conservation policies.

coastal ecosystems | upwelling | community regulation | Chile

Variation in the supply of new individuals to local populations has long been recognized as a major factor controlling species interactions and community regulation in marine ecosystems (1–3). Recruitment variation has generally been thought to add stochasticity to population and community dynamics; however, recent studies using long-term and spatially extensive databases are starting to find persistent regularities in the effect of oceanographic processes on benthic communities. One of these oceanographic processes is upwelling, which can influence larval delivery to coastal habitats (4–7). During upwelling, equatorward winds produce offshore Ekman transport (OET) of surface waters along eastern oceanic boundaries, exporting larvae of coastal organisms that are entrained in the moving waters. Reversals or breakdown of winds bring offshore waters and larvae back to the coastal zone (6–8). Regional gradients in the intensity of wind-driven upwelling that determine the rate of larval recruitment of dominant intertidal invertebrates have been discovered along the south island of New Zealand and the coasts of western North America and South Africa (9–12). Because the rate of recruitment is a major factor controlling the strength of species interactions (13, 14), atmospheric circulation

seems to determine the latitudinal variation in the strength of species interactions over thousands of kilometers (9, 11, 12). Upwelling can be modulated by meso-scale changes in coastal topography (15, 16), and these land features have been associated with spatial patterns of population structure (17–19). However, few experimental studies have directly examined which scales of oceanographic changes are linked to variations in the strength of species interactions (but see ref. 11).

Here, we examine the effects of meso- and regional-scale variation in upwelling along the southeastern Pacific. The evidence supports the hypothesis that abrupt regional-scale discontinuities in oceanographic regimes, but not meso-scale variation, can couple the dynamics of benthic and pelagic systems and regulate the strength and outcome of species interactions in intertidal communities. These discontinuities set spatial limits to ecological generalizations derived from field experiments.

Methods

Mussels, *Perumytilus purpuratus*, and chthamaloid barnacles are dominant competitors for space in the mid and high intertidal zones of southeastern Pacific shores, respectively, capable of excluding other species from the primary substratum and thereby affecting the entire intertidal community (20–22). These sessile invertebrates have broadly dispersing pelagic larvae, whose return to the adult habitat depends on cross-shelf transport processes and is often highly variable over space and time (17, 23). We characterized the patterns of recruitment of these species at 14 sites spread >900 km of coastline in central Chile between 29°S and 35°S during 72 months (January 1998 to December 2004). In addition, to evaluate in more detail the effects of variation in upwelling intensity, between 2002 and 2003, we sampled four additional sites toward the center of the study region (Fig. 1a). Thus, we had similar information for a total of 18 sites across the region. Recruitment of mussels and barnacles was quantified on larval collectors deployed over 20- to 50-m transects on wave-exposed benches at each study site at the mid and high intertidal zones, respectively (23, 24). Barnacle recruitment plates and mussel recruitment pads were replaced every 25 to 70 days. Two common species of chthamaloid barnacles are found in the upper intertidal zone at roughly similar abundances, *Jehlius cirratus* and *Notochthamalus scabrosus*. They both recruit and survive on the recruitment collectors, but they cannot accurately be identified to species at small postmetamorphic size. Thus, we pooled both species of barnacles
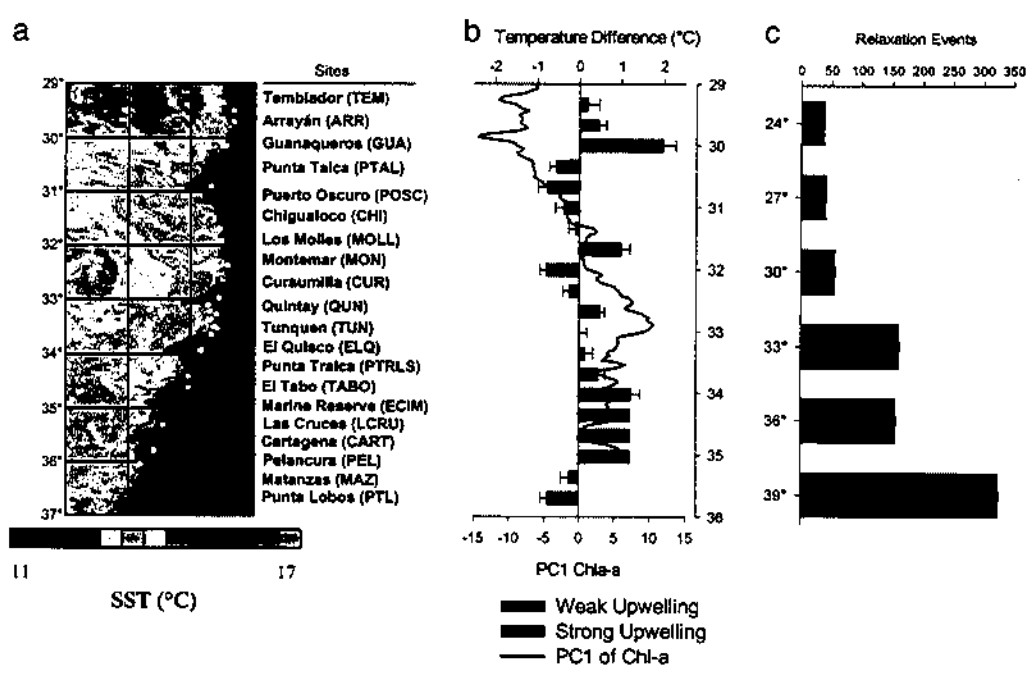
Fig. 1. Spatio-temporal oceanographic and biological patterns across the region. (a) Selected AVHRR satellite image for the study region showing spatial structure in SST during November 1999 and the locations of study sites. Abbreviations of sites listed on the right as used in other figures. (b) Mean ± SE difference in SST between pixels 2 km and 25 km offshore in front of each study site. Negative values indicate strong upwelling with water nearshore colder than offshore. The line superimposed on the figure is the first empirical orthogonal function (principal component) of chl-a concentration (mg/m³) for the study region. Data were 8-day averages of SeaWiFS satellite images every 4 km alongshore between September 1997 and August 2001. (c) Frequency of relaxation events (OET ≤ 0) across the region based on 6-hourly observations for austral spring–summer 2000–2001 and 2001–2002.

in analyses. To characterize patterns of intertidal abundance (cover) of mussels and barnacles, between spring and summer of 2001 and again in 2003, we sampled the low, mid, and high intertidal zones at each of the 18 study sites for which we had recruitment data and five additional sites interspersed among the former (Fig. 1a), which provided better spatial coverage. Between 7 and 12 50 × 50-cm quadrats with 81 intersection points were sampled along 20- to 50-m-long transects at each of three benches separated by 50–400 m.

We identified the main spatial scales of variation in hydrographic conditions across the region by using different types of information. The spatial structure of sea-surface temperature (SST) was obtained from 62 advanced very high resolution radiometer (AVHRR, 1-km resolution) images. For each of the 23 sites, we calculated the mean difference in SST between a station ca. 2 km offshore and that observed 25 and 50 km offshore. Colder temperatures inshore are indicative of strong coastal upwelling whereas warmer temperatures reflect weak upwelling conditions, and the latitudinal gradient in SST does not affect the classification of sites (25). This classification of sites as having strong or weak upwelling was contrasted with the pattern of *in situ* measured temperature recorded by loggers (StowAway Tidbit, Onset Computer Corporation, Bourne, MA; ±0.01°C precision) deployed at a 1- to 2-m depth ($n = 13$ sites). These loggers registered SST between 5- and 20-min intervals from 1997 through 2004 and are well correlated with nearshore AVHRR temperature (17). Monthly upwelling indices (OET) spanning our study region from 1997 to 2000 are publicly available from the National Marine Fisheries Service Pacific Fisheries Environmental Laboratories of the National Oceanic and Atmospheric Administration (NOAA, www.pfeg.noaa.gov). In addition, we obtained 6-hourly OET indices during the spring and summer months, when upwelling-favorable conditions are maximal. The OET is calculated over quadrats of 3° × 3° (30°S,

33°S, and 36°S) and is based on the average wind field and the Coriolis parameter for that latitude. Time series of coastal chlorophyll-*a* (chl-*a*) concentration (mg/m³) for the study region, from 1997 to 2001, were obtained from 8-day composites of the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS, 4-km resolution) satellite (26).

To distinguish spatial correlation resulting from spatial trends in recruitment and adult abundance (cover) across the entire region, from those resulting from site-to-site variation, we decomposed spatial variability into its trend (i.e., variation common to several sites adjusted throughout the study region) and the residual variation (site variation not accounted for by the trend). A locally weighted scatterplot smoothing (LOWESS) (27) was fit separately to the spatial patterns in recruitment and cover of each species as a function of the distance (km) to the southernmost site (Fig. 1a) for the smoothing factor that produced normal and symmetric LOWESS residuals and was independent from geographic distance (Kolmogorov–Smirnov Tests, $P > 0.05$) (28). We then calculated the correlations between recruitment and cover based on the regional-scale trend (predicted LOWESS), site-variation (residuals from LOWESS), and the raw data. A sequential Bonferroni correction (29) was applied to adjust significance levels for multiple comparisons. Because LOWESS smoothing will produce spatially autocorrelated data (regional trends), the effective degrees of freedom for significance tests of cross-correlations can be lower than the standard tests (30, 31). Therefore, significance values close to 0.05 should be taken with caution. The effect of meso-scale variation in upwelling intensity (strong versus weak) was evaluated by using one-way ANOVA on the raw data and on the residuals of LOWESS regression, using sites as replicates.

Two field experiments were conducted between 1999 and 2000 to quantify spatial variation in the strength of predator–prey interactions. We concentrated in the predator–mussel interac-

tion because its outcome is critical for the entire intertidal community (21, 22, 32). First, to evaluate whether regional changes in adult mussel abundance were the result of variation in predation intensity caused by changes in predator abundances and/or per capita predation rates, or by higher mussel mortality due to abiotic conditions, we transplanted mussels from a common source to different sites. Ten clumps of 100 juvenile *Perumytilus* mussels each were transplanted to the mid-low intertidal zone at each of four sites [Matanzas (MAZ), Marine Reserve (ECIM), Las Cruces (LCRU), and El Quisco (ELQ); Fig. 1] located south of 32°S, where mussel recruitment rates are relatively high, and three sites [Temblador (TEM), Punta Talca (PTAL), and Guanaqueros (GUA); Fig. 1] north of 32°S, where mussel recruitment rates are relatively low. Plastic mesh was used to hold mussels against the rock surface to allow them to reattach and to prevent predation. After two months, the mesh on five randomly chosen clumps per site was removed, exposing half of the mussel clumps to predators while the other half were protected by dome-shaped mesh predator exclusion cages. Mussel survival was monitored every 2 days for the first week and every 15 days thereafter. We present mussel survival in the two treatments after 50 days from the beginning of the experiment. In such experiments, in which a fixed number of prey are followed over time, mussel survival can be described by $N_t = N_0 e^{(-\alpha P + m)t}$, where N_t is the number of live mussels at time = t, N_0 is the initial number of mussels transplanted, αP is the total or population predator–prey interaction strength, and m is the natural mussel mortality rate (33, 34). Calculating the slopes of the regressions between $\mathrm{Log}_e(N_t/N_0)$ and time for each replicate under different treatments and using average predator density as an estimate of P allow estimation of all mussel mortality terms (35, 36).

The mussel transplant experiment evaluated whether there was geographic variation in natural mussel mortality (m) or predation intensity (αP). To determine the role of these factors in the regulation of mussel populations, a predator exclusion experiment that allows mussels to settle at natural rates must be conducted. Therefore, we set up a series of replicated predator-exclusion experiments at five sites with similar physical characteristics. Stainless-steel cages, control plots, and roofs (procedure controls) were used to exclude predators, allow all predators to access experimental plots undisturbed, and control for cage artifacts, respectively. Five replicates of each treatment were deployed over short turfs of the alga *Gelidium chilense*, which mediates mussel recruitment to the intertidal zone. Experiments were conducted in 1999 and again in 2000 at three sites south of 32°S (ECIM, Las Cruces, and El Quisco) and two to the north (Punta Talca and Guanaqueros). In all cases, no differences were observed between roofs and control plots ($P > 0.05$). Thus, for simplicity, we present results for controls and treatments.

Results and Discussion

Our analyses revealed two scales of variation in hydrographic conditions associated directly or indirectly with variation in upwelling activity across the region. First, coastal topography and coastline orientation are associated with meso-scale spatial structure in SST, which is apparent in AVHRR satellite images (Fig. 1a). Several studies in central Chile have shown that colder inshore waters in the images correspond to areas of intensification of wind-driven upwelling, whereas warmer waters correspond to areas of weak upwelling or upwelling shadows, which often occur <15 km away from upwelling centers (17, 37, 38). Superimposed on this meso-scale variation in upwelling intensity, which occurs irregularly across the entire region (Fig. 1b), there is a clear regional-scale discontinuity in oceanographic regimes. Due to the seasonal migration of the Pacific anticyclone and continental topography, upwelling-favorable winds are generally weaker, but more persistent throughout the year north of

~32°S (39–41). Indeed, OET is upwelling-favorable year-round north of ~30°S–32°S, whereas they are downwelling-favorable (OET ≤ 0) during austral winter south of this latitude (39). Analysis of high-frequency, 6-hourly upwelling indices during spring and summer months, when upwelling and therefore offshore transport are more intense, shows that there are fewer episodes of upwelling relaxation to the north of 32°S (Fig. 1c). Changes in upwelling intensity and oceanographic regimes can have important effects on larval transport to the shore (15, 42).

Results from the long-term recruitment monitoring study showed high among-site variation, but also a sharp, coincident geographic discontinuity in average recruitment rates of mussels and barnacles at about latitudes 32°S–33°S, with generally lower recruitment to the north (Fig. 2 a and b). Regional trends in barnacle and mussel recruitment were highly correlated, whereas site residuals were not (Table 1), suggesting that barnacle and mussel recruitment are similarly affected by regional-scale processes, but not by local, site-specific factors. Field surveys of adult cover of these same sessile species showed that the abrupt changes in recruitment rates were mirrored by persistent breaks in intertidal community structure. Mussel cover in the mid zone and, to a lesser extent, barnacle cover in the high intertidal zone changed abruptly at ~32°S–33°S (Fig. 2 c and d), with larger abundances to the south than to the north of this latitude. Low mussel cover at the marine reserve of ECIM, where mussel recruitment is high (Fig. 2), is attributable to locally intensified predation by the commercially collected gastropod *Concholepas concholepas*, which is protected in the reserve (21). Barnacle and mussel cover were highly correlated in terms of both their regional trends and site residuals (Table 1), suggesting that regional-scale processes as well as site-scale postrecruitment factors affect adult cover of these species in similar ways. Recruitment was highly correlated with adult cover when we examined regional trends for mussels and barnacles, presumably as a result of these groups sharing similar spatial structure across the study region (Table 1). These strong correlations indicate that, over scales of hundreds of kilometers, recruitment limitation dominates the patterns of adult abundance. In contrast, site residuals of recruitment and cover showed no correlation (Table 1), suggesting again that postrecruitment processes that vary over scales of sites are the main determinants of local adult abundance. Strong correlations between recruitment and intertidal abundance are observed in the region of low recruitment to the north of 32°S ($r = 0.91$ and 0.80, for mussels and barnacles, respectively), suggesting that, within this region, intertidal populations are recruitment-limited (3, 43). To the south of this latitude, correlations are weak and nonsignificant ($r = 0.37$ and 0.03, for mussels and barnacles, respectively).

Although regional-scale discontinuities in upwelling regimes had profound effects on mussel and barnacle recruitment, apparently leading to similar patterns of regional variation in intertidal abundances, meso-scale variation in upwelling intensity had only weak effects on these groups. Evaluating the effect of upwelling intensity by using site residuals from LOWESS regressions reduced the large variability observed across sites within upwelling condition produced by the strong regional trends (Fig. 2 *Inserts*). Analysis of these site anomalies showed that recruitment and cover of mussels and barnacles were slightly higher (lower) than expected at weak (strong) upwelling sites, as predicted by the upwelling-relaxation model (13). However, these differences were small and significant only for mussel recruitment (Fig. 2).

If discontinuous oceanographic regimes cause major breaks in benthic community dynamics, one would expect to detect this signal in the pelagic environment as well. A sharp change in chl-*a* concentration at ~32°S has been reported in nearshore waters (39, 44). Similarly, empirical orthogonal function analysis of SeaWiFS
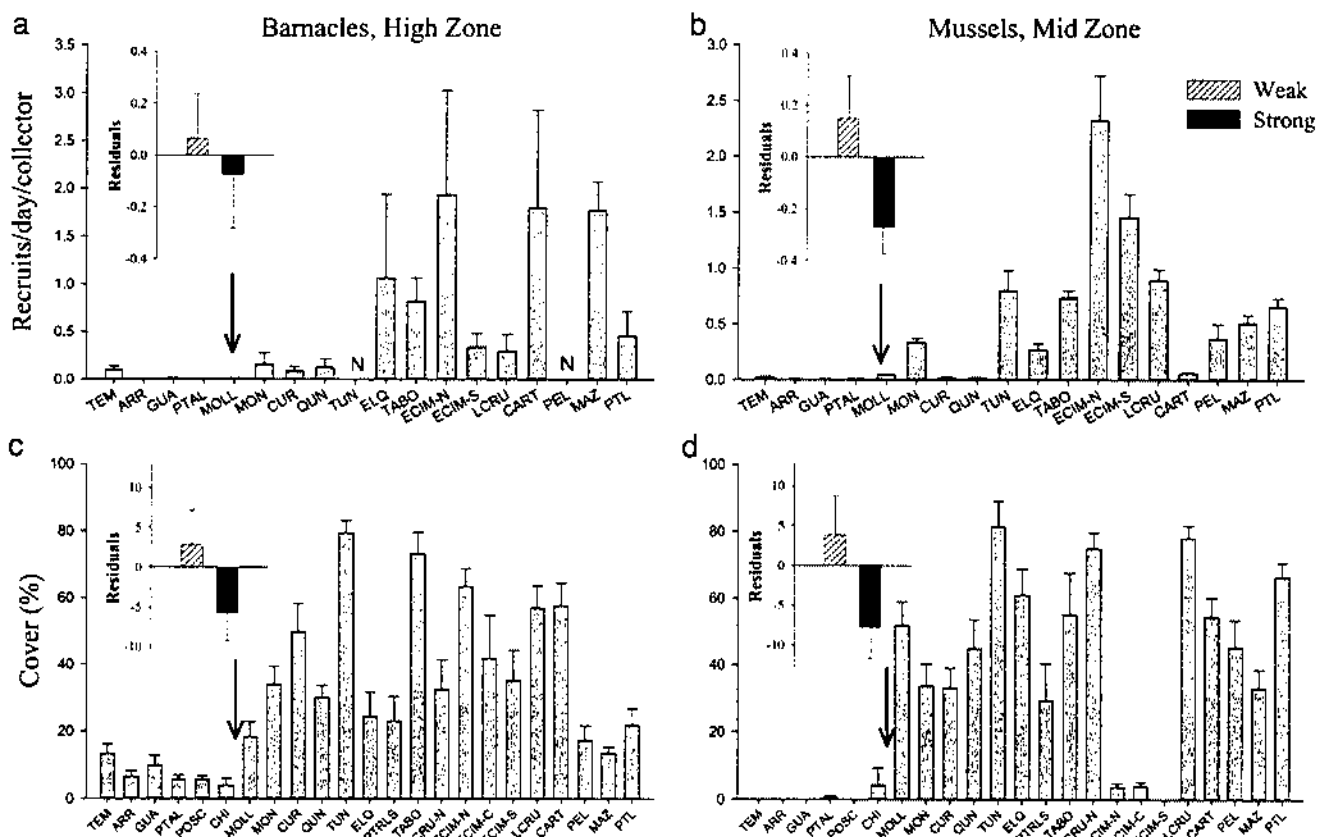
Fig. 2. Patterns of recruitment and adult abundance across the region. (a and b) Monthly recruitment to collectors, standardized by days of exposure and averaged from January 1998 through December 2004 at each study site for chthamaloid barnacles *J. cirratus* and *N. scabrosus* in the high intertidal zone settling on 10 × 10-cm Plexiglass plates coated with safety walk (a) and *P. purpuratus* mussels in the midzone settling on plastic Tuffy pads (b) (23). (c and d) The intertidal adult abundance estimated from replicated transects and 50 × 50-cm quadrats at the same sites and tidal heights for barnacles (c) and mussels (d). The segmented lines show location of the geographic discontinuity. The arrows indicate the position of Los Molles, the site located at 32°S. (*Inserts*) The average cover (a and b) or recruitment (c and d) of barnacles and mussels at sites of strong (black bars) and weak (hatched bars) upwelling, after removing the regional trend in the data by using LOWESS regression (residuals). Error bars in these panels represent variation across sites within upwelling-intensity condition.

chl-*a* time series showed a marked shift in the intensity of the annual cycle of surface chl-*a* concentration around 32°S (Fig. 1*b*). These striking coincidences in spatial structure between the benthic and pelagic communities are indicative of strong coupling over regional scales. The sharp spatial transition in phytoplankton biomass and dynamics has not yet been explored in detail, but changes in phytoplankton biomass associated with upwelling dynamics involve changes in phytoplankton species composition and cell size spectrum, which in turn can have important effects on invertebrate larval condition (45). Although our results suggest that adult mussels grow and survive well at sites north of 32°S–33°S (see below), it is possible that the lower phytoplankton availability to the north could lead to a decrease in adult reproductive output. Lower

reproductive output over such an extensive geographic region would reduce total larval production, which in turn could be responsible for low adult abundances.

Results from the mussel transplant experiment showed that transplanted mussels protected from predators survive well at all sites across the entire region (Fig. 3*a*, cross-hatched bars). Natural mortality of mussels in the absence of predators (*m*) was low and similar across sites (*P* > 0.05), suggesting that abiotic factors do not play a major role in the observed pattern of mussel abundance. High mortality of transplanted mussels was observed in the presence of predators at all sites (Fig. 3*a*, filled bars), with the largest interaction strengths (α*P*) inside the marine reserve of ECIM and the management and exploitation area of El Quisco (ELQ), where

Table 1. Pearson correlation coefficients between recruitment and cover of barnacles and mussels based on raw data

Variables	Raw data	Regional trend	Site residuals
Mussel recruitment vs. cover	0.53 (0.0220)	**0.81 (0.0001)**	0.24 (0.3453)
Barnacle recruitment vs. cover	0.31 (0.2736)	**0.67 (0.0081)**	−0.21 (0.4786)
Recruitment of mussels vs. barnacles	0.26 (0.3710)	**0.97 (0.0001)**	−0.42 (0.1310)
Cover of mussels vs. barnacles	**0.67 (0.0025)**	**0.79 (0.0001)**	0.53 (0.0240)

Regional trends fitted by LOWESS regression. Significance of correlations in parentheses. Bold face indicates significant correlations after Bonferroni adjustment.
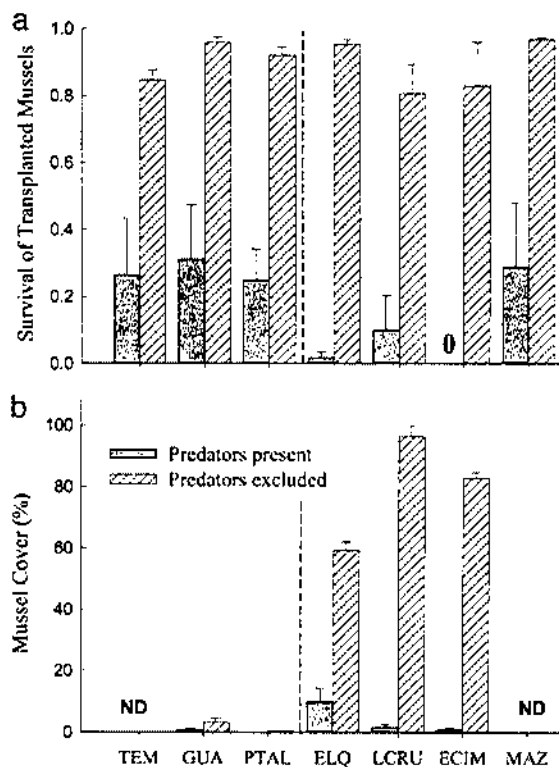
ECOLOGY

Fig. 3. Results of two independent field experiments. (a) Survival of transplanted mussels at sites north (TEM, GUA, PTAL) and south (ELQ, LCRU, ECIM, MAZ) of the recruitment discontinuity observed ~32°S–33°S (segmented line). Bars are average (± SE) survival of mussels in replicated clumps in the presence (filled bars) and absence of predators (hatched bars) after 50 days in the field. (b) Effects of predator exclusions on resultant community structure at a subset of the sites north and south of the discontinuity. Bars are the average abundance of mussels (% cover ± SE) in replicated plots in the presence of predators (filled bars) and in predator exclusions (hatched bars). For simplicity, procedural controls (roofs) are not presented.

harvesting of the carnivorous gastropod *C. concholepas* and other invertebrates is excluded or regulated, respectively (46, 47). No differences were observed between sites located north and south of 32°S. This result suggests that predation intensity can vary among sites but is similar across the geographic discontinuity. Indeed, predator abundance does not vary systematically across the region (25). Probable causes for the lack of a geographic response in abundance of the major mussel and barnacle predators are that their larvae are not affected by the same oceanographic processes influencing barnacle and mussel larvae and that they are generalists that can switch to feeding on other prey and that their own recruitment is not directly dependent on local prey consumption. In

addition, seastars and gastropod predators are long-lived and could withstand several years of low prey recruitment (48).

Do discontinuous oceanographic regimes ultimately modify the outcome of species interactions and the regulation of benthic communities? In the predator-exclusion experiments, mussels covered between 60% and 95% of the primary space within the first 3 months of initiating the experiments at sites south of 32°S (Fig. 3b) out-competing other invertebrate and algae species from the rock. In contrast, at the two northern sites, neither mussel nor barnacle cover increased in predator exclusion plots. At the three sites south of 32°S, prey abundances in exclusions differed from those in controls ($P < 0.001$), whereas no differences were found at northern sites ($P > 0.05$). Thus, predators play a major role in the regulation of intertidal communities south of ~32°S–33°S, but their role is negligible to the north, at least up to around 28°S.

The paradigm of top-down control of intertidal communities along the coast of Chile (20, 22, 32) was built on field experiments conducted in a limited geographic range in central Chile, at around 33°–34° and a few places in the south (49). Similar conclusions in other parts of the world are similarly based on geographically restricted studies where logistic limitations have constrained the geographic extent of ecological studies. The use of the comparative experimental approach (24) and the recently developed availability of long-term, spatially extensive data sets of recruitment and oceanographic conditions are starting to reveal more persistent and regular patterns than many envisioned a decade ago. With similar studies elsewhere (11, 12), our results suggest that patterns of species interactions in benthic communities can be bound by regional discontinuities in oceanographic conditions. Discontinuous upwelling regimes also cause major changes in the temporal dynamics of phytoplankton biomass, which in turn can have far-reaching effects in the pelagic food web. It is therefore not surprising that the anchovy fisheries along the coast of Chile and Peru shows a sharp decrease in total captures in an extensive region of the coast north of ~32°S (50). Considerations of the scale and geographic location where oceanographic conditions produce major changes in the pattern of species interactions, like those found here north and south of 32°S, must be incorporated in designing policies for the sustainable management of benthic and pelagic resources, as well as in establishing marine coastal reserves worldwide.

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ECOLOGY

Research

Predator–prey interactions under climate change: the importance of habitat vs body temperature

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Habitat temperature is often assumed to serve as an effective proxy for organism body temperature when making predictions of species distributions under future climate change. However, the determinants of body temperature are complex, and organisms in identical microhabitats can occupy radically different thermal niches. This can have major implications for our understanding of how thermal stress modulates predator–prey relationships under field conditions. Using body temperature data from four different sites on Santa Cruz Island, California, we show that at two sites the body temperatures of a keystone predator (the seastar *Pisaster ochraceus*) and its prey (the mussel *Mytilus californianus*) followed very different trajectories, even though both animals occupied identical microhabitats. At the other two sites, body temperatures of predator and prey were closely coupled across a range of scales. The dynamical differences between predator and prey body temperatures depended on the location of pairs of sites, at the extremes of a persistent landscape-scale weather pattern observed across the island. Thus, the well understood predator–prey interaction between *Pisaster* and *Mytilus* cannot be predicted based on habitat-level information alone, as is now commonly attempted with landscape-level ('climate envelope') models.

The temperature of a plant or animal's body can affect virtually all of its physiological processes (Buckley et al. 2001, Somero 2005). These cellular and subcellular-level processes in turn have cascading effects on the distribution and abundance of organisms and populations and the functioning of ecosystems, and have been the focus of ecological investigation for decades. Moreover, understanding the role of body temperature in driving patterns of organism distribution has taken on a new urgency in the face of global climate change (IPCC 2007) and a pressing need to forecast the impacts of climate change on natural ecosystems (Clark et al. 2001, Helmuth et al. 2006b). This need has given rise to a number of both mechanistic and statistically-based approaches, all with the common goal of explicitly hindcasting and/or forecasting the impacts of climate change on patterns of species distributions and organism abundances (Stockwell and Peters 1999, Porter et al. 2000, Hugall et al. 2002, Pearson and Dawson 2003, Kearney and Porter 2004, Pörtner and Knust 2007).

One of the most commonly used approaches (the 'climate envelope' method) relies on correlations between environmental variables (parameters such as air or water temperature) observed at the current edges of a species range boundary to estimate a species fundamental niche space (Hugall et al. 2002). By extrapolating to future climatic conditions, these approaches predict future range

boundaries by assuming that the current range edge is set by some aspect of climate. Even many individual-based approaches still rely on habitat temperature (usually surface or air temperature) as a starting point, and then predict operative body temperature based on correlation (Buckley et al. 2008, but see Kearney and Porter 2004 for a more mechanistic approach).

As emphasized by Kearney (2006), such 'climate envelope' methods generally assume that aspects of the habitat (such as air or surface temperature) are equivalent to axes of the organism's fundamental niche space (such as body temperature), thus ignoring any details of the organism's interaction with the surrounding environment. In other words, not only is the organism's realized niche space assumed to equal its fundamental niche space, but no consideration is give to the organism itself: estimates of organisms' fitness are based solely on the characteristics of current and future habitat conditions. It has long been known that the body temperatures of ectothermic organisms are driven by multiple, interacting climatic parameters and are often quite different from the temperature of the surrounding air or substrate (Porter and Gates 1969, Stevenson 1985, Huey et al. 1989). The flux of heat to and from an organism is affected by its size, color, morphology, and material properties, and two different ectothermic species exposed to identical climatic conditions

can experience markedly different body temperatures (Porter and Gates 1969, Helmuth 2002). As a result, not only are measurements of habitat temperature (e.g. air or surface temperature) insufficient proxies of a species thermal niche but they also are highly unlikely to serve as effective proxies for the current or future body temperature of more than one species (Helmuth 2002, Fitzhenry et al. 2004). While methods that estimate body temperature based on habitat temperature do allow different offsets for each species, they nevertheless assume that organism body temperature varies linearly with habitat temperature, and that this offset is constant from site to site. In other words, they are based on correlations with habitat temperature.

Recent studies have shown that predictions of the impacts of weather and climate on organismal distributions are fundamentally different when these predictions are based on body temperature rather than on environmental parameters (Hallett et al. 2004, Helmuth et al. 2006a, 2006b). Understanding the effects of weather and climate in driving body temperature is particularly important when examining predator–prey interactions (Durant et al. 2007, Pincebourde et al. 2008). While several recent studies have made significant advances to mechanistically model the effects of climate, and climate change, on the current and future distribution of species ranges by including the direct physiological effects of climate (Porter, et al. 2000, Kearney and Porter 2004) we are just beginning to understand some of the indirect effects of climate on species interactions (Sanford 1999, 2002, Pincebourde et al. 2008). Specifically, most predictions of the effects of climate change on species distributions, and indeed most ecological studies, base estimates of climate-influenced predator–prey interactions on measurements of habitat temperature. Here we show that the relative difference in body temperature between a predator and its prey varies significantly – both quantitatively and qualitatively – between sites despite exposure to identical microhabitat conditions at each site. Importantly, these patterns are unlikely to be predictable in space and time without a mechanistic understanding that includes some prediction or direct measurement of their actual body temperatures in the field. Our results highlight the importance of considering the interaction of an organism's morphology and thermal properties with its surrounding environment in determining body temperature, as well as an organism's physiological response to temperature when forecasting ecological responses to environmental stress. Moreover, they uncover strong landscape-scale variability in the degree to which predators and their prey are coupled in their thermal responses to their ambient thermal environments.

Methods

Study site and organisms

The California mussel, *Mytilus californianus* (hereafter *Mytilus*) forms dense beds in the mid-intertidal zones of rocky shores from Alaska to Baja and is a primary prey species for the predatory seastar, *Pisaster ochraceus* (hereafter *Pisaster*) (Paine 1974, Menge et al. 1994). In the absence of predation or disturbances to control its population size,

Mytilus has been shown to expand its distribution and outcompete all plant and animal species from most of the intertidal zone (Paine 1974, Robles et al. 1995). Unlike *Mytilus*, which is sessile and cannot escape thermal stress, *Pisaster* is mobile. Many intertidal predators show little or no movement during low tide (Newell 1973), and *Pisaster* in particular are inactive during low tide (Robles et al. 1995). Robles et al. (1995) found that *Pisaster* move upshore with the incoming tide to feed and then move downshore before the tide recedes again. They also found that *Pisaster* can move >3 m vertically and >10 m along the rock surface during a single tide before returning to low intertidal levels to rest during low tide. The potential for behavioral thermoregulation in *Pisaster* could thus greatly impact the consumer–resource dynamics, a process that has recently been observed in the interaction between grazing limpets and seaweeds in other intertidal systems (Harley 2003).

We examined temporal and spatial patterns in the body temperature of *Pisaster* and *Mytilus* body temperatures at four sites around Santa Cruz Island, California. Santa Cruz Island is the largest of the Northern California Channel Islands and is located in a region of high oceanographic variability in the Santa Barbara Channel on the northern portion of the Southern California Bight (Fig. 1). A persistent thermal gradient exists along the channel where higher sea surface temperatures in the southeastern portion of the channel are associated with the influx of north-flowing warm subtropical water. On the northwestern part of the channel, equatorward, upwelling-favorable winds are topographically intensified around Point Conception, and much cooler ocean temperatures prevail due to the intense advection of cold water from the nearby Point Conception and Point Arguello upwelling centers (Winant et al. 2003). These oceanic characteristics produce persistent differences in ocean temperature ($\sim 2°C$) and fog formation between the southeastern and northwestern sides of the island
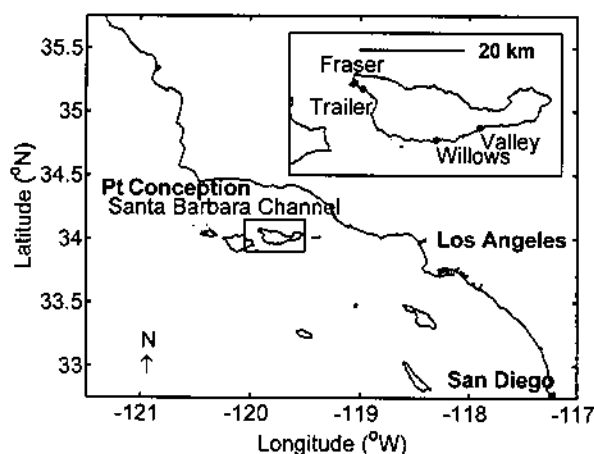
Figure 1. Location of the four study sites around Santa Cruz Island. The sites represent extremes along a steep gradient in oceanographic conditions observed along the island shores with sites located on the western end of the island (Fraser and Trailer) experiencing cooler ocean temperatures than the sites located on the southwestern side (Valley and Willows). Detailed sea surface temperature satellite imagery highlighting the thermal gradient can be found at Otero and Siegel (Otero and Siegel 2004).

(Broitman et al. 2005, Fischer and Still 2007). We selected four intertidal study sites that represent the extremes of this environmental gradient (Fig. 1, inset): two sites on the northwest shore of the island (Fraser and Trailer) and two on the southeastern shore (Willows and Valley). The number and locations of sites were limited by accessibility and other logistical constraints, and sites were selected to be as similar as possible in terms of geomorphology, wave exposure, and habitat type.

Instrumentation

We recorded temperatures corresponding to the body temperatures of *Mytilus* and *Pisaster* using pairs of biomimetic temperature loggers during the Boreal summer of 2006 (12 July to 10 October). As is true for the temperature of an organism's body, the temperature recorded by a sensor is significantly affected by the morphology, surface color, wetness and thermal properties (thermal inertia) of the instrument, and failure to match these characteristics to those of the intertidal animal of interest have been shown to lead to errors of 14°C or more (Fitzhenry et al. 2004). We thus used sensors designed to match the thermal character-istics of *Mytilus* and *Pisaster*. These instruments have previously been shown to record temperatures that are within 2-2.5 and 1°C of adjacent mussels and seastars, respectively (Fitzhenry et al. 2004, Szathmary et al. in press). Loggers were located in the mid intertidal zone, corresponding to the tidal elevations where maximal densities of each species are observed in the field (Blanchette et al. 2006). Loggers recorded temperature every 30 min and were serviced every ~40 days. In the case of seastar biomimetic loggers, the microhabitat location of sensors was intended to mimic the temperatures of animals aerially exposed while they are feeding on mussels rather than when they are concealed in crevices (Pincebourde et al. 2008). Thus, whenever possible, seastar loggers were deployed directly adjacent to biomimetic sensors mimicking mussel body temperatures so that each sensor was exposed to similar microhabitat conditions. In all, cases pairs of seastar and mussel loggers were deployed within ~20 cm vertical elevation of one another at each site. Biomimetic loggers were sometimes lost haphazardly across sites and were replaced during the next visit to the site.

Data analysis

The primary goal of our study was to determine if subtle variations in local weather affected body temperatures of predator and prey differently at each of four different sites on Santa Cruz Island. We were not able to perform a spectral analysis to establish the pattern of dynamical coupling between both records using the cross-coherence function because of repeated instrument loss and the short study period (Bendat and Piersol 1986). Alternatively, we examined the temporal cross-covariance between the body temperatures of *Mytilus* relative to the body temperatures of *Pisaster* at multiple temporal scales (i.e. frequencies). To remove serial correlation, we transformed all temperature

time series to anomalies through first-order differencing before calculating statistics (Helmuth et al. 2006a). We examined patterns of thermal covariance over different temporal scales filtering the time series from 0.5 to 24 h using a 30-min running-mean filter (48 scales) and calculating Kendall–Tau (R_τ) cross-correlations between seastar and mussel body temperatures lagging the filtered anomaly time series between ±240 min (±4 h or 8 lags back and forward in time plus lag-0, e.g. 17 lags). Negative lags in the cross-correlation correspond to the seastar temperature anomalies leading the correlation (e.g. the seastars heating or cooling before the mussels), while positive lags corresponded to the mussel temperature anomalies leading the correlation. We computed R_τ by sampling the time series at the frequencies prescribed by the filter lengths across all scales. Then, using Monte Carlo simulations, we calculated significant cross-correlations through the standard error distribution of R_τ (Sokal and Rohlf 1981). We used a Bonferroni correction for the multiple comparisons (48 time scales × 17 lags) to adjust our significance levels accordingly ($\alpha < 0.05$). In this way, we are estimating concordance (Kruskal 1958) between the two signals at different lags and time scales, and using simulations to establish their significance and accommodate error in their measurement.

Results

The body temperature of both mussels and seastars (as recorded by biomimetic sensors) showed large amplitude fluctuations during the 40-day study period. However, the body temperatures of seastars were consistently lower than those of adjacent mussels, and their body temperature fluctuations were of smaller amplitude. As expected for intertidal ectotherms, temporal variation in body tempera-ture was dominated by the daily cycle with ca 12 h fluctuations between daily thermal extremes. The periodi-city in the detrended temperature time series was uncorre-lated to the fortnightly tidal cycle at all sites (results not shown). For mussels, oscillations of approximately 8°C were observed at the beginning of the study period at the southeastern sites (Valley and Willows, Fig. 2A–B). The mean body temperature of both mussels and seastars followed a clear spatial gradient with the highest tempera-tures observed at the southeastern sites and the lowest at the northwestern sites. Both mean body temperature and variance in body temperature was higher for mussels than for seastars. For mussels, the largest variances were observed at the sites with the lowest means (Table 1). At the southeastern sites (Valley and Willows, Fig. 2A–B), daily fluctuations in seastar body temperature were smaller than those of their mussel prey. In contrast, at northwestern sites, where overall mean temperatures were lower (Trailer and Fraser, Fig. 2C–D), daily fluctuations were greater between the two species.

The dynamical association between temperature fluctua-tions showed that at the scale of sites, mussel and seastar body temperatures covary over a range of temporal scales (Fig. 3). Temporal decoupling was more pronounced at the
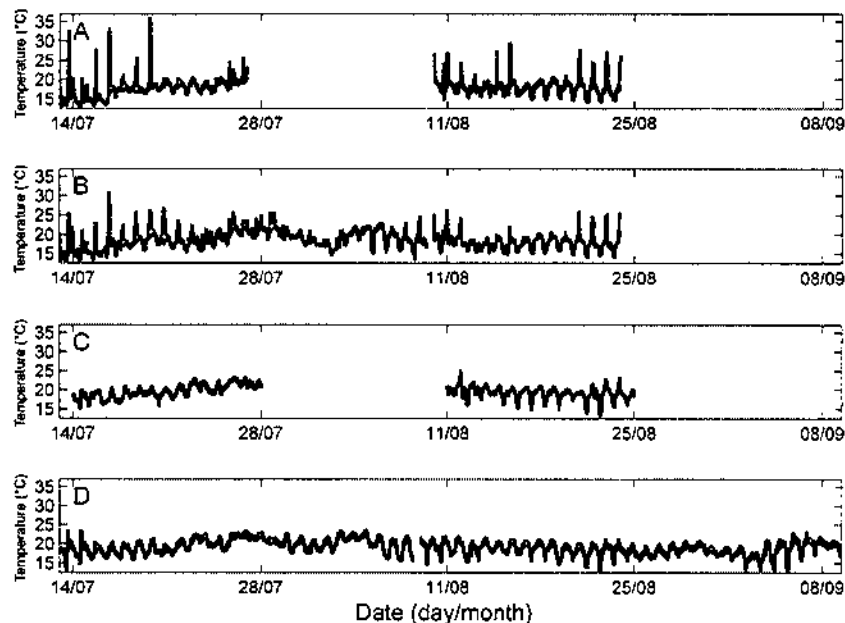
Figure 2. Temperature time series of the seastar *Pisaster ochraceus* (black lines) and the mussel *Mytilus californianus* (gray lines) during the study period (July–August 2006) at the four study sites around Santa Cruz Island in southern California. (A) Valley, (B) Willows, (C) Trailer and (D). Fraser. Note the larger amplitude of the body temperature fluctuations in the mussel. Gaps in the record are due to instrument loss.

northwestern sites, Trailer (Fig. 3C) and Fraser (Fig. 3D), where body temperatures of *Mytilus* and *Pisaster* were not correlated at scales smaller than about 6 h, and instead were restricted to the daily temperature cycle of ~12 h. Predator and prey body temperatures were more tightly coupled at the southeastern sites, with highly significant correlations between 1 and 24 h across a broad range of lags (Fig. 3A–B). At all sites, the body temperature of *Mytilus* led the correlations (i.e. *Mytilus* warmed or cooled before *Pisaster*), more notably at the 12-h scale. The rapid response of *Mytilus* body temperature was apparent through the prevalence of significant correlations at positive lags, particularly in the northwestern sites where temperatures were largely decoupled. The symmetrical pattern of lagged correlation at the 12-h scale observed at the northwestern sites suggested that body temperatures of *Mytilus* and *Pisaster* became coupled only during the extremes of the daily temperature cycle.

Table 1. Body temperature statistics of biomimetic sensors of (A) the seastar *Pisaster ochraceus* and (B) the mussel *Mytilus californianus*. Note that although the southeastern sites (Valley and Willows) are warmer, variances are generally larger at the cooler sites (Trailer and Fraser) for both seastars and mussels.

	Valley	Willows	Trailer	Fraser
(A) *Pisaster*				
Mean	19.053	18.444	18.007	17.209
Variance	2.964	2.948	3.462	2.208
Anomaly variance	0.156	0.132	0.125	0.082
(B) *Mytilus*				
Mean	19.752	19.411	18.726	18.289
Variance	3.230	3.831	7.198	7.139
Anomaly variance	0.167	0.174	0.529	1.210

Discussion

Our results showed that the body temperature of two ectotherms, a dominant intertidal mussel and its keystone seastar predator, can have very different temporal patterns of body temperature across sites, both in terms of maximum temperature and in level of dynamical coupling. Since we used standardized biomimetic sensors to monitor the body temperature of these two species, and controlled for microhabitat characteristics, we attribute the contrasting temperature dynamics to landscape–scale differences in climate and the interaction of climate with the thermal properties of *Mytilus* and *Pisaster* bodies. Importantly, it is highly unlikely that these impacts on predator and prey could be predicted by patterns in habitat alone, which appear to have a large impact on the prey species but only a very subtle impact on the predator.

Differences in climate between the southeast and northwest of the island are associated with the gradient in ocean temperature driven by the oceanographic transition zone around Point Conception (Winant et al. 2003). The gradient is particularly steep across Santa Cruz Island (Broitman et al. 2005), and the two extremes of the island experience different oceanic and atmospheric conditions, with the northwestern extreme being dominated by fog formation and much cooler temperatures, particularly during summer insolation maxima (Fischer and Still 2007). This landscape-level thermal and insolation gradient causes the body temperatures of both ectotherms to be tightly coupled at the warmer southeastern sites but not at the cooler northwestern sites.

Climate is a defining characteristic of these habitats, and it can be described without any reference to the organism. However, the niche space that an organism occupies has
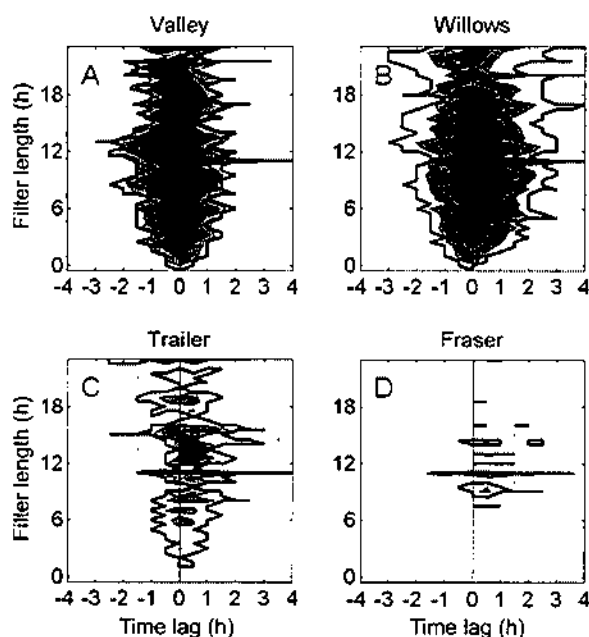
Figure 3. Kendall correlation coefficients showing the dynamical coupling between time series of body temperature anomalies of *Mytilus* and *Pisaster* at the four study sites. (A) Valley, (B) Willows, (C) Trailer and (D) Fraser. Correlations were calculated across a range of lags and filters representing scales of temporal integration. Correlations inside the black contour indicate significant correlations and the greyscale contours, from black to white, indicate the magnitude of significant correlations (0.95, 0.75, 0.65 and <0.65, respectively). Positive lags correspond to *Mytilus* body temperature anomalies leading the correlation (*Mytilus* warming or cooling before), while negative lags indicate *Pisaster* leading. Significant correlations are always maximal around lag 0 and lag 1 showing that the *Mytilus* time series usually led the correlation. Highly significant correlations extend into positive and negative lags at the 12 h filter scale indicating that the body temperatures of both species are maximally coupled during the extremes of the daily thermal cycle. The largest degree of coupling is observed on temporal scales (filters) above one hour while in Fraser, the coolest site, temperatures are significantly coupled around the extremes of the daily cycle. Note the contrasting pattern of the overall dynamical coupling with the southeastern (warmer) sites showing greater coupling between predator and prey temperatures than the northwestern (cooler) sites.

more dimensions than climate. For example, the 'environment' cannot be described without reference to a particular organism (Kearney 2006). These two species occupy basically the same habitat as suggested by their overlapping biogeographic ranges and ecological characteristics, but *Pisaster* predation regulates the abundance and vertical distribution of *Mytilus* (Paine 1974, Menge et al. 1994). Also, it is necessary to understand how morphology, physiology, and especially behavior, determine the kind of environment an organism experiences when living in a particular habitat to define its niche space. *Pisaster* is mobile and has the ability to behaviorally thermoregulate, and its feeding activity can be modulated by both submerged and aerial body temperature (Szathmary et al. in press). Pincebourde et al. (2008) showed that while *Pisaster* was

unlikely to experience body temperatures close to its lethal limit (35°C) in the field (Fig. 2A), it regularly experienced temperatures that reduced feeding. Chronic exposures (>8 days) to body temperatures above 23°C resulted in a 30–40% reduction in feeding rate on mussels and concomitantly decreased rates of growth. In contrast acute exposure caused increased feeding rates. These laboratory results were supported by field measurements conducted at Bodega Bay, CA, and at Strawberry Hill, OR which showed that the number of exposures to physiologically damaging temperatures varied with tidal height (Petes et al. 2008). These results suggest that despite *Pisaster*'s ability to move, it nevertheless is exposed to varying conditions in the field, which may compromise its ability to feed (Pincebourde et al. 2008). When mussels collected from the mainland near Santa Cruz Island were exposed to a range of aerial body temperatures, mortality rates of 100% were observed for the following condition – body temperatures of 36°C for periods of 2 h or more for 3 days (Mislan unpubl.). Mussel biomimetic logger temperatures at Valley (Fig. 2A) approached 36°C once during this study suggesting that mussels can experience harmful body temperatures at some sites and not others on Santa Cruz Island which is in broad agreement with the mosaic structure of body temperature patterns of *Mytilus* along the coast of western north America (Helmuth et al. 2002, 2006a).

Habitat alone does not determine the distribution and abundance of these two species, and additional explicit mechanisms related to more than one dimension of the species' niche may be required to understand the present and future distribution of *Mytilus* and *Pisaster*. If the predator–prey interaction is included in the calculation of the niche, one can obtain better approximation of the realized niche of either species (Hutchinson 1957, Kearney 2006). We have shown that the temporal dynamics of body temperatures of an ectothermic predator–prey pair can significantly depart under different climate scenarios. Vertical distribution of *Mytilus* may actually expand if atmospheric temperatures in the future are stressful enough to decrease *Pisaster* feeding rates but not high enough to kill *Mytilus* (Pincebourde et al. 2008). Alternatively, a milder atmospheric temperature increase can positively affect *Pisaster* feeding rates and contract Mytilus vertical distribution. Since the vertical distribution of *Mytilus* can have major community-level consequences (Paine 1974), a statistical model describing associations between the distributions of organisms across a landscape and bioclimatic features can be considered at best as a 'habitat model' (Kearney 2006). Only when interspecific interactions and their sensitivity to climate become part of the bioclimate models we may be approaching functional trait-based multispecies distribution models which are capable of reliable ecological forecasting (Kearney and Porter 2004, Kearney 2006, McGill et al. 2006).

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MOSAIC PATTERNS OF THERMAL STRESS IN THE ROCKY INTERTIDAL ZONE: IMPLICATIONS FOR CLIMATE CHANGE

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Abstract. We explicitly quantified spatial and temporal patterns in the body temperature of an ecologically important species of intertidal invertebrate, the mussel *Mytilus californianus*, along the majority of its latitudinal range from Washington to southern California, USA. Using long-term (five years), high-frequency temperature records recorded at multiple sites, we tested the hypothesis that local "modifying factors" such as the timing of low tide in summer can lead to large-scale geographic mosaics of body temperature. Our results show that patterns of body temperature during aerial exposure at low tide vary in physiologically meaningful and often counterintuitive ways over large sections of this species' geographic range. We evaluated the spatial correlations among sites to explore how body temperatures change along the latitudinal gradient, and these analyses show that "hot spots" and "cold spots" exist where temperatures are hotter or colder than expected based on latitude. We identified four major hot spots and four cold spots along the entire geographic gradient with at least one hot spot and one cold spot in each of the three regions examined (Washington–Oregon, Central California, and Southern California). Temporal autocorrelation analysis of year-to-year consistency and temporal predictability in the mussel body temperatures revealed that southern animals experience higher levels of predictability in thermal signals than northern animals. We also explored the role of wave splash at a subset of sites and found that, while average daily temperature extremes varied between sites with different levels of wave splash, yearly extreme temperatures were often similar, as were patterns of predictability. Our results suggest that regional patterns of tidal regime and local pattern of wave splash can overwhelm those of large-scale climate in driving patterns of body temperature, leading to complex thermal mosaics of temperature rather than simple latitudinal gradients. A narrow focus on population changes only at range margins may overlook climatically forced local extinctions and other population changes at sites well within a species range. Our results emphasize the importance of quantitatively examining biogeographic patterns in environmental variables at scales relevant to organisms, and in forecasting the impacts of changes in climate across species ranges.

Key words: biogeography; climate change; intertidal; mussel; Mytilus californianus; *signal analysis; temperature; thermal stress; U.S. Pacific Coast.*

Introduction

The effects of temperature on the survival and physiological performance of organisms, and the subsequent influence of physiological temperature tolerance on species distributions patterns, have been major foci of investigation for decades (Orton 1929, Hutchins 1947, Vernberg 1962, Somero 2005). Virtually all physiological

processes are affected to at least some degree by the temperature of an organism's body. Recent technological innovations at molecular and biochemical levels have precipitated major advances in our understanding of how temperature drives organismal physiology and ecology (e.g., Somero 2002, Dahlhoff 2004, Hofmann 2005). Exploring the role of organism temperature in driving species distribution patterns has assumed a further sense of urgency given changes in global climate (Intergovernmental Panel on Climate Change 2001), the observable impacts of these changes on ecological patterns in nature (Root and Schneider 1995, Parmesan and Yohe 2003, Root et al. 2003, Parmesan and Galbraith 2004, Harley et al. 2006), and a pressing need to forecast the impacts of climate change on natural

ecosystems (Clark et al. 2001, Halpin et al. 2004b, Gilman et al. 2006, Helmuth et al. 2006).

In many cases, however, our understanding of how the physical environment, and in particular aspects of climate, may limit the distribution of organisms is limited by our rather poor understanding of how physiologically relevant environmental factors vary in space and time (Hallett et al. 2004). In particular, we often know little of how "climate" is translated into patterns of body temperature, especially at spatial and temporal scales relevant to organisms (Helmuth 2002). Thus, while we have a general understanding of how large-scale climatic indices change over large geographic gradients (Stenseth et al. 2003), we often are at a loss as to how to explicitly test hypotheses relating to the influence of climate on levels of physiological performance (Chown et al. 2004, Hallett et al. 2004, Helmuth et al. 2005).

Mechanistically exploring the impacts of climate, and climate change, on the distribution of organisms in nature thus mandates a detailed knowledge of (1) how physiologically relevant environmental factors vary in space and time (Hallett et al. 2004, Holtmeier and Broll 2005); (2) how organisms interact with and perceive those environmental signals (Helmuth 2002, Helmuth et al. 2005, Gilman et al. 2006); and (3) what the physiological consequences of those varying signals are to the organism (Chown et al. 2004, Hofmann 2005, Somero 2005), including how organisms may adapt and physiologically acclimate to those signals (Clarke 2003, Stillman 2003). While significant progress has been made in all of these arenas, recent studies have emphasized that the physical environment can vary on scales that are not only highly complex but often counterintuitive (Underwood and Chapman 1996, Helmuth and Hofmann 2001, Helmuth and Denny 2003, Denny et al. 2004, Wright et al. 2004). The body temperatures of ectothermic organisms are often quite different from the temperature of the surrounding air or substratum (Porter and Gates 1969, Stevenson 1985, Huey et al. 1989). Subsequently, two organisms exposed to identical climatic conditions can experience markedly different body temperatures and thus very different levels of physiological stress, even when physiological responses to temperature are similar. Thus, patterns of organism temperature can vary over a wide range of temporal and spatial scales, even when broad-scale climatic patterns appear far simpler (Holtmeier and Broll 2005, Gilman et al. 2006). Moreover, physiological responses to fluctuating temperatures are often complex, and simple metrics such as average temperature may not be a sufficient indicator of physiological stress (Buckley et al. 2001, Halpin et al. 2004a). Knowing how and when to look for the effects of climate change, either through direct empirical observation or through modeling, therefore requires an explicit understanding of how potentially limiting factors such as body temperature vary over space and time, as well as knowledge of how physiological tolerance to those parameters varies along comparable scales (Halpin et

al. 2002, 2004a, Clarke 2003, Stillman 2003, Tomanek and Sanford 2003, Kearney and Porter 2004, Wright et al. 2004, Dethier et al. 2005, Stenseng et al. 2005).

The intertidal zone, the interface between marine and terrestrial environments, has long served as a model for examining the effects of climate on species distributions (Connell 1972) and may also prove an excellent model for the effects of climate change on species distributions (Hawkins et al. 2003, Harley et al. 2006, Helmuth et al. 2006). Here, we explicitly quantify spatial and temporal patterns in the body temperature of an ecologically important species of intertidal invertebrate, the mussel *Mytilus californianus*, along the majority of its latitudinal range from Washington to southern California, USA. We present long-term (5-yr) temperature records recorded at multiple sites along the west coast of the United States. We show that patterns of body temperature vary in potentially physiologically meaningful and often counterintuitive patterns over large sections of this species' geographic range. We use temporal autocorrelation to evaluate year-to-year consistency and temporal predictability in the mussel body temperatures along this large-scale gradient. Additionally, we evaluate the spatial correlations among sites to explore how body temperatures change along the latitudinal gradient, and explore the role of wave exposure at a subset of sites to explore the relative importance of wave splash in driving patterns of body temperature.

The roles of aerial and aquatic body temperatures in the intertidal zone

The upper zonation limits of many rocky intertidal organisms are thought to be set by some aspect of thermal or desiccation stress related to aerial exposure at low tide (Connell 1972), and organisms living in this habitat have been shown to exist at or near the edges of their thermal tolerance limits (Davenport and Davenport 2005). The intertidal zone is a model ecosystem for exploring the effects of climate, and climate change, on natural communities (Fields et al. 1993, Southward et al. 1995, Sagarin et al. 1999, Helmuth et al. 2006). The body temperature of intertidal invertebrates and algae at low tide is a crucial determinant of organism survival and performance (Somero 2002, 2005). Many studies have documented that the production of heat shock proteins (hsps) occurs after exposure to temperatures experienced during low tide (Sanders et al. 1991, Roberts et al. 1997, Hofmann 1999, Somero 2002, Tomanek 2002, Tomanek and Sanford 2003, Dahlhoff 2004, Halpin et al. 2004a, Li and Brawley 2004, Snyder and Ross 2004) and that the production of these proteins and their use in chaperoning activity exerts a metabolic cost (Heckathorn et al. 1996, Iwama et al. 1998). Other studies have shown physiologically significant impacts of aerial body temperature on the heart function of intertidal invertebrates (Stillman 2003, Stenseng et al. 2005).

Water temperature has also been shown to be an important limiting environmental factor, affecting rates

of feeding (Sanford 1999, 2002), larval mortality, and reproductive success (Hoegh-Guldberg and Pearse 1995). It may also influence the body temperature of intertidal organisms during low tide by setting the initial temperature following emersion, and by influencing rock temperature (Wethey 2002, Gilman et al. 2006). Moreover, it is an indicator of upwelling, another important driver of geographic distributions (Broitman et al. 2001, Leslie et al. 2005, Blanchette et al. 2006). While the relative importance of aerial and aquatic body temperatures to organismal survival remains unresolved, evidence suggests that both are likely important determinants of the physiological function and geographic distribution of intertidal species. As a result, the local and geographic responses of intertidal organisms are expected to display strong responses to changes in both terrestrial and aquatic climatic conditions (Lubchenco et al. 1993, Sanford 1999, Somero 2002, Harley 2003, Helmuth et al. 2006).

However, to date most studies have focused exclusively on the role of water temperature in driving temporal and spatial patterns of intertidal assemblages (e.g., Barry et al. 1995, Schiel et al. 2004). Moreover, physiological evidence suggests that not only the magnitude of extremes in temperature, but also the duration, frequency, and time history of these events may be important determinants of survival (Buckley et al. 2001, Crozier 2004, Halpin et al. 2004a, Wright et al. 2004). Explicitly quantifying spatial and temporal patterns in both aerial and aquatic body temperature is thus a necessary first step in generating hypotheses regarding the likely impacts of climatic variability on the geographic distributions of intertidal invertebrates.

Recent studies suggest that patterns of aerial body temperature may be more geographically complex than anticipated in coastal communities (Helmuth et al. 2002). Multiple factors interact to drive the body temperature of an intertidal alga or invertebrate during aerial exposure. The absolute tidal height of an organism on the shore, the amount of wave splash that it receives, and the local tidal cycle all interact to determine the timing and duration of exposure to terrestrial conditions at low tide. While exposed, substratum angle plays a major role in determining the amount of solar radiation received (Schoch and Dethier 1996, Helmuth and Hofmann 2001). Patterns of local climate such as fog can also have a significant modifying effect. Many of these factors (such as the effects of substratum aspect) can be very localized (Helmuth and Hofmann 2001). Other factors, such as regional differences in the timing of low tide (Denny and Paine 1998), may be sufficiently extensive to have biogeographic consequences for intertidal organisms (Helmuth et al. 2002). Yet other modifying influences, such as wave splash, may operate at intermediate scales (Schoch and Dethier 1996). As a result, while climatic conditions generally become increasingly colder moving poleward along coastlines, the occurrence of local "modifying factors" may theo-

retically override the impacts of climatic gradients, leading to mosaic patterns of temperature (Helmuth et al. 2006), as has been suggested for terrestrial ecosystems (Holtmeier and Broll 2005). This model suggests that the impacts of climate change will be most effectively detected by conducting investigations throughout species ranges rather than just at the margins of species ranges (Helmuth et al. 2002, Sagarin and Somero 2006). Specifically, this concept suggests that climate change may exhibit disproportionately large impacts at a series of "hot" and "cold" spots within species ranges (Helmuth et al. 2006), rather than causing simple latitudinal range shifts. Helmuth et al. (2002) for example, showed that because summer-time low tides occur in the middle of the day at northern latitudes, aerial body temperatures of mussels at sites in Oregon were as hot as some sites in Southern California, where summertime low tides seldom occur midday. As a result, Helmuth et al. (2002) predicted that mortality and physiological stress due to climate change would likely be detected not only at range margins, but also at hot spots within the species range. However, this study was conducted over only a one year time period, and at a limited number of sites.

Here, we explore this concept in detail using long-term, high-frequency measurements of temperatures relevant to the body temperatures of intertidal mussels (*Mytilus californianus*). We use this data set to test the hypothesis that aerial thermal regimes do not decrease monotonically with increasing latitude, and that "hot spots" and "cold spots" exist along the west coast of the United States. We furthermore explore the role of local patterns of wave splash in driving aerial thermal regimes, and patterns of temporal variability to investigate the concept that there exist geographic patterns in the predictability of thermal stress that may be detectable by intertidal organisms.

METHODS

Temperature instrumentation

Like terrestrial ectotherms (Porter and Gates 1969), the body temperatures of intertidal invertebrates during low tide are driven by multiple, interacting climatic factors such as solar radiation, wind speed, relative humidity and air and ground temperatures (Johnson 1975, Helmuth 2002). Furthermore, the shape, color, and mass of the organism also affect body temperature. Thus, two organisms exposed to identical climatic conditions can display very different temperatures (Porter and Gates 1969, Etter 1988, Helmuth 2002). As a result, during aerial exposure the body temperatures of intertidal organisms are often quite different from the temperature of the surrounding air, and can vary from one another by more than 15°C, even over scales of <20 cm (Bertness 1989, Helmuth 1998, Helmuth and Hofmann 2001).

As is the case for organisms, the shape, size and color of a data logger can influence the temperature that it records while in air (Heath 1964), and one type of logger
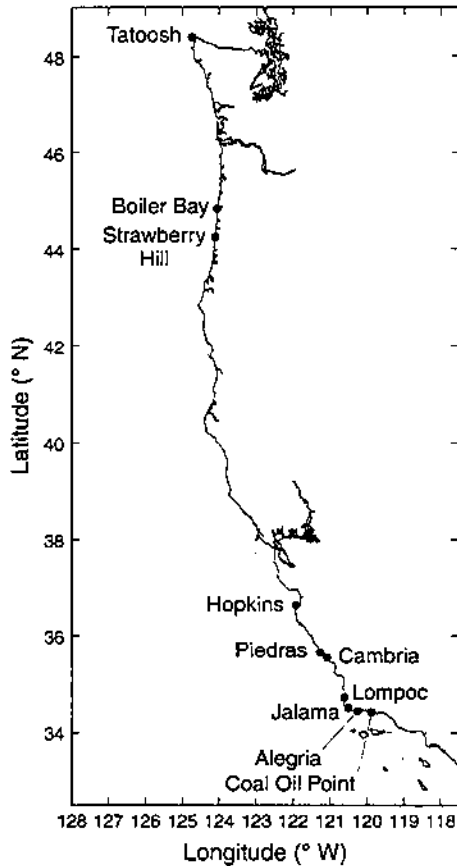
Fig. 1. Map of all deployment sites along the U.S. Pacific Coast.

site in Washington (Tatoosh Island; see Plate 1); two sites in Oregon (Boiler Bay and Strawberry Hill); and seven sites in California (Hopkins, Piedras Blancas, Cambria, Lompoc, Jalama, Alegria, and Coal Oil Point [COP]). At three sites (Strawberry Hill, Boiler Bay, and Hopkins), loggers were additionally deployed at wave-protected (sheltered) areas adjacent to the wave-exposed sites to explore the role of wave splash. It should be noted, however, that the "wave protected" site at Boiler Bay, a bench landward of the wave-exposed bench, is less sheltered than the Hopkins or Strawberry Hill sites (Fitzhenry et al. 2004). All loggers were deployed on approximately horizontal substrata, which was verified using a Brunton inclinometer. Deployment durations varied from site to site, and were interrupted by instrument loss and damage. Our longest continuous deployment was at Hopkins (Monterey Bay, California), which was initiated in 1998 (Helmuth and Hofmann 2001) and is ongoing, while our shortest deployment was 431 days at Tatoosh Island. For some analyses, we grouped these sites into three regions: Washington–Oregon (WaOr; Tatoosh, Boiler Bay, and Strawberry Hill), Central California (CenCal; Hopkins, Piedras Blancas, and Cambria), and Southern California (So-Cal; Lompoc, Jalama, Alegria, and COP). Data from a few additional sites were not included in the analysis because of data sparseness (short deployment or very recent deployment) but are included in the Appendix for comparison (Bamfield [Seppings Island], British Columbia; Cattle Point, Washington; Collin's Cove, Washington; Bodega Bay, California; and Boat House, California).

Instrument deployment

Previous results indicated that variability between microsites at any given location was generally rather low, as long as instruments were deployed in regions with similar wave exposure, and on a uniform substratum angle (Helmuth et al. 2002, Harley and Helmuth 2003, Fitzhenry et al. 2004). Wave splash was quantified at each site using the method of Harley and Helmuth (2003) which compares the timing of "effective shore level" (the tidal height at which loggers are cooled by the returning tide) against the absolute tidal height (as measured using a laser level or theodolite; Table 2). The difference between the two values is estimated as the average wave run-up (AWR), i.e., the average distance that waves "run up" the shore above the still tide line after breaking. Loggers were affixed to the rock surface using Z-spar epoxy putty (Splash Zone compound A-788, Kop-Coat, Inc., Rockaway, New Jersey, USA) oriented in approximate growth position (Helmuth et al. 2002). The number of loggers retrieved varied due to instrument loss, ranging from three to six (Table 2). Each logger recorded average temperature at an interval of 10 or 15 min. Using the daily extremes of these high-frequency observations across all loggers deployed at a site, we calculated the average daily minima and

is unlikely to serve as an effective proxy for all species at a site (Fitzhenry et al. 2004). We therefore matched the thermal characteristics of living mussels using a series of biomimetic sensors. Commercially available Tidbit loggers (Onset Computer Corporation, Bourne, Massachusetts, USA) were either encased in black-tinted epoxy (Fitzhenry et al. 2004) or were placed in real mussel shells that were filled with silicone (Helmuth and Hofmann 2001). Fitzhenry et al. (2004) have previously shown that this species does not appear to cool via the evaporation of water even when forced to gape, and so does not behaviorally thermoregulate. Our loggers thus recorded the body temperatures of living mussels to within ~2–2.5°C during aerial exposure at low tide (Helmuth and Hofmann 2001, Fitzhenry et al. 2004).

Deployment sites

The primary goal of this study was to explore the role of the timing of low tide in driving latitudinal patterns in body temperature. We attempted to hold other local modifying factors such as wave splash, substratum aspect, and relative tidal height constant. Loggers were deployed at the seaward (wave-exposed) margins of 10 sites along the U.S. Pacific Coast (Fig. 1, Table 1): one

TABLE 1. Names and positions of all sites and locations discussed in the study, ordered from north to south.

Region	Location	Alongshore position (km)	Latitude (° N)	Longitude (° W)
WaOr	Tatoosh Island, WA	1660.1	48.39	124.74
WaOr	Boiler Bay, OR	1260.7	44.83	124.05
WaOr	Strawberry Hill, OR	1196	44.25	124.12
CenCal	Hopkins, CA	327.1	36.62	121.90
CenCal	Piedras Blancas, CA	208.11	35.66	121.28
CenCal	Cambria, CA	185.66	35.54	121.10
SoCal	Lompoc, CA	84.175	34.72	120.61
SoCal	Jalama, CA	57.722	34.50	120.50
SoCal	Alegria, CA	37.284	34.47	120.28
SoCal	Coal Oil Point (COP), CA	0	34.41	119.88

Notes: All coordinates were measured using the WGS84 system. State abbreviations: WA, Washington; OR, Oregon; CA, California.

maxima. Temperature observations during high tide (estimated by comparing temperature records against tide tables) were used to calculate average daily seawater temperature. We then used these daily statistics to calculate the average daily maxima and minima for the entire period of record for each site, a measure of "chronic" stress that incorporates both water and aerial temperature (Helmuth and Hofmann 2001), as daily extremes over the time period reflect extremes from both environments. We also calculated the highest and lowest temperatures recorded at each site for the period of February 2002–February 2003 in order to compare patterns of extreme or "acute" temperatures (Helmuth and Hofmann 2001), a reflection of aerial temperature extremes (Table 3). This time period represents the longest nearly continuous record available for most sites, with the exception of 2001, which was discussed in an earlier paper (Helmuth et al. 2002).

From the daily statistics, we calculated monthly summary statistics for each logger for every month with at least 25 days of data. Data for all sites, when available, are presented in the Appendix. For these long-term estimates, we applied a filter of 30 min as a smoothing function, calculating the highest and lowest temperature that occurred for a minimum of 30 min/d (the 97.9 and 2.1 percentile, respectively; Fitzhenry et al. 2004; Appendix).

Data analysis

Our hypothesis-testing framework was geared toward dissecting the main spatial and temporal patterns of variation of daily extremes in mussel body temperature. In order to examine spatial patterns, we relied on standard regression techniques to test for a latitudinal thermal gradient. Temporal patterns were examined with two different analyses to characterize the thermal regimes at every site with suitable temporal records. First, using temperature return times we examined the cumulative risk of experiencing a physiologically critical temperature. Second, we used temporal autocorrelation to examine the time-varying predictability in temper-

ature extremes. These spatial and temporal analyses are detailed in the next two subsections.

Spatial patterns

We tested for latitudinal gradients in daily maximum and minimum mussel body temperature using a regression model of the alongshore distance between sites and mussel body temperature statistics. This regression analysis tested the hypothesis that mussel body temperature extremes change with the large-scale (latitudinal) gradient in solar radiation and air temperature. We used the alongshore distance instead of latitude in order to appropriately represent the two Santa Barbara Channel sites (Alegria and COP), which are located along the same latitude (Table 1, Fig. 1), and preserve the spatial relationship across sites. The use of this criterion does not affect the general trend of decreasing temperature with latitude as the Santa Barbara Channel sites experience much warmer atmospheric and oceanographic conditions than the open coast sites (Lompoc and Jalama) located at approximately the same latitude (Cudaback et al. 2005). In order to examine the

TABLE 2. Descriptions of each wave-exposed site and of logger deployments.

Location	Average wave run-up (cm)	No. loggers	Tidal height (cm)	Tidal height (proportion of range)
Tatoosh Island	67.9	4–5	170	0.71
Boiler Bay	66.1	3–6	112	0.48
Strawberry Hill	47.4	3–5	157	0.68
Hopkins	94.3	4	175	1.09
Piedras Blancas	81.8	6	162	1.01
Cambria	NA	3	139	0.87
Lompoc	58.2	3–4	133	0.84
Jalama	50.0	4–6	114	0.72
Alegria	36.7	4	110	0.68
Coal Oil Point	31.0	3–4	81	0.50

Notes: Loggers were deployed near the middles of mussel beds at each site (reported as both height above mean lower low water [MLLW] and scaled as proportion of diurnal tidal range). Data are not shown for wave-protected subsites. Note that absolute tidal range increases with latitude and is ~50% higher at northern latitude sites than at southern sites.

TABLE 3. Long-term means of daily statistics and extremes for the period February 2002–February 2003 at all wave-exposed locations.

| | Intertidal mussel temperature (°C) | | | | |
| | Daily average | | | | |
Location	Average	Minimum	Maximum	Yearly maximum†	Month of maximum‡
Tatoosh Island	9.9604	8.0302	13.249	25.44 ± 4.36	May
Boiler Bay	11.465	8.6199	18.179	34.72 ± 2.22	July
Strawberry Hill	11.22	8.8817	16.621	27.08 ± 7.00	July
Hopkins	13.905	11.178	19.518	33.59 ± 2.38	April
Piedras Blancas	13.234	10.539	19.794	33.64 ± 3.59	April
Cambria	13.786	10.208	21.416	35.30 ± 0.86	April
Lompoc	13.871	11.134	19.861	31.15 ± 3.13	June
Jalama	14.995	11.645	22.452	35.46 ± 1.43	May
Alegria	15.691	11.92	23.434	39.50 ± 3.83	June
Coal Oil Point	15.713	12.688	20.636	34.32 ± 1.89	June

† Hottest temperature recorded for at least half an hour (mean ± SD for all loggers at each site).
‡ Month in which the extreme high temperature was recorded.

hypothesis that hot-spots and cold-spots may exist regardless of their latitudinal position we used a third-order polynomial regression of alongshore position with the long-term means of daily maximum and minimum temperature and plotted the bivariate relationship between residuals for each site using all data. The polynomial fit was used to remove the large-scale spatial structure in the data. Residuals from the large-scale model represent temperature variations due to local-scale processes (Legendre and Legendre 1998). We statistically tested the presence of cold and hot spots by fitting the polynomial regression across all sites during the only period when all sites had concurrent temperature measurements (13 January–18 July 2001, 183 days) and using a one-tailed t test to examine if the daily deviations from the large-scale model at every site were significantly smaller or greater than zero for average daily minima and maxima, respectively.

To compare the magnitude of variation within and among sites, we used variance components analysis to quantify the magnitude of variation in average daily maximum logger temperature among sites, replicate loggers within sites, and replicate days of observations within loggers. We independently tested for the influence of wave splash on mussel temperature, by regressing the residuals from the polynomial regression (i.e., deviations from the expectations based on latitude) against the average wave run-up (AWR) for each site. We similarly tested for the effects of logger intertidal height (both absolute and as a percentage of tidal range, Table 2) using linear regression analysis.

Temporal patterns

Because high-temperature stress is known to affect mussel distribution and physiology, we examined the distributions of daily maxima for all exposed sites for which we had a concurrent, continuous data set. We used a period from 12 January to 13 November 2001 at all exposed sites except Cambria and COP, where data were lacking. Previous data indicate that brief exposure

to temperatures above 30°C are sufficient to induce production of hsps in *M. californianus* (Halpin et al. 2004a), so we used this temperature as a basis for comparing the potential for thermal stress among exposed sites. We calculated a survival distribution function $(1 - F(x)$, where $F(x)$ is the cumulative distribution function), from which we derived the probability of observing a daily maximum above 30°C.

We used the daily statistics to study the dynamical behavior of mussel body temperature by examining patterns of temporal autocorrelation using data from January 2000 through December 2004. We examined daily patterns of variation at short but physiologically relevant time scales with our maximal temporal scale being 28 days. The raw daily time series showed a strong seasonal cycle that can bias autocorrelation estimates through serial correlation (i.e., inflate autocorrelation at short time lags). Due to the limited number of years in the record and temporal gaps in several of the time series, it was not possible to remove the annual cycle using harmonic regression. Thus, we removed seasonality by first-order differencing such that the first difference, D, at time t and temperature T is $D = T(t) - T(t - 1)$. We then centered each time series by subtracting the mean and dividing by the standard deviation and calculated the unbiased temporal autocorrelation of mussel body temperature (Bendat and Piersol 1986, Denny et al. 2004). We computed conservative confidence intervals for autocorrelation by calculating them for the time series with fewer degrees of freedom at each lag in the comparisons by regions (see *Results*). Due to the limited length of the time series, autocorrelation estimates were calculated using all available pairs of data at each time lag.

Wave exposure

To examine the role of wave splash, we separately compared the three sites where a suitable record of different wave-splash regimes existed (Boiler Bay, Oregon; Strawberry Hill, Oregon; and Hopkins, Cal-

Fig. 2. Daily maximum mussel body temperature at all sites from 1 January 2000 to 31 December 2004. Sites are sorted latitudinally from north (top) to south (bottom). The color bar on the right side of the figure is the key to the temperatures shown in the figure, which range from 6° to 42°C.

ifornia). Specifically, we tested the hypothesis that mussels at wave-protected locations experience hotter and less variable temperature than their wave-exposed counterparts. In order to follow a hierarchical approach to examine temperature variability, we compared mussel body temperature extremes through correlation and examined their temporal dynamics through their auto-correlation functions at all three pairs of sites. This allowed us to examine temperature variations at the regional and local scales, over a range of temporal scales. Thus, we examined nested scales of variation, exploring the effect of wave splash on temperature over tens of meters and comparing differences in temperature due to latitude over hundreds of kilometers. All analyses were performed using Matlab 7.01 v.14 (Mathworks, Natick, Massachusetts, USA) or SAS (SAS Institute, Cary, North Carolina, USA).

RESULTS

Spatial patterns in extreme temperatures

In accordance with our previous results from 2001 (Helmuth et al. 2002), yearly extremes in maximum body temperature from 2002 revealed a highly variable thermal mosaic (Table 3, Fig. 2), with no clear latitudinal pattern. The probability of exposure to a temperature over 30°C, at which induction of the heat-

shock response is likely, also showed a complex spatial pattern, with sites having a relatively high probability interspersed with sites having a lower probability (Fig. 3). In contrast, the long-term averages of daily minimum and daily high tide body temperature did show a fairly strong latitudinal gradient (Table 3, Figs. 4 and 5).

Results of the ANOVA confirmed that between-site variability in logger temperature were greater than within-site variability. Separate analysis on daily maxima and minima both showed greater variance among sites than within sites (20% vs. 8% for maxima, 45% vs. 3% for minima). In both analyses, day-to-day variation within loggers represented the greatest variance component. The observation of greater variance among than within sites suggests that microsite differences were indeed quite low, and were unlikely to be driving site-level temperature differences. The regression of residuals vs. average wave run-up (a measure of wave splash) and logger height showed that there were no relationships between either maximum or minimum temperature for both of these metrics, again confirming that the patterns observed were not due to variability in logger placement.

The results of the polynomial regression of the daily minimum and maximum temperatures aid in elucidating the complex geographic pattern. Moreover, the analysis provides a means of objectively identifying sites as hot
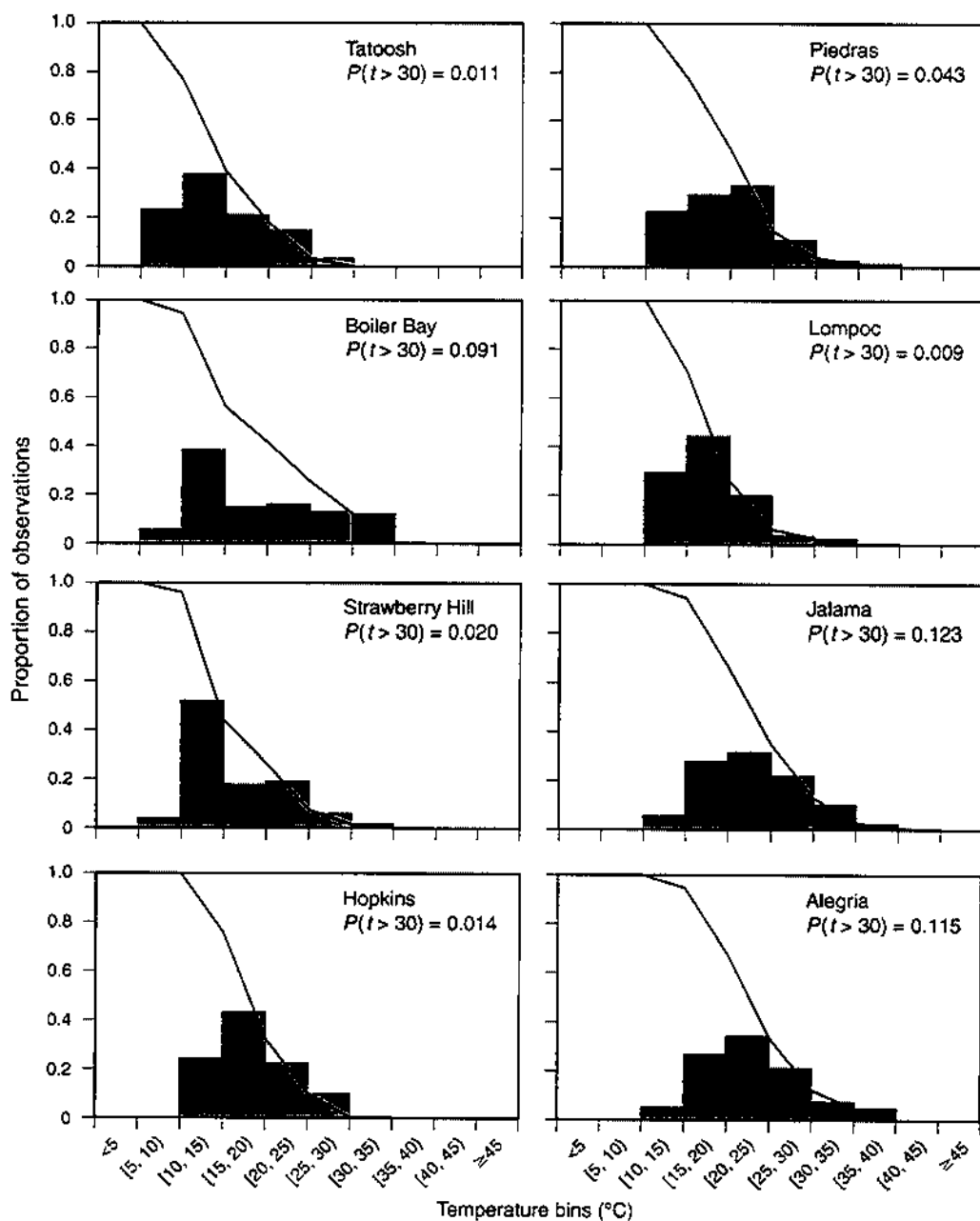
Fig. 3. Distributions and survival function for daily maximum body temperature at all wave-exposed sites (except Cambria and Coal Oil Point) ranging from northernmost to southernmost from top left panels to bottom right panels, for the period 12 January–13 November 2001. Temperatures are binned in 5° temperature bins, and histograms represent the proportional occurrences of temperatures in these bins in the time period. The $P(t > 30)$ in each case represents the probability that any given temperature will exceed 30°C.

and cold spots based on long term trends in daily minima and maxima. The polynomial regression demonstrates that while a simple spatial model can explain some variation in long-term measurements in daily maxima and minima (Fig. 6), important deviations from predicted temperatures remain, with sites having colder daily minima and hotter daily maxima than expected. The bivariate relationship between minimum and maximum temperature residuals from the polynomial regression shows that departures from the latitudinal model are not sorted geographically (Fig. 7, Table 4). Here, we define a hot spot as a site with maximal daily temperatures that are warmer than expected based on the expectation of latitudinal gradient and a cold spot as a site with daily minimal temperatures that are colder than expected based on the latitudinal gradient. There

PLATE 1. Measurements of intertidal heights were conducted at most sites with a laser level, using a reference point obtained by observing still tidal height on multiple days. The site shown here is Strawberry Draw, Tatoosh Island, Washington, USA. Photo credit: B. Helmuth.

were at least four major hot spots among the locations examined: Boiler Bay (WaOr), Cambria (CenCal), and Alegria and Jalama (SoCal). The long-term average of the average daily maximum temperatures at these sites was around a full degree Celsius hotter than predicted by the geographic structure, with Alegria being 1.73°C hotter. Although departures from the latitudinal model were smaller in the case of average daily minima, the analysis identified four sites as cold-spots during the period of time examined: Boiler Bay (WaOr), Cambria (CenCal), and Alegria and Jalama (SoCal; Table 4). Strikingly, three sites appeared as both a hot and cold spot suggesting they experienced extreme thermal variability with respect to the rest of the sites used as the latitudinal sample. The one-tailed t test for the residuals of the daily latitudinal model supported the conclusions reached by examining only the residuals of the long-term means (Table 4).

Temporal patterns

In order to examine the dynamical behavior of extremes in mussel body temperature, we calculated the temporal autocorrelation at all exposed locations within each region. In the SoCal region, the dominant signal related to tidal forcing as evidenced by the positive autocorrelation estimates around 14- and 28-d lags (Fig. 8E and 8F). Similarly, negative autocorrelation is evident around opposite phases of the tidal cycle (i.e., 7- and 14-d lags). The tidal signal is more pronounced in the autocorrelation of maximum body temperatures. Although the strength of the tidal signal is still evident in the autocorrelation of maximum and minimum daily mussel body temperature in the CenCal region (Fig. 8C and 8D), the tidal pattern is completely absent in the WaOr region (Fig. 8A and 8B). One of the most prominent features of the autocorrelation function is the large negative autocorrelation observed at short time lags. The pattern of temporal variability over short time lags is in striking contrast with the tidal signal, with the WaOr region showing the largest and more persistent negative autocorrelation estimates at short time lags (1–3 d) in the three regions. In the CenCal region, negative autocorrelation at short time lags was largely confined to 1-d lags and to the opposite phases of the tidal cycle. The SoCal region showed a moderate day-to-day variation in maximum body temperatures with marginally significant negative autocorrelation observed 1-d lags in maximum body temperatures, but with a persistent negative autocorrelation pattern over 1- to 10-d lags in minimum body temperatures.

Contrasts between exposed and protected locations

Daily maximum and minimum mussel body temperatures were always correlated between exposed and protected locations within sites (Fig. 9, Table 5). Tighter correlations were observed with measures of minimum temperatures at exposed and protected sites, and the linear trends tended to closely follow a 1:1 relationship
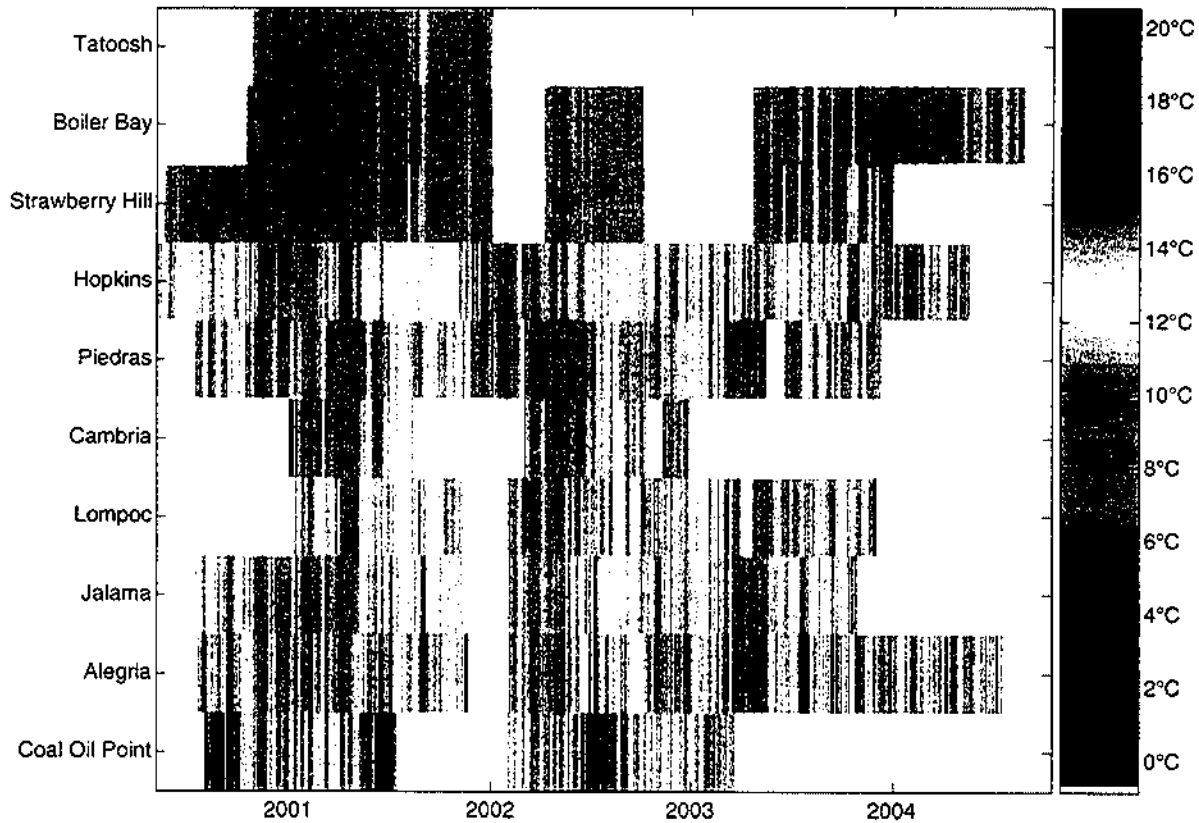
Fig. 4. Time series of daily minimum mussel body temperature at all sites from 1 January 2000 to 31 December 2004. Sites are sorted latitudinally from north (top) to south (bottom). Temperatures range from −1° to 21°C.

(Fig. 9A, C, and E; Table 5). In agreement with the correlation patterns, we did not find differences in minimum daily mussel body temperatures within any site (t test; Hopkins, P = 1; Strawberry Hill, P = 1; Boiler Bay, P = 0.32643, Table 5). Protected locations were hotter (on average) than their exposed counterparts when we compared maximum daily mussel body temperatures (t test; all locations, P < 0.0001, Table 5). It was apparent that at higher daily minimum temperatures, the temperatures at the exposed and protected locations converged (Fig. 9E) perhaps because the minima on those days reflect water temperature at high tide, when both protected and exposed locations are submerged. In contrast, at higher average daily maximum temperatures, exposed locations tended to stay cooler than protected locations, probably indicating the amelioration of high temperatures in exposed area by wave splash (Fig. 9F).

We found that patterns of autocorrelation in extreme temperatures at exposed and protected at any given site showed almost identical patterns. The autocorrelation function of minimum temperatures is strikingly similar at any given site regardless of wave exposure (Fig. 10A, C, and E). An interesting feature was the presence of a small-scale (1–2-d lags) negative autocorrelation indicating that minimum temperatures were extremely variable

from day to day. A similar picture was evident in the autocorrelation of maximum temperatures where exposed and protected locations behaved similarly across exposed and protected locations at all sites (Fig. 10B, D, and F). As we had detected before for all exposed locations, the tidal signal became stronger with decreasing latitude (Fig. 7) for both exposed and protected locations at all three sites. The magnitude of the negative autocorrelation at 1-d lag at the protected location in Strawberry Hill was the largest detected in the present study (Fig. 10D, r = −0.36056).

DISCUSSION

The significance of latitude

Geographic patterns of environmental variables play an important role in the ecology and evolution of broadly distributed species. Because abiotic factors such as solar radiation, day length, wave height, upwelling, the timing of low tide, and air and water temperature can all vary with latitude, physiological stress, and organismal performance are expected to change with latitude as well, but often in nonintuitive ways. Here, we show that the latitudinal patterns in the aerial body temperatures of Mytilus californianus are complex, and that patterns vary depending on whether one looks at water temperature, long-term averages of daily maxima and

FIG. 5. Time series of daily mussel body temperature during high tide at all sites from 1 January 2000 to 31 December 2004. Sites are sorted latitudinally from north (top) to south (bottom). Temperatures range from 5° to 22°C.
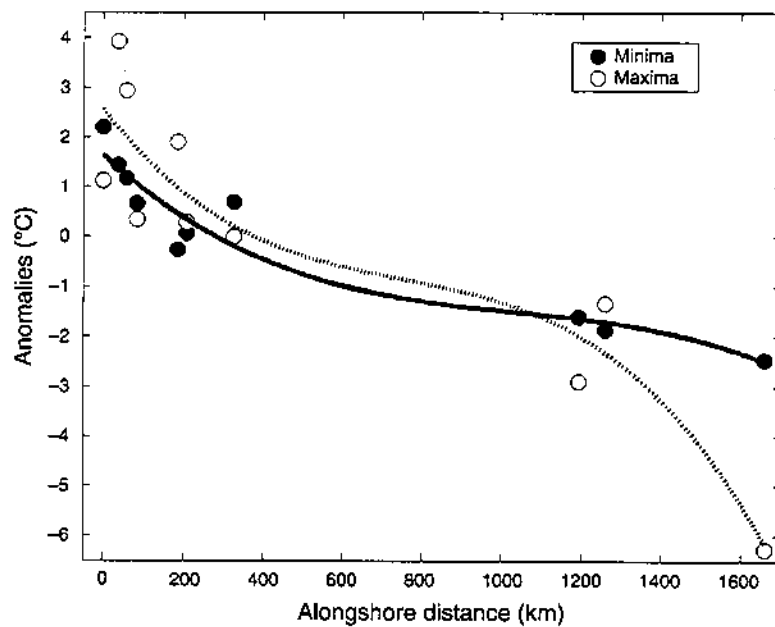

FIG. 6. Third-order polynomial regression of the alongshore position of all sites and their long-term means of maximum (open circles) and minimum (solid circles) mussel body temperatures. The solid line is the least-squares polynomial fit of alongshore position and maximum temperatures ($r^2 = 0.8604$, $F_{3,6} = 12.326$, $P < 0.001$) while the segmented line corresponds to the least-squares fit of the minimum temperatures ($r^2 = 0.90963$, $F_{3,6} = 20.132$, $P < 0.001$).
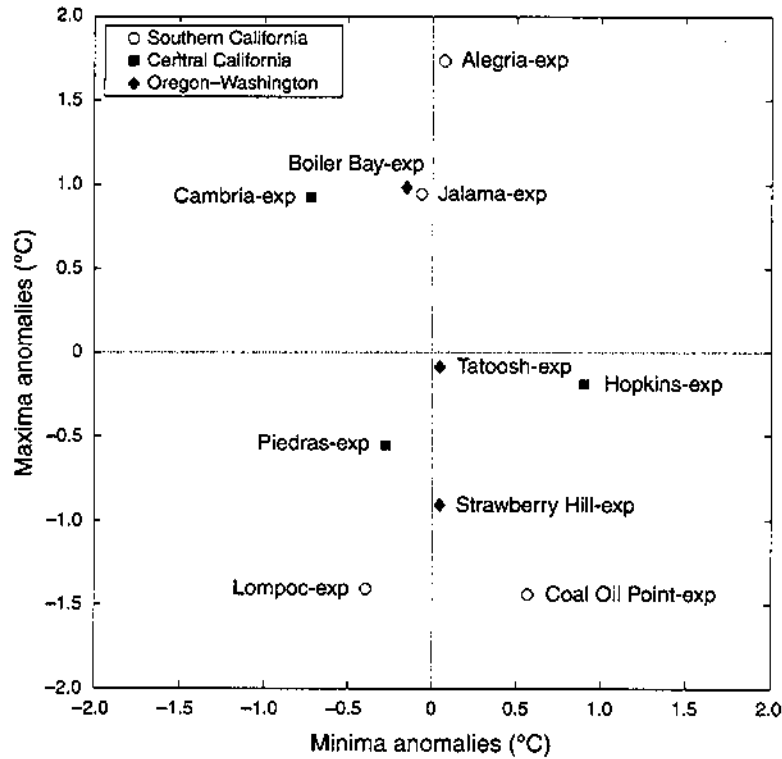
FIG. 7. Bivariate relationship between residuals from the polynomial regression of alongshore position and long-term daily maximum and minimum mussel body temperature for all exposed (exp) locations. Locations lying above the horizontal line show average daily maxima that are hotter than expected by their geographic position, while locations falling below the horizontal exhibit maxima that are less hot than expected. The vertical line depicts the same relationship for average daily minima, with sites lying on the left being colder and sites on the right being less cold than predicted by the latitudinal gradient. Sites are grouped by geographic region, with solid circles corresponding to the southern California locations, open squares to the central California locations, and solid diamonds to the Oregon–Washington locations.

minima (chronic stress), patterns of predictability, or at yearly extremes (acute stress). Specifically, latitudinal variation in average temperature increases with decreasing latitude. This is not surprising, since this metric is in part driven by water temperature, which shows a clear

TABLE 4. Results of one-tailed *t* test for differences between anomalies from the latitudinal model for maximal and minimal daily temperature values.

Location	Maximum daily temperatures		Minimum daily temperatures	
	t	*P*	*t*	*P*
Coal Oil Point	−17.125	1	13.512	1
Alegria	14.424	<0.001	−1.0371	0.1505
Jalama	14.941	<0.001	−9.0401	<0.001
Lompoc	−19.267	1	1.5765	0.9416
Cambria	7.9847	<0.001	−13.472	<0.001
Piedras	2.0411	0.0213	−5.2718	<0.001
Hopkins	−5.6733	1	15.389	1
Strawberry Hill	−14.567	1	4.5958	1
Boiler Bay	14.983	<0.001	−8.2764	<0.001
Tatoosh	−14.697	1	16.666	1

Notes: The alternative hypothesis is that the anomaly is greater (for maximal temperatures) or smaller (for minimal temperatures) than 0. Boldface *P* values indicate rejection of the null hypothesis with $P < 0.01$ (all df = 184).

decrease with increasing latitude (Fig. 5). In contrast, while long-term averages of daily maxima and minima show a general trend with latitude over large scales (which likewise is not unexpected since daily maxima and minima during neap tidal cycles are reflective of body temperature during submersion), large deviations from this model occur in the daily maxima and minima at specific locations (hot and cold spots; Figs. 6 and 7) likely due to the impact of modifying factors such as the timing of low tides and local microclimates.

The complexity of the latitudinal pattern is even more apparent when examining values of yearly extremes (Table 3), which reflect only the influence of aerial body temperatures. For example, the maximum temperatures experienced at Boiler Bay (WaOr) in 2002 differ more from the neighboring site at Strawberry Hill, 60 km away, than they do from Hopkins (CenCal), even though the latter is >900 km south (Table 2) and loggers at the latter site were higher in the intertidal (Table 2). (It should be noted, however, that, in other years, Strawberry Hill and Boiler Bay displayed very similar high temperature extremes; Appendix.) Similarly, freeze events were recorded at Boiler Bay (November 2003), Hopkins (December 1998), and Lompoc (November
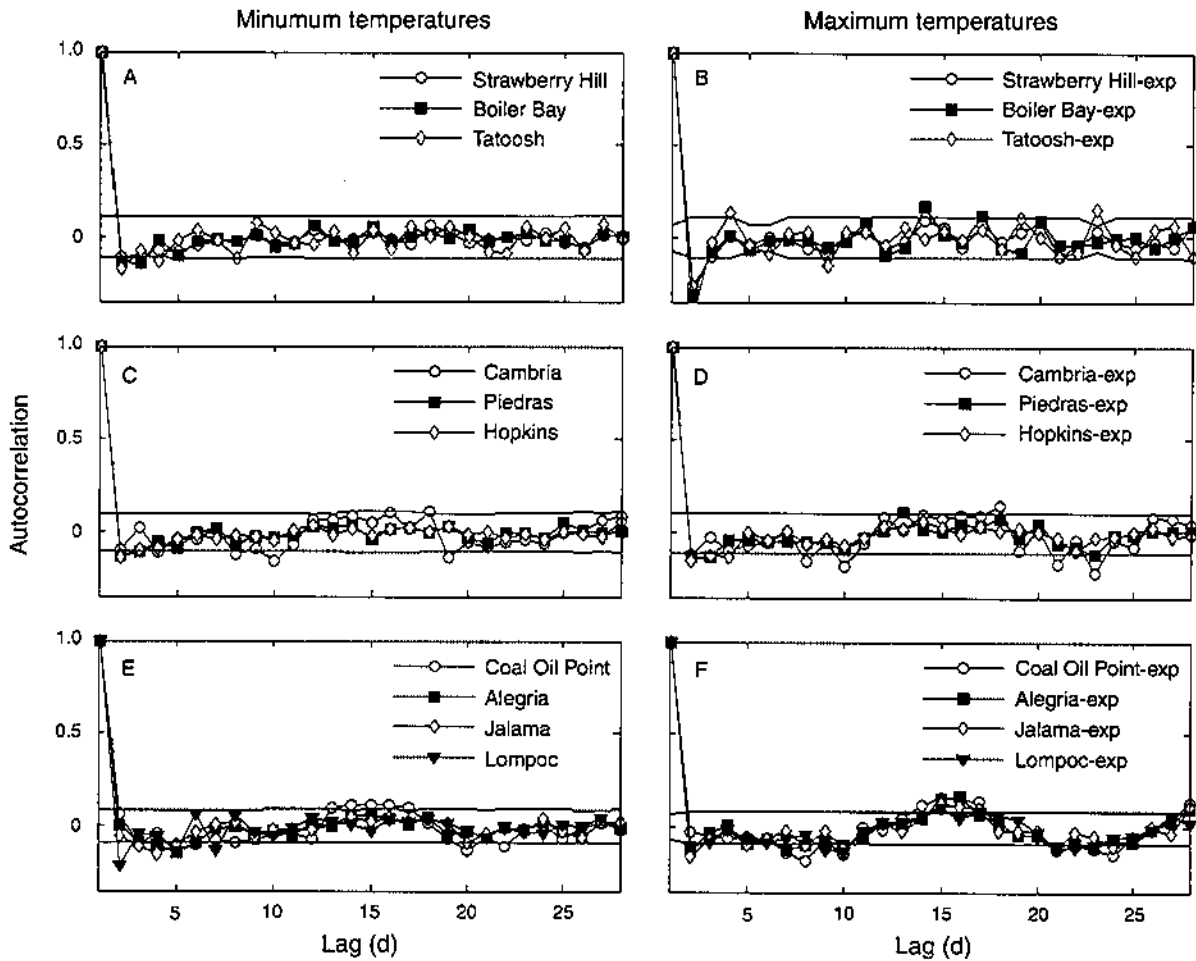
Fig. 8. Autocorrelation functions of daily minimum (A, C, and E) and maximum (B, D, and F) mussel body temperatures at all sites. Horizontal lines are Bonferroni-corrected ($\alpha = 0.05$) confidence intervals for significant autocorrelation. Notice the weakening of the tidal signal toward high-latitude sites, particularly for the autocorrelation of maximum daily temperatures and the presence of strong negative autocorrelation in both maximum and minimum temperatures at one- and two-day lags for all high-latitude sites. Autocorrelation trends show that the tidal signal is significantly negative at lags (distance in time) equivalent to half of a tidal cycle (~7 d) and is positive around a full tidal cycle (~14 d). This pattern is more evident in the maximal temperatures at lower latitudes (F); the harmonic characteristics of the signal are less evident at higher latitudes (panels D and B). To illustrate the decay in the tidal signal, sites are sorted latitudinally, from higher latitudes (top panels, WaOr region) toward lower latitudes (CenCal, mid panels, and SoCal, lower panels).

2003), but not at any of the other outer-coast sites (but see data for Puget Sound sites in Appendix).

As discussed by Helmuth et al. (2002), the daily pattern of immersion and emersion, as determined by tides and wave splash, interacts with the local terrestrial climatic regime to determine an intertidal organism's aerial thermal regime. Generally organisms with body temperatures driven largely by solar radiation experience maximum body temperatures in mid-day and early afternoon hours, especially during summer when levels of solar radiation are greatest. But, depending on the tides, intertidal organisms may be submerged and thus avoid exposure to solar radiation during this part of the day. Such is the case in southern California where low tides seldom occur midday in summer months (Helmuth et al. 2002). While many of the physical forcing factors

controlling body temperature exhibit strongly cyclical variation (e.g., solar radiation and wave heights on an annual cycle, tidal immersion on a 14-d cycle embedded in an 18.6-yr cycle [Denny and Paine 1998]), variability within these forcing mechanisms and the combination of their signals contribute to the thermal mosaic observed. The importance of the tidal cycle in driving geographic patterns of temperature is confirmed by our observation that peak temperatures at southern California sites typically occur in April and May, while those at northern sites occur in June and July (Table 3). Latitudinal variation in wave exposure may also contribute to observed patterns in temperature, especially at sites south of Point Conception where levels of wave splash are typically very low. In southern California, where low tides in summer seldom occur in

Minimum temperatures   Maximum temperatures
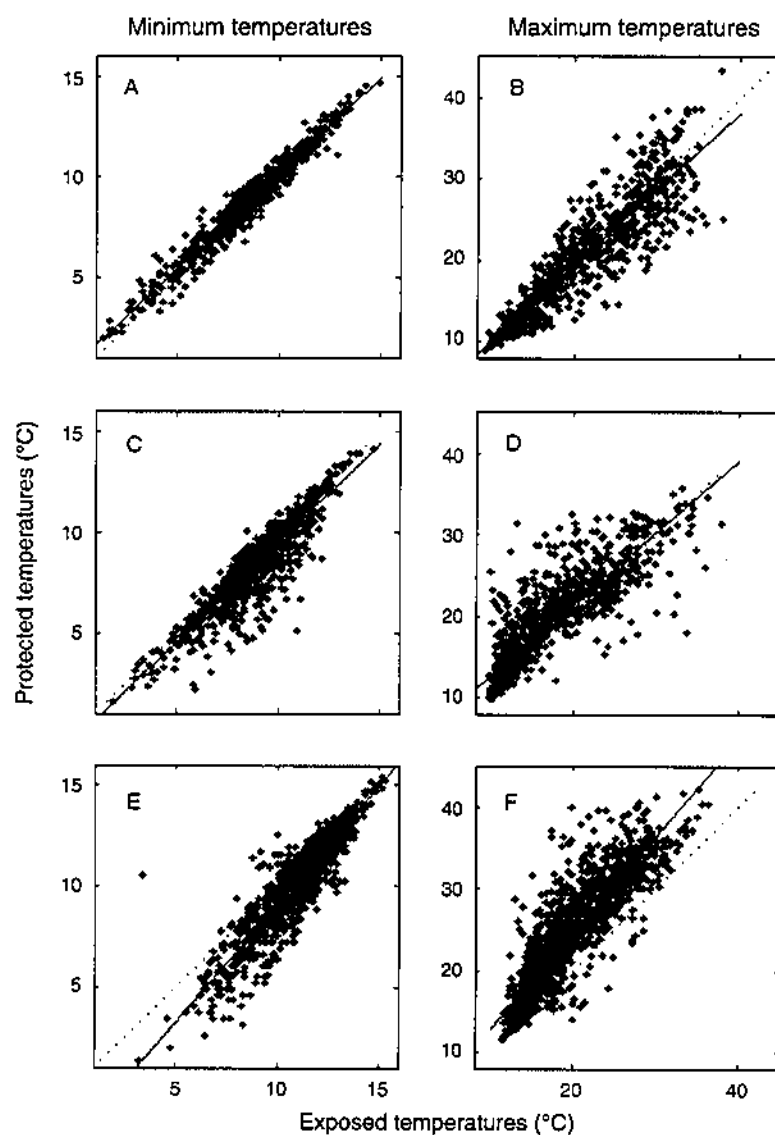

Exposed temperatures (°C)

Fig. 9. Scatter plots between exposed and protected locations for minimum (A, C, and E) and maximum (B, D, and F) daily mussel body temperatures in the three sites with paired locations: Boiler Bay (A and B), Strawberry Hill (C and D), and Hopkins (E and F). All correlations are highly significant (see Table 2 for statistics). The solid line is the least-squares fit to the data, while the dotted line shows the 1:1 relationship.

Table 5. Statistics for the correlation between exposed and protected locations at all three sites where the comparison was possible for average daily minimum temperatures and average daily maximum temperatures.

Location	Average daily minimum temperatures				Average daily maximum temperatures			
	r	t	df	P	r	t	df	P
Hopkins	**0.90901**	10.958	3111	1	**0.87063**	−21.458	3111	<0.001
Strawberry Hill	**0.89441**	6.1634	2060	1	**0.86023**	−7.1008	2060	<0.001
Boiler Bay	**0.97806**	−0.4499	1128	0.32643	**0.92838**	−6.3482	1128	<0.001

Notes: Values of r in boldface indicate significant correlations ($P < 0.001$); t is the t statistic after testing the alternative hypothesis that the mean of the protected location is greater than the mean of the exposed location with $\alpha = 0.05$; P is the probability that the null hypothesis is true; and rejections are shown in boldface type.
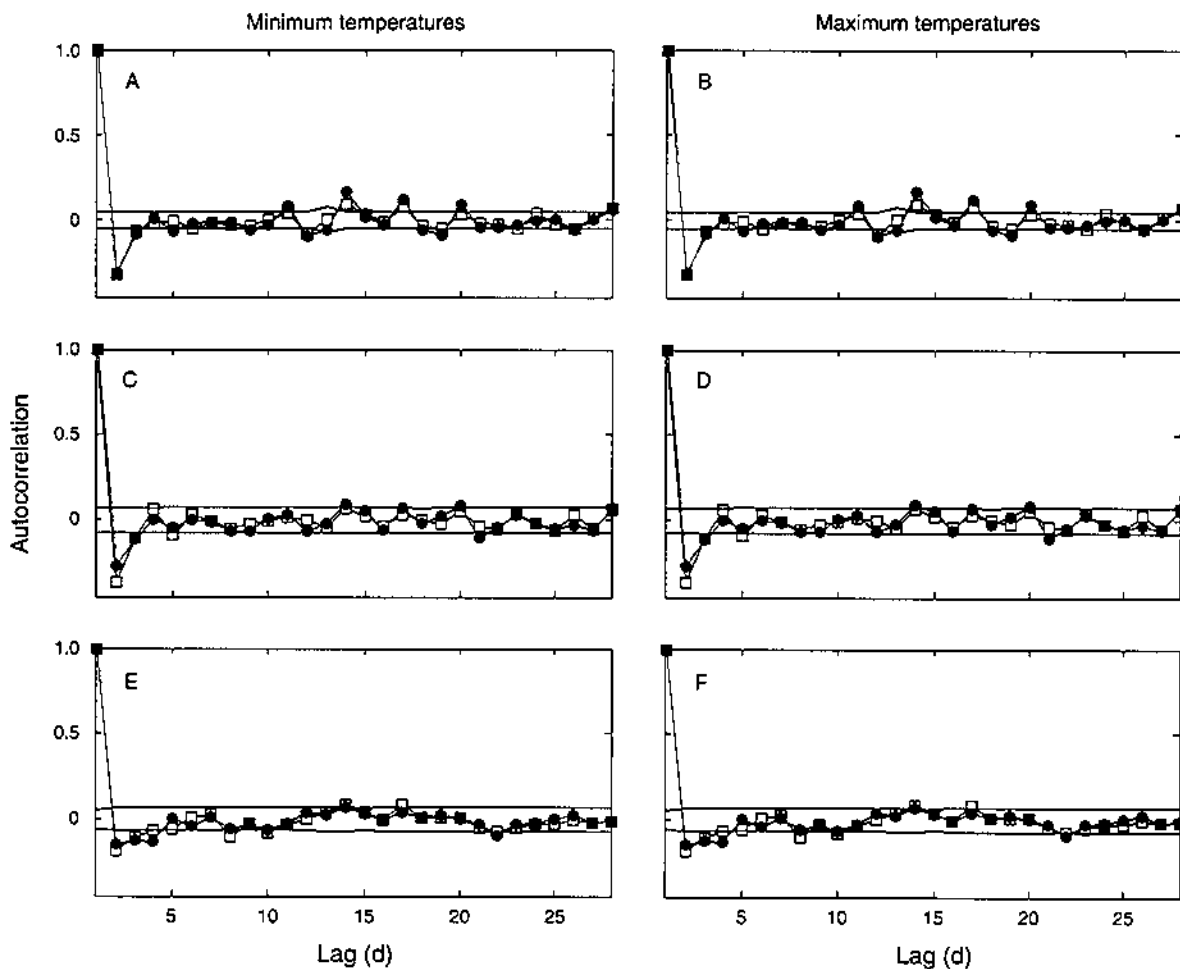
FIG. 10.   Autocorrelation functions of daily minimum (A, C, and E) and maximum (B, D, and F) mussel body temperatures at exposed and protected locations at Boiler Bay (A and B), Strawberry Hill (C and D), and Hopkins (E and F). Horizontal lines are Bonferroni-corrected ($\alpha = 0.05$) confidence intervals for significant autocorrelation. Solid circles are protected locations, and open squares are exposed locations. Note the extreme similarity in the autocorrelation functions and the presence of large and significant negative autocorrelation over 1–2 d lags in the high-latitude sites (A–D).

the middle of the day, the risk of extreme body temperatures may typically be fairly low, especially in wave-exposed areas, even when terrestrial climatic conditions are hot (Helmuth et al. 2002). Thus yearly temperature extremes at Jalama (SoCal) were very similar to those at Boiler Bay (WaOr; Table 3).

At northern sites, thermal conditions at wave-exposed and wave-protected sites can be quite similar during periods of calm waves at extreme low tide (Fitzhenry et al. 2004; Appendix). For example, yearly maximum temperatures recorded at Strawberry Hill wave-exposed and wave-protected sites during the course of this study were very similar in magnitude, even though values of average daily maximum temperatures were higher in the wave-protected site (Fitzhenry et al. 2004; Appendix). Consequently, because animals may be less acclimated to elevated temperatures, they may be more at risk for

physiological stress in these wave-exposed areas than at wave-protected areas.

Physiological implications of spatial variation in thermal stress

We observed clear differences among regions in the frequency and magnitude of extreme events, as well as the thermal history of these events, which may have important physiological and biogeographic consequences. Interpreting the importance of these patterns requires a better understanding of the relative importance of submerged temperature, aerial body temperature, and thermal history on the physiology of *M. californianus*. Mussels living in southern California experience predictable cycles of thermal stress over a lunar tidal cycle. Because of this environmental predictability at relatively short time scales, mussels may be able to acclimate to stressful thermal conditions (Weber

1992, Dahlgaard et al. 1998, Horowitz 2002). At higher latitudes, tidal rhythms in thermal stress are absent, and negative autocorrelations suggest that day-to-day thermal variability is highly unpredictable. In this context, organisms may be more vulnerable to damage from temperature maxima after periods of lower temperatures, and conversely, organisms at low-latitude sites may be less vulnerable, even when the absolute magnitude of the temperature maxima are the same. The interplay of the duration and magnitude of heat stress on an individual's subsequent acclimation to thermal stress is complex and poorly understood, although the process of "thermal hardening" is thought to be important (Krebs and Feder 1998). Clearly, more information on the time course of thermal acclimation will be of use in predicting organismal response to environmental variation. Interpreting the biological consequences of these complicated thermal will require that information about the physiological performance and tolerance of the organisms living along the North American west coast be collected on concomitant spatial scales (Hofmann 2005).

Implications for climate change

The mosaic of hot and cold spots across the distribution of *M. californianus* suggests a number of hypotheses regarding the geographic response of this species to future climate change. Latitudinal range shifts are commonly predicted consequences of climate change (e.g., Fields et al. 1993, Barry et al. 1995) and have been observed empirically in many systems (Parmesan et al. 1999, Walther et al. 2002). Local hot-spots may facilitate such poleward expansions by providing footholds for advancing populations, as has been hypothesized for some invasive populations (Ruiz et al. 1999). Alternatively, cold spots may function as thermal refugia as the ranges of colder water species contract to higher latitudes. If hot spots become sufficiently large, or occur adjacent to regions of unsuitable habitat, they could instead serve as barriers to dispersal, in effect creating disjunct populations (Helmuth et al. 2006). Because complex tidal regimes where latitudinal variability in the timing of low tide in summer and winter may be commonplace, the potential for hot spots and cold spots to be a worldwide phenomenon is very real. As a result, if thermal mosaics are a pervasive feature of many species' latitudinal ranges, a narrow focus on population changes only at the margins may overlook climatically forced local extinctions and other population changes at sites well within a species range. Our results therefore stress the importance of quantitatively examining patterns in environmental variables at scales relevant to organisms, and in forecasting the impacts of changes in climate across species range distributions.

Latitudinal trends in the temporal predictability of thermal stress also have implications for population responses to climate change. The temporal unpredictability (i.e., the low autocorrelation) of more northern

intertidal sites renders the organisms within them vulnerable to unsystematic deviations from the local mean. The true physiological impact of this prediction for a potential climate change scenario remains untested as far as we know. The level of temperature variability also influences the abilities of organisms to survive extreme temperature events (Kelty and Lee 2001) thus mussels at sites such as Cambria, which appeared as both a hot and a cold spot, may be better suited for rare climatic extremes than those from sites such as Tatoosh which exhibit more thermal stability.

Ultimately, however, the ecological and geographic responses of *M. californianus* to climatic change will depend not only on the direct physiological effects of temperature change on mussels, but also on ecological interactions with other species. For example, wherever the upper distributional limit of *M. californianus* shifts lower into the intertidal due to increases in aerial climatic stress, but that of its primary predators *(Pisaster ochraceous)* remains unaffected or shifts upward due to warming seawater temperatures (Sanford 1999), the prey will be "squeezed" out of the intertidal leading to local extinction (Harley 2003). In contrast, wherever the upper limits of both predator and prey are shifted downward by climatic stress, there will be no net effect of climate change on mussel beds. Moreover, all species are likely to be affected not only by shifts in aerial and aquatic climate, but by changes associated with sea level rise and wave height (Harley et al. 2006), both of which will determine emersion time.

Additional considerations

In sum, our results suggest that local patterns of wave splash and tidal regime can overwhelm larger-scale climatic gradients in driving patterns of body temperature (Helmuth et al. 2006), akin to what has been suggested for terrestrial ecosystems (Holtmeier and Broll 2005). Understanding the ecological relevance of these patterns, however, requires at least two other important areas of information not included in this study. First, the ability of organisms to evolve or physiologically acclimate to thermal stress must be considered (Clarke 2003, Chown et al. 2004) when determining when and where thermal extremes will cause mortality events. Second, if mortality events are to matter, then they must be of sufficient magnitude that larval supply is unable to repair or span the damage that occurs (Sotka et al. 2004). In other words, the spatial extent of the mortality must exceed the maximum dispersal of the larva to reinvade or traverse the hot spot or cold spot. Such an event may be particularly likely when a hot spot occurs adjacent to a region of unsuitable habitat.

Importantly, some of the patterns we describe here may be specific to the intertidal height at which they were measured. For example, organisms that live higher on the shore than *Mytilus californianus* may not experience predictable, two-week variation in thermal stress because daylight emersion occurs throughout the

fortnightly tidal cycle. Conversely, organisms that live very low in the intertidal will only be exposed by the low "spring tides" that coincide with new and full moons, and those at southern sites will almost never be exposed in the summer. Thus, tidal height can modulate the regional patterns observed in this study and our results may not apply to other species in this habitat. Thus the hot spots for mussels found in this study may not be hot spots for other groups living, for instance, in the high intertidal (Sotka et al. 2004). We strongly stress that the thermal environment in the intertidal zone must be considered from the perspective of the organism's interaction with the physical environment, as well as the physiological response of the organism to that environment.

Conclusions

In agreement with previous studies, we found a complicated pattern of organismal body temperatures along a large latitudinal gradient (Helmuth et al. 2002). The four major hot spots and cold spots identified here are spread along the entire geographic gradient with at least one hot spot and one cold spot in each of the three regions (WaOr, CenCal, and SoCal). Interestingly three sites, one in each region, appeared as both hot and cold spots, suggesting extreme thermal variability. These results suggest that extreme care must be exercised when choosing sites to serve as representatives of range edges and range centers, and are consistent with recent findings that several species do not display an "abundant center" distribution along the west coast of the United States (Sagarin and Gaines 2002a, b, Sagarin and Somero 2006). We also showed that considerably more information is present in the thermal signal when analyses of thermal data move beyond mean temperatures and water temperature. Investigations of the physiological or ecological effects of climate on organisms must carefully consider what metrics are most relevant (Gilman et al. 2006). Depending on the organism and the question, it will be essential to understand temporal patterns of thermal variability and predictability within sites, as well as differences in means and extremes among sites. With so many variables, ecologists must be careful to explicitly record environmental conditions relevant to organismal physiology and not rely on simple proxies, such as air or water temperature. Obviously, this complicates the work of the investigator, especially when choosing sites for comparison through space or time. However, without this degree of detail, ecologists and physiologists may miss crucial features of the physical environment that determine individual fitness, population and community dynamics, biogeographic patterns, and ecological responses to climate change.

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APPENDIX

Monthly summary statistics for temperatures at the study sites (*Ecological Archives* M076-017-A1).

Dirección Ejecutiva

Departamento de Control de la Contaminación

Área Control de la Contaminación Hídrica

GOBIERNODECHILE

COMISION NACIONAL
DEL MEDIO AMBIENTE

DOCUMENTO ENVIADO POR CORREO ELECTRÓNICO

"Proceso de Revisión DS 90"

Enviado por : CORMA- Julio de la Fuente

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Fecha : Lunes, 13 de abril 2009

Hora : 17:08 hrs

DOCUMENTOS ANEXOS

N°	DOCUMENTO
1	Antecedentes de Boro
2	Respuesta de CONAMA frente a antecedentes de Boro presentados

De:	Julio de la Fuente (Papeles) [Jdelafuente@papeles.cmpc.cl]
Enviado el:	Lunes, 13 de Abril de 2009 17:08
Para:	Claudia Galleguillos
CC:	Pedro Navarrete (CMPC Celulosa G.Tecnica)
Asunto:	Abatimiento de boro
Marca de seguimiento:	Seguimiento
Estado de marca:	Púrpura

Estimada Claudia

Hemos revisado con nuestros asesores los antecedentes sobre tecnologías para el abatimiento de boro que nos enviaste, nuestros comentarios al respecto son los siguientes:

Reparos de extrapolar al tratamiento industrial los proyectos ASITEC Ltda./Universidad de Tarapacá y ABAR/Fundación Chile
sobre sistemas de tratamiento de aguas con contendidos de boro.

1. Ambos proyectos están desarrollados sólo a nivel experimental, y no dan cuenta de ninguna experiencia aplicada en su respaldo, ni en Chile ni en el exterior.

2. El objetivo principal de ambas iniciativas no es el tratamiento industrial (aunque el proyecto ASITEC Ltda/UTA indique, sin mayor fundamento, que puede configurarse para este fin). Son aplicaciones específicas para regadío en zonas del norte de Chile donde se supera la norma de riego (NCh.1333).

3. Por definición los parámetros de calidad del agua para riego son más estrictos que los de una norma de emisión como el D.S.90.

4. Esos proyectos experimentales tampoco son extrapolables al resto del país, por falta de evidencia empírica suficiente y porque los períodos de déficit hídrico, que son los que justifican la necesidad de riego, son muy inferiores a los del norte de Chile, lo que diferencia notablemente el efecto sobre los cultivos.

5. Una norma de emisión de boro debe considerar las peculiaridades de las distintas regiones agro-climáticas en lo relativo a tipo de cultivos, disponibilidad hídrica, niveles naturales de cursos de agua y caudales de dilución.

6. Las tecnologías existentes a nivel mundial para abatimiento de boro, se relacionan con la osmosis inversa y con el intercambio iónico.

7. Existe un ejemplo de planta de tratamiento en base a osmosis inversa para grandes caudales, pero para fines de desalinización de agua de mar para agua potable. Se trata de la Planta *Ashkelon* de Israel (la más grande del mundo, construida el año 2006) que, con un costo de US$ 250 millones, tiene capacidad para tratar 320.000 m3 al día de agua de mar, produciendo alrededor del 13% del agua potable consumida a nivel domiciliario en Israel. Esta planta ocupa una superficie de 75.000 m2 (7,5 Há) y cuenta, entre otras instalaciones, con unidades desalinizadoras, líneas de bombeo desde el mar, caminos y una planta termoeléctrica especialmente dedicada a su operación. Es decir, tiene una envergadura física y de inversión que tampoco permite extrapolarla para fines de tratamiento industrial.

8. Una norma de emisión de boro debe balancear los niveles deseados y la factibilidad del tratamiento necesario para alcanzarlos (tecnologías y costos actualmente disponibles – BAT–). Para ello no basta una revisión solamente a nivel de investigación y desarrollo.

Atte
Julio De la Fuente Ibar
CORMA

20-04-2009

De: Claudia Galleguillos [mailto:cgalleguillos@conama.cl]
Enviado el: Lunes, 13 de Abril de 2009 18:00
Para: Julio de la Fuente (Papeles)
CC: Pedro Navarrete (CMPC Celulosa G.Tecnica); Mariela Arevalo
Asunto: RE: Abatimiento de boro

Estimado Sr. Julio de la Fuente, agradecemos la información enviada y acusamos recibo de la misma, sin embargo, al hacer una exhaustiva revisión, hemos constatado que no contiene lo solicitado en conversación sostenida el día 27.03.09, respecto a analizar las diversas tecnologías disponibles para abatir boro, ver cuales se ajustan a las necesidades de la empresa, cuanto es el porcentaje de remoción (propuesta de nuevo valor con tecnología de abatimiento) y cuales son sus costos de implementación y operación.

Saluda atentamente,

Claudia Galleguillos C.
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