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Efectos de la variabilidad climática y la pesca en
ecosistemas costeros de América Latina

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RESUMEN

Las pesquerías de pequeña escala (SSF por su sigla en inglés) son sistemas sociales-ecológicos que desempeñan un papel crítico en términos de la seguridad alimentaria y la mitigación de la pobreza en América Latina. Estas pesquerías se ven cada vez más amenazadas por factores antropogénicos y climáticos que actúan en múltiples escalas. En esta Tesis se investigan los efectos de la variabilidad climática y la pesca en los ecosistemas costeros de América Latina. En este sentido se analiza la importancia de las variables climáticas en las variaciones de abundancia de recursos pesqueros explotados las SSF. Asimismo se discuten los efectos combinados adicionales de dos factores humanos: la globalización de los mercados y la gobernanza. Para determinar la relevancia de la temperatura en la dinámica poblacional de la almeja amarilla (*Mesodesma mactroides*) explotado por una SSF de Uruguay se implementaron dos modelos edad-estructurados. Se compararon los ajustes de un modelo estándar y otro donde se consideró la sobrevivencia del recurso en función de la anomalía de temperatura superficial del mar en la zona costera (SSTA por sus siglas en inglés). La inclusión de esta función mejoró sensiblemente el ajuste del modelo, lo cual sugiere que la temperatura juega un papel importante en la explicación de las tendencias de largo plazo de dicho recurso. Asimismo se evaluaron los efectos combinados de gran escala y largo plazo de la pesca, el clima y las variables económicas en la almeja antes mencionada y la almeja congénica *Mesodesma donacium* que habita las playas del Océano Pacífico de América del Sur. Las variaciones en las capturas o abundancia de las almejas se relacionaron con variables bioeconómicas (precios unitarios) y climáticas, como las SSTA y los índices climáticos a gran escala (Oscilación Decadal del Pacífico y Oscilación Multidecadal del Atlántico). La captura o abundancia de los recursos variaron de forma diferencial según la latitud y las características oceanográficas de cada región. Para *M. donacium*, las relaciones entre las capturas y las variables explicativas difirieron entre unidades bioclimáticas. Los eventos El Niño Oscilación del Sur cálidos contribuyeron a la disminución de las capturas en Perú y el norte de Chile, mientras que se incrementaron en el sur de Chile, lo que sugiere un efecto positivo en el borde sur del rango de distribución de esta especie. En el caso de *M. mactroides*, las tendencias de largo plazo en las variaciones de la abundancia estuvieron relacionadas con la intensidad de pesca y las SSTA, observándose las mayores abundancias durante el período frío que durante el cálido; además las mortandades masivas ocurridas a partir de 1994 diezmaron la población. Por otra parte el déficit de la oferta respecto a la demanda, agravada por los bajos costos de operación asociados a estas pesquerías estimularon el aumento del esfuerzo de pesca, elevaron los precios, llevando a estas especies de almejas a niveles cercanos a la extinción (efecto Allee antropogénico). La falta de respuesta de los recursos a las clausuras pesqueras implementadas después de las mortandades masivas sugiere que estos sistemas superaron ciertos umbrales críticos que impiden su recuperación. Esto lleva a la necesidad de intensificar las investigaciones para lograr identificar las señales que permitan establecer alertas tempranas para gestionar las pesquerías de estos moluscos costeros con riesgos de conservación. Entre los factores que amenazan estas pesquerías y la fauna

asociada a las playas arenosas, están los derivados de las actuales tendencias climáticas que afectan su hábitat (e.g. aumento del nivel del mar, incremento en la frecuencia de tormentas fuertes). En este sentido se analizaron los efectos de las tendencias a largo plazo de la variabilidad climática en la morfodinámica de dos playas arenosas en la costa Atlántica de Uruguay, una reflectiva y otra disipativa. Se observó que el cambio hacia una fase cálida de la Oscilación Multidecadal del Atlántico a partir de 1995, resultó en un predominio de las SSTA positivas en el área de estudio, el cual se vio asociado a un aumento de las anomalías de velocidad del viento, en particular los de componente sur, sobre todo después de 1997. Las tendencias climáticas anteriormente mencionadas afectaron las características morfodinámicas de las playas en forma diferencial: la playa disipativa mostró un incremento de las características disipativas y la playa reflectiva mostró una intensificación de las características reflectivas. El tamaño de grano del sedimento fue una variable perdurable que se mantuvo a lo largo del tiempo. Si bien la playa reflectiva mostró una mayor resiliencia frente a los forzamientos climáticos, los procesos erosivos asociados a estos, sumados al desarrollo urbano, actividades extractivas y otros emprendimientos sobre la costa podrían afectar la biodiversidad y la pérdida de hábitats críticos que sustentan servicios ecosistémicos. Estos efectos, así como el impacto de la variabilidad climática detallado en esta Tesis en numerosas SSF de América Latina, destacan la necesidad de mejorar los sistemas de gestión, de gobernanza así como el desarrollo de programas y estrategias de conservación para mitigar los impactos antropogénicos y del clima en los sistemas biofísico y social pertenecientes a los sistemas sociales-ecológicos definidos por las SSF.

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CAPÍTULO 1 - INTRODUCCIÓN GENERAL

1.1 Variabilidad climática y su efecto en la biodiversidad

El calentamiento global terrestre es ampliamente aceptado en la actualidad. En el último siglo la temperatura media global terrestre ha aumentado 0.74°C y la temperatura superficial oceánica 0.67°C (Trenberth et al. 2007, IPCC 2007). En este contexto, los Océanos Pacífico, Atlántico e Índico en el Sur juegan un papel crítico en la transmisión de señales al clima mundial, principalmente debido a la no existencia de barreras continentales entre ellos (Bard & Rickaby 2009). Se ha constatado una tendencia similar de incremento en la temperatura para estos océanos, incluso con falta de información detallada al sur de la latitud 30°S (Gille 2002). Estos cambios en la temperatura son consistentes con la migración sur de la Corriente Circumpolar Antártica, tanto en el Pacífico como en el Índico y Atlántico (Swift 1995). Recientes estudios paleoclimáticos indican a la migración del Frente Subtropical (STF, por sus siglas en inglés) como modulador del clima durante los períodos glaciales (Bard & Rickaby 2009). Por definición, el STF es el límite entre las aguas subtropicales y las aguas subantárticas, originándose en la zona de la convergencia de las Corrientes de Brasil y de Malvinas, constituyendo una zona frontal que cruza todo el Atlántico sur, el Índico y el Pacífico aproximadamente a 40°S (Stramma & Peterson 1989). Sin embargo, dicha zona muestra una amplia variabilidad en su localización latitudinal, que podría ser producto de las condiciones atmosféricas y variabilidad a gran escala de la circulación oceánica (Stramma et al. 1995). Además del calentamiento del mar, los modelos de Cambio Climático predicen un aumento de la estratificación de los océanos y cambios en la circulación (FAO 2008).

Los procesos climáticos tienen efectos drásticos en el funcionamiento de los ecosistemas marinos, operando en una amplia gama de escalas temporales y espaciales (Bakun 1996, Rouyer et al. 2008). La variabilidad del clima oceánico incluye corrientes cambiantes y cambios de temperatura, que alteran la alimentación, el crecimiento y los patrones migratorios de fauna marina (Miller et

al. 2010). En América del Sur, estos escenarios se relacionan con variaciones interanuales (por ejemplo, El Niño Oscilación del Sur: ENSO por su sigla en inglés) y multidecadales (e.g la Oscilación Decadal del Pacífico (PDO, por su sigla en inglés) y la Oscilación Multidecadal Atlántico (AMO, por su sigla en inglés).

Los episodios de El Niño se caracterizan por períodos con temperaturas superficiales del mar excepcionalmente cálidas en el Pacífico tropical oriental debido a la relajación de los vientos alisios. Mientras que durante los episodios de La Niña los vientos alisios se intensifican, potenciando los afloramientos y determinando la presencia de aguas superficiales con temperaturas por debajo de las medias históricas. El Niño suele durar 9-12 meses, y La Niña suele durar 1-3 años. Ambos tienden a desarrollarse durante marzo-junio, alcanzan su máxima intensidad entre diciembre y abril, y luego se debilitan durante mayo-julio (Figura 1) (<http://www.cpc.ncep.noaa.gov/products>).

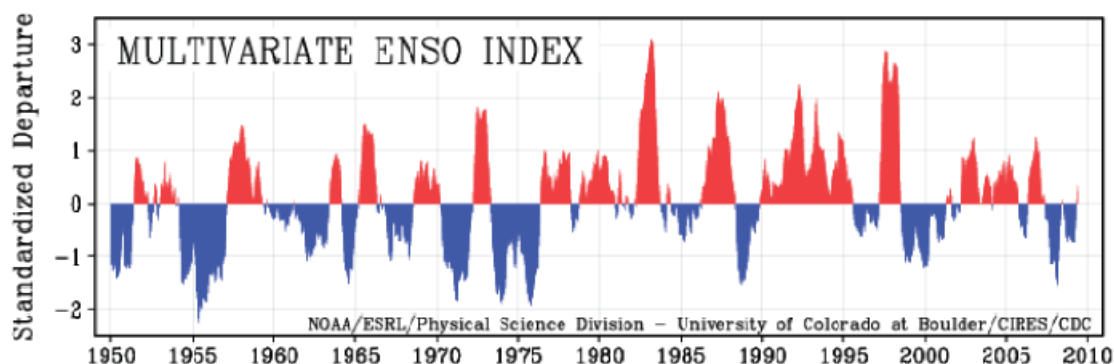


Figura 1.1. Serie cronológica de variaciones el Índice ENSO Multivariado, los positivos son eventos ENSO cálidos o Niños (rojo) y los negativos son los eventos ENSO fríos o Niñas (azul) (<http://www.esrl.noaa.gov/psd/data/climateindices/list/>).

Esta variabilidad ambiental oceánica a gran escala influye en las corrientes y las propiedades de las masas de agua. El PDO se define como el componente principal de la variabilidad de la temperatura mensual superficial del mar del Pacífico Norte (del 20N hacia los polos) (Zhang et al. 1997), presentando fases cálidas y frías que pueden durar de 20 a 30 años (Figura 1.2).

Los ciclos del PDO han influido en la abundancia de pequeños pelágicos en el Pacífico tropical y templado (Chavez et al. 2003, Montecino & Lange 2009), al igual que en las poblaciones de salmones del Pacífico norte (Finney et al. 2010) e incluso en las comunidades de fitoplancton (Cloren & Dufford 2005).

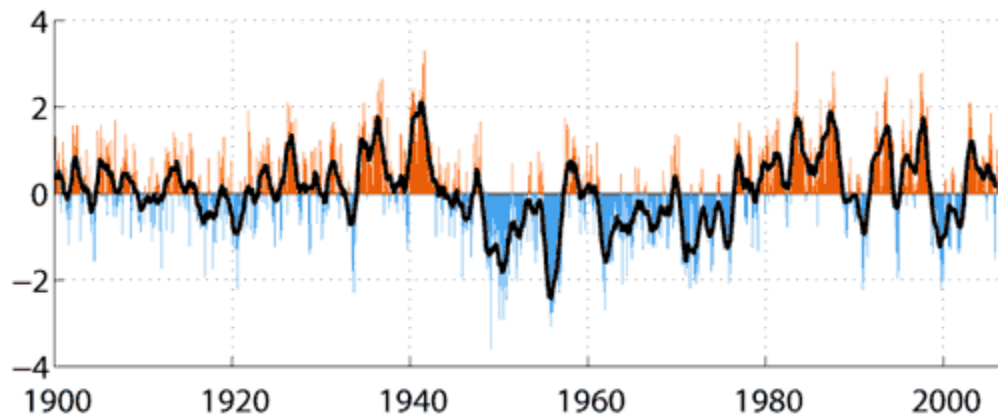


Figura 1.2. Serie cronológica de la Oscilación Decadal del Pacífico, mostrando fases cálidas (rojo) y frías (azul) (<http://www.esrl.noaa.gov/psd/data/climateindices/list/>)

Las series de tiempo del AMO se calculan a partir del conjunto de datos SST mensuales. Se trata básicamente de un índice de las temperaturas Atlántico Norte al cual se le quita la tendencia. Presenta fases frías y cálidas que pueden durar de 20 a 40 años y una diferencia de alrededor de 1°C entre los extremos (Figura 1.3). Estos cambios son naturales y han estado ocurriendo durante al menos los últimos 1000 años (Enfield et al. 2001).

Los ciclos del AMO han sido señalados como responsables de cambios en la abundancia y distribución de peces, la biomasa de fitoplancton y zooplancton en el Atlántico Norte (Edwards et al. 2013) y el clima en América del Sur (Seager et al. 2010).

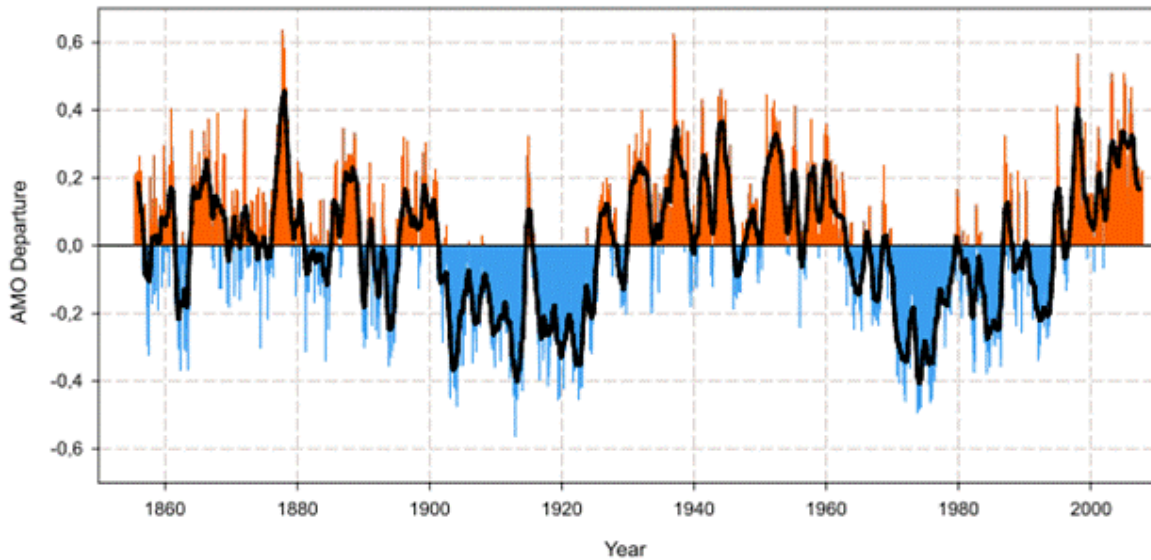


Figura 1.3. Serie cronológica de la Oscilación Multidecadal del Atlántico mostrando fases cálidas (rojo) y frías (azul) (<http://www.esrl.noaa.gov/psd/data/climateindices/list/>)

Los ciclos climáticos afectan diferentes niveles organizacionales, incluyendo poblaciones, comunidades y ecosistemas. Creciente evidencia científica muestra que las fluctuaciones climáticas afectan la abundancia y biogeografía de los organismos (Stenseth et al. 2002, Cheung et al. 2012), operando tanto directamente a través de procesos fisiológicos (metabolismo o reproducción) o indirectamente a través de alteraciones en la estructura del ecosistema y los procesos relacionados a éste (e.g. relaciones predador-presa y competencia: Stenseth et al. 2002). Por ejemplo, los cambios en la temperatura superficial del mar afectan la estructura de las comunidades fitoplanctónicas, pudiéndose trasladar este efecto a niveles tróficos más altos (Richardson & Schoeman 2004). Estos cambios determinan a su vez variaciones en la magnitud de interacciones interespecíficas e incluso generan nuevas interacciones, con sus consecuentes repercusiones en la abundancia y una eventual aceleración en las tasas de extinción (Thomas et al. 2004). Estudios de interacciones tróficas han demostrado que el Cambio Climático genera diversas presiones en los organismos, sopesando la necesidad de permanecer en sincronía con los períodos de una máxima disponibilidad de alimento y los beneficios de minimizar la predación (Both et al. 2008). Asimismo, un adelanto de los eventos reproductivos producto del

incremento en la temperatura podría generar alteraciones en las interacciones tróficas en especies que carecen de suficiente plasticidad para adecuarse a dichos cambios (Brook 2009).

1.1.1 Variabilidad climática y pesca

La pesca juega un papel importante en la seguridad alimentaria y como fuente de ingreso económico, además de emplear a millones de personas entre pescadores y trabajadores asociados a las actividades pesqueras y acuicultura. El alimento acuático proporciona 20% de la proteína animal per capita, incluyendo a más de 2800 millones de personas, la mayoría en los países en desarrollo (FAO 2008). El aumento de la temperatura de los océanos, ríos, y lagos, cambios en la precipitación, salinidad de las aguas y acidez de los océanos, e inclusive el incremento en la frecuencia e intensidad de los eventos climáticos extremos, aumentan la incertidumbre en la disponibilidad de recursos pesqueros para su captura (FAO 2008).

Los cambios inducidos por el clima pueden ser agravados por otras variables antropogénicas actuando simultáneamente, particularmente la presión pesquera (Harley et al. 2006). De hecho, la existencia de muchas especies está comprometida como resultado de varias fuentes de estrés, en su mayoría provocadas por el hombre (Hare 2003). No obstante, los efectos relativos de la explotación pesquera y de los forzamientos climáticos son difíciles de discernir y participan conjuntamente sobre las poblaciones explotadas. Más importante aún, los efectos acumulativos no son simplemente aditivos, sino que el clima y la pesca interactúan de manera tal que el clima puede provocar fallos en un sistema de gestión pesquera y la explotación pesquera también puede impedir la capacidad de una población para soportar o ajustarse a los cambios climáticos (Planque et al. 2010). Además, los cambios climáticos incrementan los riesgos de invasión de especies y propagación de enfermedades transmitidas por diferentes vectores, que pueden amenazar la calidad y disponibilidad de alimento (FAO 2008).

Asimismo, han sido documentados cambios en la distribución de especies marinas, los cuales en general consisten en una expansión hacia los polos en las especies de aguas cálidas y una contracción hacia los polos de las especies de aguas frías (FAO 2008). En el Atlántico Sudoccidental se han registrado cambios los rangos de distribución de peces asociados a la variabilidad climática donde se observó una mayor influencia de aguas cálidas lo que permitió aumentar el rango de distribución de peces asociados a aguas tropicales y subtropicales (e.g. Segura et al. 2009, Izzo et al. 2010), en este caso corresponde a variaciones climáticas y oceánicas interanuales.

En los últimos años, una serie de evaluaciones e iniciativas internacionales han establecido la necesidad de un enfoque ecosistémico a los desafíos que plantea el manejo de los sistemas marinos (Sinclair et al. 2003, Ommer 2006, Bianchi et al. 2008). El objetivo de la planificación y desarrollo de las políticas marítimas es mantener saludables los sistemas sociales-ecológicos (SES por su sigla en inglés, ver Ostrom 2009) que sustentan los servicios ambientales y los medios de subsistencia de las poblaciones humanas. Los SES marinos se encuentran afectados por factores ambientales y los efectos de la globalización de los mercados. El cambio climático es un estrés adicional que puede afectar estos sistemas, apartándolos de los rangos de variabilidad históricamente observados (Perry et al. 2010). Uno de los principales retos es identificar los factores que determinan los cambios de régimen que afectan a los SES marinos. El término “cambio de régimen” estaba restringido a la descripción de procesos atmosféricos multidecadales y sus consecuencias en el ambiente físico (e.g. Rahmstorf 1999). Actualmente es aplicado de manera más amplia, por ejemplo en investigaciones tróficas en lagos (Scheffer et al. 2001) y estuarios (Petersen et al. 2008). De esta manera, cambios en la abundancia y composición de especies de una comunidad a nivel regional o escalas espaciales mayores, producto de factores físicos externos o antropogénicos, pueden constituir un cambio de régimen (Kraberg et al. 2011).

Las economías que dependen de la pesca, las comunidades costeras y los pescadores, experimentarán los efectos del cambio climático de diversas maneras. La vulnerabilidad de las comunidades pesqueras depende de la capacidad de los individuos y los sistemas para prever dichos cambios y adaptarse a ellos. Esta capacidad de adaptación depende de las características de la comunidad y puede verse limitada por factores culturales, marcos institucionales o de gobernanza (FAO 2010). De esta manera, la vulnerabilidad varía entre países, comunidades y entre grupos demográficos de una misma sociedad. En general, los países y los individuos más pobres son más vulnerables a los efectos del cambio climático. Las pesquerías como SES dinámicos están experimentando un rápido cambio en los mercados, la explotación y la gobernanza. Los efectos combinados de estos cambios y los del cambio climático hacen que sea difícil predecir las repercusiones futuras del cambio climático para los SES pesqueros (FAO 2010).

El rango de la variabilidad climática es un tema de escala temporal y depende de la experiencia y las capacidades del SES para adaptarse a los cambios que esta variabilidad produce en los sistemas. En una típica vida de trabajo de un pescador del Pacífico es de esperar que haya experimentado varios eventos ENSO, y al menos un evento interdecadal. En el caso de la variabilidad climática de mayor escala temporal, no puede ser experimentada por los individuos, pero probablemente debe haber sido experimentada por los antepasados y/o por la comunidad, integrándose de esta manera al conocimiento ecológico tradicional (Trosper 2003). Las transiciones entre esas escalas más largas serán percibidas como “cambio” en lugar de variabilidad (Perry et al. 2010).

1.1.2 Playas arenosas y variabilidad climática

Las playas arenosas ocupan gran parte de las costas expuestas de los márgenes continentales a nivel mundial (McLachlan & Brown 2006) y constituyen uno de los ambientes físicamente más estresantes de todos los ecosistemas marinos (Defeo

& McLachlan 2005). Numerosos factores, como tamaño de grano, pendiente, mareas y altura y período de la ola, interactúan determinando un amplio rango de estados morfodinámicos que se extiende desde playas disipativas a reflectivas (Short 1996). Las playas disipativas están definidas por arenas finas, pendientes suaves, baja penetrabilidad del sustrato y alto contenido de agua, mientras que, en el otro extremo, las playas reflectivas presentan arena gruesa, pendiente pronunciada, alta penetrabilidad del sustrato y bajos contenidos de agua y materia orgánica (Short 1999). Estos sistemas se encuentran interconectados con ecosistemas adyacentes tales como el sistema de dunas y la zona de barrido y tienen su biota propia, conformando una unidad geomorfológica denominada zona litoral activa (Short & Hesp 1982). Como consecuencia de esta interconexión, los efectos del clima en estos ecosistemas arenosos pueden actuar directamente en sus subsistemas (e.g. dunas o zona de barrido) o indirectamente, en los ecosistemas adyacentes (e.g. estuarios). A esto se agregan efectos acumulativos derivados de otras presiones humanas, tales como la construcción, actividades extractivas (arena) y pesca (Defeo et al. 2009).

Las playas arenosas son altamente valoradas a nivel mundial debido a que constituyen los tipos de costa más utilizados por la sociedad (McLachlan et al. 2013). A los valores económicos y sociales que poseen, debe sumársele las características distintivas desde el punto de vista ecológico y de su biodiversidad. Actualmente, estos ecosistemas únicos deben enfrentar una escalada de intervenciones antrópicas generalmente relacionadas con la recreación y el Cambio Climático (Defeo et al. 2009). Los factores ambientales, tales como cambios en los patrones de vientos y aumento del nivel del mar, generan erosión y retracción de las líneas de costa, los cuales, sumados a un incremento de la temperatura, pueden afectar severamente a las comunidades faunísticas. Esto cobra especial importancia si se considera que las fluctuaciones demográficas de las poblaciones que habitan playas arenosas son causadas por la acción conjunta de factores abióticos y bióticos, incluyendo factores ambientales exógenos e interacciones intra e interespecíficas (Defeo et al. 1992, 1997, Defeo & de Alava

1995) y actividades humanas (Lima et al. 2000). En este contexto, el incremento de la temperatura del mar puede tener efectos diferenciales a distintas latitudes y en taxa con diferentes capacidades para dispersarse. Por ejemplo, muchas especies de playas arenosas (e.g. crustáceos peracáridos) carecen de fases larvales dispersivas, por lo que cambios en el clima les pueden afectar en mayor grado. Las especies endémicas y estenotermas son particularmente vulnerables a los efectos del Cambio Climático y podrán ser reemplazadas por especies de bajas latitudes (O'Hara 2002). La biota de una playa también responderá a los efectos provocados por el cambio de temperatura. Por ejemplo, grandes cambios en el ecosistema planctónico en el Atlántico Norte han sido asociados con pequeños incrementos ($\sim 0.6^{\circ}\text{C}$) en la temperatura detectados en las últimas cinco décadas (Richardson & Schoeman 2004, Edwards et al. 2013). Siendo el plancton una fuente de alimento clave para las especies suspensívoras de las playas, cambios en la comunidad planctónica tendrán efectos impredecibles en la macrofauna que habita estos ecosistemas.

El aumento del nivel del mar es una de las consecuencias directas del calentamiento global. Se estima que el nivel del mar está subiendo $1.7 \pm 0.5 \text{ mm}\cdot\text{año}^{-1}$ (IPCC 2007), con posibilidades de aumento (Rahmstorf et al. 2007). Esto, sumado a un pronóstico de mayor frecuencia de episodios de tormenta fuertes, potenciaría la erosión de las playas y afectaría a la biota residente (IPCC 2007). Asimismo, las predicciones respecto a la acidificación de los océanos reduciría las tasas de calcificación y metabolismo del calcio en organismos marinos (Feely et al. 2004), incluyendo moluscos y crustáceos de playas arenosas (Hall-Spencer et al. 2008), determinando costos sociales y económicos significativos en el futuro (Narita 2012).

En consecuencia, un adecuado manejo de las playas arenosas requiere estrategias de mitigación o adaptación a largo plazo, incluyendo la regulación del uso de la faja costera (Finkl & Walker 2004). Las medidas para promover la resiliencia incluyen la protección de la vegetación, la estabilización de las dunas,

el mantenimiento del suministro de sedimento y la existencia de zonas buffer, además de una fuerte regulación gubernamental en cuanto al uso de la faja costera (Defeo et al. 2009).

1.1.3 Las almejas de playas arenosas

Las pesquerías de invertebrados en las playas arenosas tienen fuertes connotaciones socioeconómicas, principalmente en los países en desarrollo (McLachlan et al. 1996, Defeo 2003). Las pesquerías artesanales representan una fuente de subsistencia, suministrando empleo a las comunidades de pescadores, e incluso exportaciones para el país. Muchas de las especies que sustentan estas pesquerías muestran una restringida distribución geográfica, son endémicas o tienen un rol ecológico importante en la comunidad macrobentónica (Defeo et al. 1993, McLachlan et al. 1996). Asimismo, muchas especies de la playa tienen un fuerte componente recreacional que dificulta su administración, debido a que el número de recolectores es difícil de controlar y se hace problemática la obtención de información y la estimación de la captura y esfuerzo pesquero (Defeo 1987, 1989, Schoeman 1996, Kyle et al. 1997). La longevidad de estas especies depende de la latitud, pero en promedio va de 2 a 8 años y en general presentan un rápido crecimiento y maduración temprana (McLachlan et al. 1996).

Muchas poblaciones de playas arenosas que sustentan pesquerías artesanales y/o recreacionales muestran grandes fluctuaciones en su abundancia, debidas, entre otros factores, a tasas de reclutamiento muy variables y ocurrencia de mortandades masivas (McLachlan et al. 1996, Defeo 2003). En relación a éstas, se ha observado acumulación de toxinas producto de las floraciones algales nocivas que pueden provocar problemas sanitarios en el hombre. El fenómeno de las floraciones de algas nocivas ha aumentado espectacularmente en los últimos 30 años en las cercanías de estos ecosistemas (McLachlan & Brown 2006, Hallegraeff 2010). Aunque se desconocen las razones de dicho incremento, se postula que se debe al calentamiento global (IAEA 2004, Hobday et al. 2006). En

zonas oceánicas costeras, en particular playas arenosas donde se han implementado medidas de ordenamiento pesquero que han resultado exitosas, se han observado mortandades masivas que han generado una evidente disminución de las poblaciones de almejas en toda su área de distribución (Defeo 2003). Esto sugiere la existencia de otros efectos a gran escala asociados al clima que aumentan la incertidumbre acerca del comportamiento del recurso en el largo plazo, lo cual dificulta la implementación de cualquier medida de manejo (Defeo 2003).

1.1.4 Las almejas del género *Mesodesma* en América del Sur

Las almejas del género *Mesodesma* de las costas del Atlántico (*Mesodesma mactroides*) y Pacífico (*Mesodesma donacium*) de América del Sur dominan en términos de biomasa las comunidades de playas arenosas en miles de km de extensión de costa (Defeo 2003). Además de su importancia clave en los flujos de energía en estos ecosistemas, estas especies de origen antártico (von Ihering 1907) son objeto de explotación artesanal y recreacional. Dicha explotación ha pasado por diferentes fases históricas en su explotación (Castilla & Defeo 2001), las cuales se describen a continuación.

***Mesodesma mactroides* del Atlántico**

La almeja amarilla *Mesodesma mactroides* Deshayes, 1854 (Bivalvia: Mesodesmatidae) habita playas arenosas de la costa atlántica de América del Sur, desde San Pablo, Brasil (24°S) hasta el sur de Buenos Aires, Argentina (41°S) (McLachlan et al. 1996, Fiori & Defeo 2006). La pesca artesanal o recreacional de *M. mactroides* se desarrolla en los tres países que abarca su distribución (Brasil, Uruguay y Argentina) ya sea para alimento, carnada, actividad turística y/o comercial (Defeo 1996, 1998, Defeo et al. 1993, McLachlan et al. 1996).

La información sobre la pesquería en Brasil es escasa; la almeja amarilla puede llegar a desaparecer al final de la temporada estival en los alrededores de balnearios

importantes, donde es consumida como alimento y carnada (Gianuca 1983). En Argentina, la explotación de la almeja amarilla se ha llevado a cabo desde 1940, conjuntamente con el desarrollo de la industria del enlatado (Olivier et al. 1971). Las capturas llegaron a su máximo en 1953 con 1078 t, luego declinaron y la clausura total de la pesquería fue implementada desde 1958 (Olivier et al. 1971). Incluso con la pesquería cerrada, el stock siguió disminuyendo por extracción ilegal en la cual se incluye la actividad del turismo estival (Bastida et al. 1991, Dadón 2001).

En Uruguay, la almeja amarilla constituyó durante mucho tiempo el segundo recurso malacológico más explotado, después de *Mytilus edulis platensis* (Defeo 1989). La distribución de la población principal de almeja amarilla en Uruguay está limitada por dos descargas de agua dulce, el Arroyo Chuy al norte y otra artificial al sur, el Canal Andreoni, ocupando una playa disipativa de 22 km de extensión (Defeo 1987, 1989). La demanda de este producto pesquero determinó un aumento en la captura durante los años ochenta, con 62 t en 1981 a un máximo de 219 t en 1985. Luego las capturas disminuyeron rápidamente y se decretó una clausura de la pesquería entre abril 1987 y diciembre 1989. Entre 1990 y 1991 se dio una fase de estabilización, donde la pesquería fue reabierta con la determinación de medidas operacionales de manejo, tales como cuotas de captura por estación, rotación de áreas, talla mínima legal y cuotas individuales de pesca (Defeo 1993). Durante esa fase las capturas variaron entre 50 y 60 t por año, pero la captura por unidad de esfuerzo se duplicó respecto a las cifras anteriores a la clausura. El manejo de la pesquería fue mejorando gracias a la aplicación de las medidas de regulación antes mencionadas, conjuntamente con la adopción del co-manejo pesquero como estrategia institucional de gobernanza (Defeo 1996, 1998). La ocurrencia de una mortandad natural masiva en noviembre de 1994 (Méndez 1995) determinó la clausura de la pesquería, la cual fue reabierta en 2009, también bajo un esquema de co-manejo.

La dinámica de la población de *M. mactroides* en la playa Barra del Chuy es afectada por factores antropogénicos, en especial por la descarga del Canal

Andreoni (Defeo 2003). La descarga del Canal Andreoni afecta la dinámica poblacional de *M. mactroides* y de otras especies, tales como *Emerita brasiliensis* (Lercari & Defeo 1999) y *Donax hanleyanus* (Defeo & de Alava 1995). En la cercanía del canal, la almeja amarilla presenta altas tasas de mortalidad, baja longevidad y bajos niveles de abundancia y reclutamiento (Defeo 1993, 1998). Estudios de largo plazo han demostrado que dicha actividad humana juega un importante rol en las fluctuaciones a largo plazo de esta población (Defeo & de Alava 1995, Defeo 1996, 1998, Lima et al. 2000). Además el estrés físico (disturbios del sedimento) y los daños (en las valvas) generados por la técnica de recolección (con palas), aumenta la mortalidad natural de las almejas que están por debajo de la talla mínima legal para la explotación comercial (< 50mm: Defeo 1996, 1998).

En cuanto a los procesos físicos que actúan sobre la dinámica poblacional en el corto plazo, la temperatura es un factor preponderante en las oscilaciones del crecimiento, el cual es mínimo durante el otoño tardío e invierno (a bajas temperaturas) y aumenta en primavera y verano en concurrencia con aumentos de la temperatura (Defeo et al. 1992). Además, durante el período de mínimo crecimiento hay una migración hacia la zona sublitoral, para evitar escasez de alimento y temperaturas extremas (Defeo et al. 1986).

Un reciente análisis a escala continental ha mostrado que la almeja amarilla ha disminuido notoriamente su abundancia a lo largo de todo su rango de distribución debido a la ocurrencia sistemática de mortandades masivas en Brasil, Uruguay y Argentina (Fiori et al. 2004, Fiori & Defeo 2006). En este contexto, la mortandad masiva de *M. mactroides* a lo largo de su rango de distribución, ocurridas en marzo de 1993 a lo largo de 350 km del sur de Brasil (Odebrecht et al. 1995), en noviembre de 1994 en Uruguay (Méndez 1995) y diciembre de 1995 en Argentina (Fiori & Cazzaniga 1999), determinaron la virtual desaparición de la especie. La ocurrencia de frentes atmosféricos fríos que acumularon grandes cantidades de dinoflagelados en la zona de rompiente ha sido postulada como una de las causas

de dicha mortandad en Brasil (Odebrecht et al. 1995). Sin embargo, este factor no explica la caída de las poblaciones de Argentina (Fiori & Cazzaniga 1999) y de Uruguay, por lo cual no sería la única causa de mortandades masivas a gran escala. Virosis específicas pueden ser una explicación alternativa, pero no ha podido ser confirmada científicamente (Fiori & Cazzaniga 1999, Fiori et al. 2004).

Lo anterior sugiere que las variaciones de abundancia de la almeja amarilla en el largo plazo estarían siendo afectadas por condiciones oceanográficas y anomalías térmicas. En este contexto, el sudeste de Sudamérica es una de las regiones más afectadas por la ocurrencia de fenómenos ENSO, donde anomalías de la temperatura superficial del mar (SSTA, por su sigla en inglés) positivas (negativas) en el Pacífico ecuatorial determinan la tendencia a precipitaciones por encima (debajo) de la media (Cazes-Boezio et al. 2003, Barreiro 2009). Estos eventos, sumados a la variabilidad climática pueden afectar la demografía y dinámica de las poblaciones que habitan playas arenosas, lo cual tiene fuertes implicancias ecológicas debido a que estos organismos utilizan una buena parte de la energía producida en dichos ecosistemas (McLachlan & Brown 2006). No obstante, no existen estudios de largo plazo que evalúen la relevancia de factores climáticos-oceánicos en la demografía de poblaciones de playas arenosas a nivel mundial en general (Defeo & McLachlan 2005), y en el caso de la almeja amarilla en particular.

***Mesodesma donacium* del Pacífico**

Mesodesma donacium se distribuye en la costa Pacífica de América del Sur desde Perú (ca. 5°S) hasta Isla Chiloé (ca. 43°S) en Chile (Tarifeño 1980). Las capturas en Perú mostraron un aumento sostenido desde 1964 (36 t) hasta 1977 (597 t), alcanzando un máximo entre 1978 y 1979, donde se capturaron cerca de 4000 t. La caída desde 1980 a 1985 podría deberse al efecto combinado de sobreexplotación del recurso (1980-1981) y efectos negativos causados pero el evento ENSO cálido en las poblaciones de *M. donacium* (Castilla & Camus 1992).

En Chile, las almejas son capturadas por pescadores artesanales en la zona de rompiente durante las mareas bajas. La mayoría de la captura se hace de manera manual e incluso durante días calmos la especie es extraída por buzos en el submareal, en plena zona de barrido (McLachlan et al. 1996). La explotación de esta almeja es regulada por un tamaño mínimo de 50 mm en la zona central y sur de Chile (ca. 38-42°S) y de 60 mm para el resto del país, además de otras regulaciones aplicadas en la zona central (e.g., Áreas de Manejo y Explotación de Recursos Bentónicos a partir de 1997: Castilla et al. 2007). Las capturas mostraron un sostenido incremento entre 1966 y 1991, particularmente a partir de 1983, producto de una gran diversificación en la exportación de moluscos por parte de Chile (Defeo et al. 1993). Llegaron a un máximo de ca. 18000 t en 1989, declinando a 9000 t entre 1990-1991, probablemente debido a sobreexplotación y fluctuaciones en el mercado. Asimismo, se observó una tendencia del mercado internacional, en especial de España, a seleccionar tamaños menores a los legalmente permitidos (Defeo et al. 1993).

Los eventos ENSO cálidos han provocado cambios en la temperatura superficial del mar del Océano Pacífico, afectando parámetros demográficos y de la dinámica de las poblaciones de *M. donacium* y alterando la estructura de la comunidad bentónica (Arntz et al. 1987). Particularmente en Perú, el aumento de la temperatura superficial del mar durante el evento ENSO de 1982-83 provocó mortandades masivas y drásticas disminuciones de la abundancia de *M. donacium*, así como fluctuaciones en sus parámetros poblacionales y cambios en el período de desove, disminución y/o cese del crecimiento (Arntz et al. 1987). A partir de registros arqueológicos se ha detectado que las poblaciones de *M. donacium* han sufrido los efectos ENSO desde hace 4000 años, virtualmente desapareciendo de la fauna malacológica de los sitios estudiados en diferentes periodos (Ávalos & Rodríguez 1994; Guzmán et al. 2000). No obstante, al igual que en el caso de la almeja amarilla de la costa atlántica, no existen estudios de largo plazo dirigidos a evaluar la relevancia de dichos factores en la demografía de la macha a lo largo de su rango de distribución.

1.2 Propósito del estudio

1.2.1 Planteamiento del problema

El género *Mesodesma* en América del sur

Aunque la magnitud exacta de los cambios físicos provocados por el calentamiento global es todavía incierta (IPCC 2007), éstos, sumados a los de la variabilidad climática, son cada vez más evidentes en las playas arenosas (Brown & McLachlan 2002, Jones et al. 2007). No obstante, no existen estudios directos sobre los efectos a largo plazo de estos agentes forzantes externos en ecosistemas de playa. Tal como se mencionara previamente, la abundancia de almejas del Género *Mesodesma* muestra una tendencia decreciente en el tiempo. Teniendo en cuenta que ambas especies han sido afectadas durante las últimas décadas por mortandades masivas, la declinación en la abundancia no sería explicada únicamente por el impacto pesquero sino también por eventos climáticos de largo plazo. En efecto, dado que en el caso de *M. mactroides* la pesquería fue cerrada en 1993, la sobrepesca no puede explicar por sí sola la tendencia observada en las últimas décadas. En el caso de *M. donacium*, la pesquería ha sido objeto de medidas de manejo (en la zona central de Chile) que han resultado exitosas para otras especies intermareales de litoral rocoso, tales como las Áreas de Manejo y Explotación de Recursos Bentónicos referidas anteriormente (Castilla et al. 2007). Por tanto, sus fluctuaciones de abundancia tampoco podrían ser explicadas enteramente por el proceso pesquero. Se postula que la declinación de ambas especies podría ser explicada por variaciones de largo plazo en la temperatura del mar, que no solo modifica sus parámetros demográficos sino también su hábitat.

Dado que los estudios de largo plazo y macroescala en especies de playas arenosas son raros o fragmentarios, para evaluar la relevancia de fenómenos climáticos, es necesario desarrollar estudios a dichas escalas de espacio y tiempo. Esto permitiría cuantificar variaciones en descriptores biológicos y detectar cuales

son los forzamientos que los determinan, tal como se ha documentado para algunos sistemas terrestres, dulceacuícolas y marinos (de Young et al. 2008).

1.2.2 Hipótesis

Las variaciones en la abundancia del género *Mesodesma* están asociadas a cambios ambientales de meso y macroescala, los cuales regulan su demografía. Esta dependencia de las variables ambientales, sumada a efectos generados por la explotación humana, hace que dichas especies presenten fuertes fluctuaciones en el tiempo. Teniendo en cuenta el aumento de la temperatura del mar en el largo plazo (IPCC 2007) y que dichas especies son de origen antártico (von Ihering 1907), la variabilidad climática asociada a dichos incrementos constituye un agente forzante externo crítico que afecta negativamente su demografía. Dicho agente forzante, actuando en conjunto con el impacto generado por la pesca, explicaría los patrones de largo plazo en la abundancia de dichas especies.

En el caso específico de la costa atlántica uruguaya, se postula que el aumento en la velocidad y frecuencia de vientos de componente sur afectan negativamente las características físicas de las playas arenosas en dicha costa. En particular, para el cinturón de playas donde habita principalmente la almeja amarilla *M. mactroides* en Barra del Chuy (Uruguay), se postula que este forzamiento climático afecte negativamente la actividad pesquera de la comunidad local.

1.1.3 Objetivo general

El objetivo general de esta Tesis es analizar la variación en el largo plazo de la abundancia de *M. mactroides* en Barra del Chuy (Uruguay) y de indicadores pesqueros de *M. donacium* en Perú y Chile en función de las anomalías de temperatura, el esfuerzo pesquero y variables económicas (e.g. precio unitario del producto). Asimismo se evalúa el potencial efecto de los vientos de componente sur en la morfodinámica de dos playas arenosas de Uruguay, una disipativa y otra reflectiva. Por último se evalúan los impactos de la variabilidad climática en las pesquerías artesanales de América Latina.

1.2.4 Objetivos específicos

1. Evaluar el rol del ambiente en las tendencias de largo plazo de la estructura de tallas y biomasa de la almeja amarilla *Mesodesma mactroides* en una playa arenosa de Uruguay.
2. Modelar las variaciones de abundancia (y/o índices relacionados) de las dos especies del género *Mesodesma* en el largo plazo en función de la anomalía de temperatura superficial del mar (SSTA), esfuerzo pesquero y/o variables económicas (e.g. precio unitario). Relacionar las fluctuaciones en la abundancia o captura de estas especies con eventos climáticos interanuales (ENSO, en el Pacífico) y decadales (PDO y AMO).
3. Evaluar respuestas diferenciales en las características físicas de playas arenosas con características morfodinámicas contrastantes (i.e. disipativa y reflectiva) a los forzamientos climáticos, así como sus potenciales implicancias sociales y ecológicas.
4. Examinar el efecto de la variabilidad climática en las pesquerías artesanales de América Latina desde el punto de vista ecológico, social y bioeconómico.

1.2.5 Organización de la Tesis

Los Capítulos 2, 3, 4 y 5 de esta tesis fueron elaborados como trabajos autocontenidos bajo el formato estándar de trabajo científico. El Capítulo 2 evalúa un modelo edad-estructurado de la almeja amarilla (*Mesodesma mactroides*) con la inclusión de variables ambientales en los procesos de su dinámica poblacional. El Capítulo 3 analiza el efecto de la variabilidad climática, la pesca y el mercado en los índices de abundancia del género *Mesodesma* en América del Sur. El Capítulo 4 analiza los efectos de la variabilidad climática en la morfodinámica de 2 playas arenosas de la costa oceánica de Uruguay. El Capítulo 5 hace una revisión de los efectos de la variabilidad climática en las pesquerías artesanales de América Latina.

CAPÍTULO 2

**Modelo edad estructurado de la almeja amarilla (*Mesodesma mactroides*)
con la inclusión de variables ambientales en los procesos de su dinámica
poblacional**



Proyecto
Gestión Pesquera en Uruguay
UTF / URU / 025 / URU

Evaluación de recursos pesqueros de Uruguay mediante modelos dinámicos

**Nicolás L. Gutiérrez
y Omar Defeo**
E d i t o r e s

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Modelo edad-estructurado de la almeja amarilla (*Mesodesma mactroides*) con la inclusión de variables ambientales en los procesos de su dinámica poblacional

Leonardo Ortega y Diego Lercari

RESUMEN

La almeja amarilla *Mesodesma mactroides* presenta una fuerte asociación con las variables ambientales, lo cual hace que experimente fuertes fluctuaciones en su abundancia y eventos de mortalidades masivas. En este trabajo se implementaron dos versiones de modelos edad-estructurados (MEE). El primer MEE no consideró el efecto de la anomalía de temperatura superficial del océano en la sobrevivencia del recurso, constatándose un ajuste pobre. El segundo MEE consideró la sobrevivencia del recurso como función de la anomalía de temperatura superficial del océano. La inclusión de esta función permitió una mejora importante en el ajuste del modelo. No obstante, en ninguno de los dos casos no se logró un ajuste razonable para la totalidad de la serie temporal analizada. Esto se atribuye a que los MEE desarrollados pueden considerarse demasiado simples para representar la compleja dinámica del recurso. Los resultados sugieren la importancia de integrar variables ambientales, en especial la temperatura, al momento de modelar la dinámica de la población y para obtener indicadores y puntos de referencia para el manejo del recurso.

1. Introducción

La almeja amarilla *Mesodesma mactroides* (Bivalvia: Mesodesmatidae) habita playas arenosas de la costa atlántica de América del Sur, entre Brasil (23°S) y Argentina (41°S) (McLachlan et al. 1996, Fiori & Defeo 2006). En Uruguay, la distribución de la población principal está limitada por dos descargas de agua dulce, el Arroyo Chuy al norte y otra artificial al sur, el Canal Andreoni, ocupando un arco de playa de 22 km de extensión con características disipativas, definidas por una suave pendiente, arena fina y fuerte acción del oleaje (Defeo 1987, 1989) (Fig. 1).

La pesca artesanal o recreacional de *Mesodesma mactroides* se desarrolla en los tres países que abarca su distribución (Brasil, Uruguay y Argentina). El producto es usado principalmente para consumo humano (Defeo 1996, 1998, Defeo et al. 1993, McLachlan et al. 1996). En Uruguay constituyó durante mucho tiempo el segundo recurso malacológico más explotado, después de *Mytilus edulis platensis* (Defeo 1989). La dinámica de la población de *Mesodesma mactroides* la playa Barra del Chuy es afectada por la pesca y por la descarga del Canal Andreoni (Defeo 2003). Dicha descarga afecta también la dinámica poblacional de otras especies, tales como *Emerita brasiliensis* (Lercari & Defeo 1999) y *Donax hanleyanus* (Defeo & de Alava 1995). En la cercanía del canal, la almeja amarilla presenta altas tasas de mortalidad, baja longevidad y bajos niveles de abundancia y reclutamiento (Defeo 1993, 1998). Se ha demostrado que la actividad humana juega un importante rol en las fluctuaciones a largo plazo de esta población (Defeo & de Alava 1995, Defeo 1996, 1998, Lima et al. 2000). Además del efecto obvio que provoca la explotación sobre la población, el estrés físico (disturbios del sedimento) y los daños generados por la técnica de recolección con palas, aumenta la mortalidad natural de las almejas que están por debajo de la talla mínima legal para la explotación comercial (< 50mm) (Defeo 1996a, 1998).

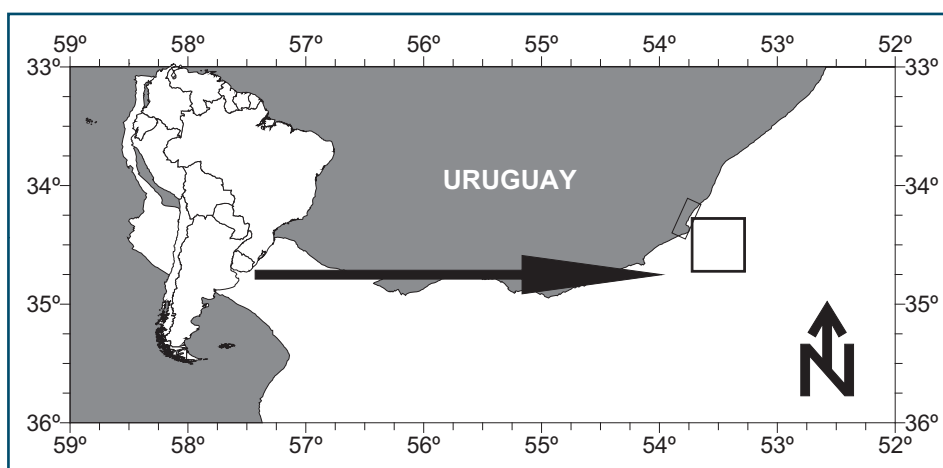


Figura 1. Ubicación del área de estudio, resaltándose la distribución de *Mesodesma mactroides* entre La Coronilla y Barra del Chuy (zona sombreada) y la zona oceánica (rectángulo) para la cual se obtuvieron los datos de temperatura y su anomalía.

Varios factores físicos actúan en la dinámica poblacional de *Mesodesma mactroides* en el corto plazo. Por ejemplo, la temperatura es un factor preponderante en las oscilaciones del crecimiento, el cual es mínimo durante el otoño tardío e invierno (a bajas temperaturas) y aumenta en primavera y verano en concurrence con aumentos de la temperatura (Defeo et al. 1992). Además, durante el período de mínimo crecimiento hay una migración hacia la zona sublitoral, para evitar escasez de alimento y temperaturas extremas (Defeo et al. 1986). Lima et al. (2000) sugirieron que el comportamiento en el largo plazo de esta población estaría siendo afectado además por condiciones oceanográficas y anomalías térmicas. No obstante, no existen estudios de largo plazo que evalúen la relevancia de dichos factores en la demografía y dinámica poblacional de la almeja amarilla.

Lo anterior resalta la necesidad de desarrollar estudios de largo plazo para evaluar tendencias demográficas y de la dinámica poblacional de la macrofauna que habita playas arenosas. Esto cobra especial importancia si se considera que un reciente análisis continental ha mostrado que la almeja amarilla se encuentra comprometida debido a la ocurrencia sistemática de mortalidades masivas a lo largo de miles de kilómetros de la costa atlántica, incluyendo Brasil, Uruguay y Argentina (Fiori et al. 2004, Fiori & Defeo 2006). Sin embargo, no existen estudios detallados que muestren variaciones en el largo plazo en esta especie en particular, y en poblaciones de playas arenosas a nivel mundial en general (Defeo & McLachlan 2005).

1.1. EL PROBLEMA

Las estimaciones de abundancia de almeja muestran una tendencia decreciente en el tiempo. Teniendo en cuenta que la pesquería fue cerrada en 1994, la pesca no puede explicar esta tendencia. Los datos históricos de abundancia de almeja amarilla muestran altas variaciones interanuales conjuntamente con una caída sistemática en el tiempo, y esta disminución en la abundancia concuerda con un sostenido aumento de las anomalías de temperatura observadas para la zona (Fig. 2). Por tanto, se postula que la declinación de la especie podría ser explicada por un efecto conjunto de la pesca y de la temperatura o anomalías de temperatura superficial del agua de mar (SSTA por sus siglas en inglés).

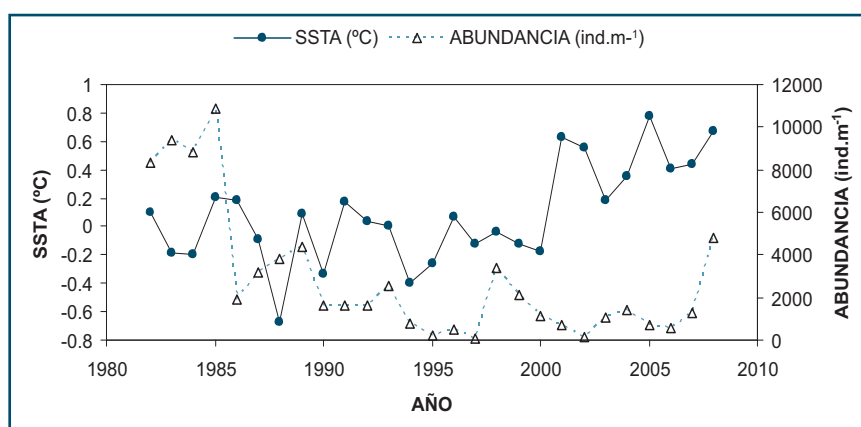


Figura 2. Series temporales de abundancia de *Mesodesma mactroides* y de anomalías de temperatura superficial del agua de mar (SSTA) para el área de estudio.

1.2. OBJETIVOS

El objetivo principal de este trabajo consistió en el desarrollo de un modelo edad estructurado (MEE) para el stock de *Mesodesma mactroides* de la playa de La Coronilla – Barra el Chuy.

Particularmente se buscó:

1. Obtener estimaciones de biomasa por clases de talla.

2. Estimar la biomasa explotable del stock.
3. Ajustar los parámetros del modelo para obtener una representación realista de la tendencia histórica del stock.
4. Incluir una variable exógena (anomalía de temperatura) en la estructura del modelo.
5. Evaluar el impacto de la pesca sumado a la variabilidad ambiental (anomalías de temperatura) en la abundancia de *Mesodesma mactroides*.

1.3. ESTRATEGIA

Se evaluó la evolución histórica de la abundancia-biomasa de la almeja amarilla mediante un MEE, el cual fue construido seleccionando variables de la dinámica poblacional de *Mesodesma mactroides*. Para esto se siguió la siguiente estrategia:

1. Identificación de las preguntas a formular:
 - a. ¿Cuáles son las series temporales de biomasa por componentes poblacionales del stock?
 - b. ¿Cuál es la serie temporal de la biomasa explotable del stock?
 - c. ¿Cuál es la importancia de la anomalía de temperatura en la explicación de los patrones temporales de biomasa?
2. Selección de supuestos sobre los cuales formular el modelo:
 - a. La pesca ocurre al comienzo del año.
 - b. No hay emigración o inmigración.
 - c. La fecundidad, mortalidad natural, peso individual y vulnerabilidad no cambian con el tiempo.
 - d. La vulnerabilidad y el peso individual no cambian con cambios en la intensidad de pesca (i.e. los parámetros no son dependientes de la densidad).
 - e. La fecundidad, mortalidad natural, peso individual y vulnerabilidad se consideran constantes para todas las edades.
3. Selección del valor de los parámetros (ajuste del modelo a los datos).
 - a. Evaluación de las tendencias y consistencia de las predicciones del modelo, incluyendo información auxiliar.
4. Modificación del modelo basándose en los resultados del paso 3.

2. Métodos

La metodología seguida en este trabajo comprendió 3 etapas: 1) recopilación de información; 2) implementación del MEE; y 3) ajuste del modelo.

2.1. RECOPIACIÓN DE INFORMACIÓN

El MEE necesita como insumos a diversos parámetros poblacionales del recurso, los que fueron recopilados de comunicaciones personales y publicaciones (Tabla 1).

Tabla 1. Insumos del MEE de almeja amarilla y fuentes consultadas.

Insumos	Fuente
Serie temporal de capturas pesqueras	Defeo, O. com pers
Serie temporal de evaluación poblacional	Defeo, O. com pers
Parámetros de crecimiento (L_{∞} ; K ; t_0)	Defeo (1998)
Coefficientes alométricos	Defeo (1998)
Sobrevivencia	Brazeiro & Defeo (1999)
Edad-longitud	Brazeiro & Defeo (1999)
Vulnerabilidad	Defeo, O. com pers
Fertilidad	Brazeiro & Defeo (1999)
Serie de anomalía de temperatura (SSTA)	Smith et al. (2008)

2.2. IMPLEMENTACIÓN DEL MEE

Se construyó un MEE básico con la formulación que se detalla a continuación. La dinámica poblacional de los individuos de edad 0 y mayores estuvo dada por:

$$N_{y+1,a+1} = \begin{cases} (\tilde{B}_{y+1} / \tilde{B}_0) / \{\alpha + \beta(\tilde{B}_{y+1} / \tilde{B}_0)\} & \text{para } a = 0 \\ N_{y,a}(1 - V_a F_y) S_a & \text{para } 1 \leq a \leq x-1 \\ N_{y,x}(1 - V_x F_y) S_x + N_{y,x-1}(1 - V_{x-1} F_y) S_{x-1} & \text{para } a = x \end{cases}$$

donde

- $N_{y,a}$: número de individuos de edad a al comienzo del año y
- x : grupo de edad agrupado (grupo 1+)
- V_a : vulnerabilidad de una almeja de edad a , asumiendo una función de filo de cuchillo
- F_y : tasa de explotación durante el año y
- S_a : tasa de supervivencia para individuos de edad a
- β, α : parámetros de la relación stock-reclutamiento
- $\tilde{B}_y$: biomasa desovante/reproductora al inicio del año y , la cual se expresa como:

$$\tilde{B}_y = \sum_{a=a_m}^x w_a N_{y,a}$$

- a_m : edad de madurez sexual
- w_a : peso a la edad a , definido por la ecuación de crecimiento de von Bertalanffy (e y f son los parámetros alométricos):

$$w_a = e \{ \ell_{\infty} (1 - \exp(-\kappa(a - t_0))) \}^f$$

Las capturas se asumen extraídas de la biomasa vulnerable:

$$F_y = C_y / B_y$$

Donde:

C_y : captura en peso durante el año y
 B_y : biomasa vulnerable al inicio del año y

$$B_y = \sum_{a=0} w_a V_a N_{y,a}$$

Los valores de α y β (modelo de stock-reclutamiento de Beverton & Holt 1956) fueron determinados a partir del reclutamiento virgen, R_0 , y el parámetro "steepness" de la relación stock-reclutamiento. Steepness (h) se define como la fracción de R_0 que se espera si la biomasa desovante es reducida al 20% de su biomasa virgen. El modelo de Beverton & Holt (1956) fue reestructurado en función de "steepness" y se despejaron los parámetros a y b a incluir en el modelo:

$$b = \frac{5h-1}{4hR_0} \quad a = \left(\frac{1-h}{R_0 4h} \right)$$

Cabe mencionar que si bien existe para la población un ajuste del modelo de reclutamiento de Ricker (1958) (Defeo 1998) las pruebas iniciales del ajuste no fueron satisfactorias, por lo que se utilizó el modelo de Beverton & Holt (1956).

2.3. AJUSTE DEL MODELO

El ajuste de los modelos a los datos proveyó las bases para determinar los valores de los parámetros del modelo y por ende calcular los valores de las variables de estado/interés. Asimismo, permitió evaluar si el MEE puede replicar los datos existentes en forma adecuada. La metodología genérica seguida para el ajuste del MEE comprendió:

- Definir la función $f(\theta)$ que determinó la "diferencia" entre los datos observados y los predichos por el modelo. Esta función midió la bondad de ajuste del modelo a los datos.
- Seleccionar los valores de los parámetros de forma tal de minimizar la diferencia entre las observaciones y estimaciones. La función de suma de cuadrados (SC) fue utilizada para evaluar el ajuste óptimo de los parámetros del modelo (i.e. minimizar la diferencia de los valores residuales) y estuvo definida en este caso por dos componentes: uno proveniente de la información generada por el modelo y el otro proveniente de los datos de las campañas de investigación.

$$SC = \sum_y (\ln B_y - \ln \hat{B}_y)^2$$

Donde :

B_y : estimación de biomasa en la campaña de investigación para el año y ,
 $\hat{B}_y$: predicción de biomasa del modelo.

En primera instancia se intentó ajustar el modelo utilizando los 26 años en los cuales se realizaron evaluaciones del recurso (1982 - 2008). Sin embargo, la serie incluye un período en el cual la especie registró mortalidades masivas y por lo tanto la abundancia (biomasa) fue nula. Esto hizo imposible ajustar el modelo a los datos observados, por lo que se ajustó el modelo a la información comprendida entre 1982 y 1991, con abundancias obtenidas de las campañas de evaluación y capturas declaradas para cada año. El MEE fue desarrollado: 1) sin incluir la SSTA; y 2) adicionando a la SSTA como variable exógena de forma que la supervivencia para cada clase de edad a se dio por la ecuación:

$$Sa = \alpha + \beta \cdot \left(\frac{SSTA}{T} \right)^\gamma$$

Donde T es la temperatura media de la serie, y α , β y γ son parámetros. Finalmente la función de SC fue minimizada mediante un método de cómputo de optimización no lineal (Solver), estimándose los parámetros R_0 , h y los parámetros de la relación supervivencia-SSTA a efectos de minimizar la diferencia entre los valores observados y estimados.

3. Resultados

En la Figura 3 se muestra el ajuste inicial del modelo, sin incluir el efecto de la SSTA en la supervivencia del recurso. Se observó una pobre concordancia entre las predicciones del MEE y las observaciones. Por el contrario, el modelo que incluyó el parámetro supervivencia-SSTA permitió un mejor ajuste a los valores observados (Fig. 4), obteniendo una SC sensiblemente menor que el modelo más simple (3.01 y 2.85 respectivamente).

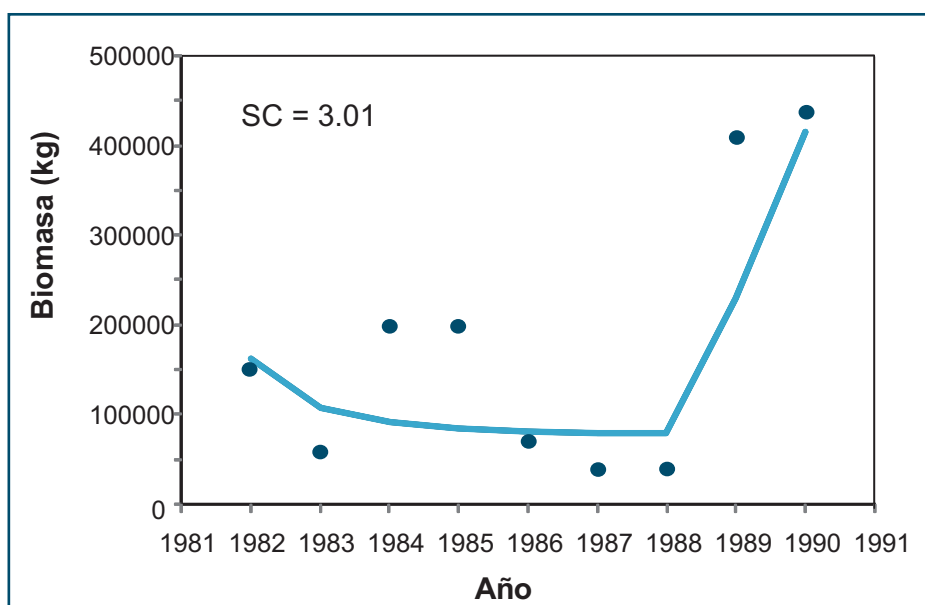


Figura 3. Serie temporal de biomasa de almeja amarilla predicha por el modelo preliminar (línea continua) ajustado a los datos observados (círculos). SC = Suma de cuadrados.

En la Tabla 2 se muestran los resultados del mejor MEE obtenido para *Mesodesma mactroides*, que incluye la función sobrevivencia-SSTA (Fig. 4).

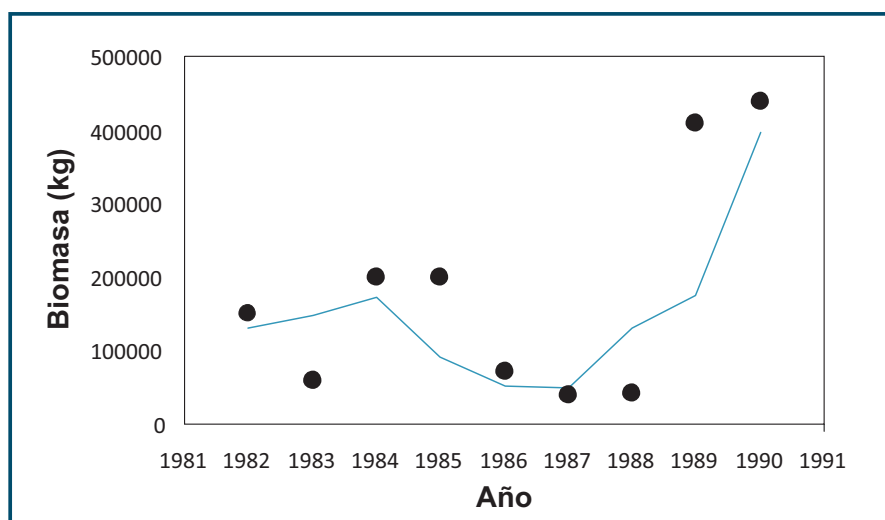


Figura 4. Serie temporal de biomasa de almeja amarilla predicha por el mejor MEE que incluye la función sobrevivencia-SSTA (línea continua) ajustado a los datos observados (círculos). SC = Suma de cuadrados.

Tabla 2. Estimaciones del MEE implementado para *Mesodesma mactroides*.

Año	Biomasa explotable (kg)	Sobrevivencia	Biomasa desovante (kg)	Tasa de explotación
1981	32134	0.21	45435148	0.99
1982	18990	0.23	31302387	0.99
1983	21389	0.38	35249628	0.99
1984	24907	0.39	41045887	0.99
1985	13244	0.18	21826698	0.99
1986	7544	0.19	12431859	0.99
1987	7281	0.32	11999747	0.99
1988	18853	0.87	31070362	0.00
1989	25273	0.23	35573338	0.00
1990	57245	0.48	81154802	0.90
1991	30901	0.19	49773647	0.99

4. Discusión

La amplia distribución latitudinal del recurso determina que existan diferencias en las características ambientales a que están expuestos (e.g. régimen térmico) y en la estrategia de vida, observándose una temporada de reclutamiento casi continuo en las poblaciones del límite norte de distribución, mientras que el reclutamiento estacional es mínimo en las poblaciones del límite sur. Asimismo, la expectativa de vida y la talla individual de la especie tienden a aumentar con la latitud (Fiori & Defeo 2006). Además, la almeja amarilla exhibe fuertes oscilaciones en su abundancia

a nivel local, probablemente asociadas a la variabilidad ambiental. Por tanto, para una adecuada modelación deben considerarse en forma conjunta las actividades pesqueras y alteraciones del hábitat. En particular, la degradación del hábitat costero sumado a las presiones causadas por el cambio climático determinan impactos ecológicos sin precedentes (Defeo et al. 2009).

La fuerte asociación del recurso con las variables físicas hace que experimente, además de las fluctuaciones antes mencionadas, eventos de mortalidades masivas. La modelación de estos eventos se hace difícil por los métodos clásicos, por lo cual para un manejo racional deben conjugarse no solo los principios básicos de manejo ecosistémico, y un estricto monitoreo biológico-ambiental, y el compromiso de los tomadores de decisiones para mantener ese hábitat lo menos alterado posible y los monitoreos en el tiempo.

El ajuste del MEE sin la inclusión del efecto de la SSTA en la sobrevivencia del recurso no fue satisfactorio. En contraste, cuando la sobrevivencia del recurso se estimó en función de la SSTA, se logró un mejor ajuste del modelo. Esto demarca por un lado el efecto sustancial que esta variable ambiental puede tener sobre la especie y también indica la necesidad de considerarla al momento de modelar su población para obtener indicadores y puntos de referencia para el manejo del stock.

Es necesario realizar un análisis comparativo más detallado sobre las dos versiones del modelo. En este sentido, si bien el modelo que incluye la SSTA presentó un mejor ajuste, presenta un mayor número de parámetros, por lo que las bondades de uno u otro deberían ser evaluadas considerando este hecho. Para esto sería conveniente ajustar el modelo utilizando la función de máxima verosimilitud a efectos de seleccionar los valores de los parámetros de forma tal que el modelo generado reproduzca la tendencia temporal de las observaciones de la mejor manera posible. Contando con un ajuste de este tipo y adicionando los perfiles de SC y máxima verosimilitud, es posible realizar una comparación estadística del ajuste de los modelos en base al número de parámetros en cada uno.

Las limitaciones de los modelos implementados se hacen evidentes al no lograr un ajuste razonable para la totalidad de la serie temporal de datos (26 años). La existencia de períodos en los que el recurso tuvo muy baja o nula presencia en el área de estudio condujo a que las estimaciones del modelo no fueran realistas. Esto podría deberse principalmente a que la estructura del modelo considera las capturas de un año (mediante la tasa de explotación) en la estimación de la biomasa explotable del año siguiente, por lo que al “pasar” por un período de varios años sin captura se predicen incrementos en la biomasa predicha. Sin embargo, la disminución de las capturas se debió a la virtual desaparición de la especie en el área, hecho constatado en las campañas de evaluación del recurso. De aquí se genera una contradicción entre los datos observados y estimados, que en definitiva lleva a no lograr el ajuste del modelo en los períodos en que las capturas y las biomásas observadas fueron nulas.

En conclusión, el MEE aplicado al stock de *Mesodesma mactroides* resultó apropiado para la serie temporal de datos analizada, pero puede considerarse demasiado simple para representar la complejidad de la dinámica del recurso. En este sentido sería necesario incluir los fenómenos de mortalidades masivas (catástrofes) en la estructuración del modelo, identificando las causas que las producen.

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CAPÍTULO 3

Effects of fishing, market price, and climate on two South American clam species



Effects of fishing, market price, and climate on two South American clam species

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ABSTRACT: Coastal shellfish are being threatened by several drivers acting at multiple temporal and spatial scales, including fishing, climate, and globalization of markets. We evaluated large-scale and long-term combined effects of fishing, climate, and economic variables on 2 congeneric clams that inhabit sandy beaches of the Pacific (*Mesodesma donacium*) and the Atlantic (*M. mactroides*) in South America. Bioeconomic and climatic variables, such as coastal sea surface temperature anomalies (SSTA) and broad-scale climatic indices (Pacific Decadal Oscillation and Atlantic Multidecadal Oscillation), were related to variations in clam populations in a differential way according to latitude and oceanographic features. For *M. donacium*, the nature and sign of the relationships between landings and explanatory predictors markedly differed between bioclimatic units. El Niño Southern Oscillation events negatively affected landings in Peru and northern Chile, whereas landings increased in southern Chile and showed a positive correlation with increasing SSTA, suggesting a positive effect at the southernmost edge of the species distribution. Long-term trends in the abundance of *M. mactroides* were related to fishing intensity and SSTA. As anticipated by basic economic theory, deficit of supply relative to demand, exacerbated by very low harvesting costs, pushed the price up and has driven these clam species to levels close to extinction (anthropogenic Allee effect). The lack of response of the stocks to long-term closures suggests that these systems exceeded critical thresholds (tipping points). Information on early warnings of tipping points is needed to help manage coastal shellfisheries that are increasingly threatened by long-lasting and large-scale stressors.

KEY WORDS: Intertidal clams · Sandy beaches · Climate variability · Fisheries bioeconomics

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INTRODUCTION

Many small-scale shellfisheries in the world are data-poor and have critical socioeconomic connotations worldwide (Caddy & Defeo 2003, McClanahan et al. 2009). In Latin America, these fisheries are based on high-value species and represent sources of food for subsistence and employment, generating important direct incomes to fisher communities and, in

some cases, export earnings (Castilla & Defeo 2001). However, shellfisheries sustainability has been difficult to achieve. Nowadays, many shellfish populations in Latin America are overexploited or depleted (Carranza et al. 2009a, b). In addition to local drivers affecting shellfish condition, global change drivers have exacerbated stock depletion rates, particularly (Defeo & Castilla 2005, 2012, Beck et al. 2011, Perry et al. 2011): (1) increasing prices for shellfish highly em-

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bedded in global markets, and (2) climate variability, such as temperature rise. Thus, the resilience of these social-ecological systems can be degraded by several drivers acting simultaneously (Ling et al. 2009, Miller et al. 2010). However, the integration of biophysical and socioeconomic information in long-term fisheries modeling has been more complex than previously thought (Cury et al. 2008).

Climatic processes have drastic effects in the functioning of marine biological systems at a wide range of temporal and spatial scales (e.g. Bakun 1996, Rouyer et al. 2008). Ocean climate variables, such as shifting currents and temperature changes, alter feeding, growth, and migratory patterns of marine fauna (Miller et al. 2010). In South America, these scenarios are related to interannual (e.g. El Niño Southern Oscillation [ENSO]) and multidecadal (e.g. Pacific Decadal Oscillation [PDO] and Atlantic Multidecadal Oscillation [AMO]) environmental variability associated with broad-scale oceanic climatic variations, which influence currents and water mass properties. This atmospheric-oceanic multiscale variability affects ecosystems, including their fishery resources (Chavez et al. 2003, Montecino & Lange 2009).

The effects of climate change may be profoundly felt in the macrofauna present in sandy beaches, a largely forgotten ecosystem despite its coverage of >70% of the open coasts of the world (Defeo et al. 2009). The position at the land-sea margin renders sandy beaches highly vulnerable to climate change, being at risk of significant habitat loss and ecological impacts from warming and erosion caused by sea-level rise and increased storms (Dugan et al. 2010). These cumulative effects are also exacerbated by the extraction of easily accessible and high-value resources inhabiting intertidal sandy shores, notably clams (McLachlan et al. 1996). Although these fisheries are generally of small scale, fishing impacts can be significant and can be amplified or reinforced by: (1) continuous erosion of beaches that reduced clam habitats (Beentjes et al. 2006), and (2) mass mortalities (Fiori et al. 2004, Riascos et al. 2009).

Sandy beach clams of the genus *Mesodesma* are a valuable resource along the Atlantic and Pacific coasts of South America (Defeo 2003). Humans have been harvesting these marine invertebrates for a long time (Rivadeneira et al. 2010). In the Pacific, the surf clam *M. donacium* (macha) is one of the most important shellfishes exploited in Chile and Peru, even though it is also a data-poor fishery where effective fishing-effort estimates are rarely available. In the Atlantic, the yellow clam *M. mactroides* is commercially exploited in sandy beaches of Brazil, Uruguay, and

Argentina (Herrmann et al. 2011). The genus *Mesodesma* has an Antarctic origin and can be associated with cold water systems, both in the Pacific and Atlantic. This genus invaded South American coasts in the late Pliocene or possibly in the early Pleistocene, during a major migration of mollusks from Antarctica, following 2 cold currents: Malvinas on the east coast and the Humboldt Current System (HCS) on the west coast (von Ihering 1907). This migration was probably triggered by decreasing temperatures at the end of the Tertiary and early Quaternary periods. According to von Ihering (1907), the dispersion of *M. mactroides* on the Patagonian coast occurred during the Pleistocene and has only recently encompassed the Brazilian littoral, delayed by the strong zoogeographic barrier represented by the Rio de la Plata (Marins & Levy 1999). These filter-feeding clams inhabit the intertidal and shallow subtidal zones of exposed, high-energy dissipative sandy beaches, where they typically burrow to a depth ~30 cm (McLachlan et al. 1996).

Mass mortalities decimated populations of both *Mesodesma* species along their entire geographic ranges during the last 30 yr. These mass mortalities have been attributed to a number of factors, namely positive sea temperature anomalies, harmful algal blooms, environmental stress, parasitism, and storms (Odebrecht et al. 1995, Fiori et al. 2004, Riascos et al. 2009, 2011, Carstensen et al. 2010). In the case of *M. mactroides*, it has been suggested that the effect of these mortalities may swamp management measures (Defeo 2003). However, large-scale and long-term records that could be used to evaluate the relative importance of climate and fishing in these sandy beach species are lacking. In the present paper, we evaluate the relative explanatory power of fishing and climate variability in explaining long-term fishery and abundance trends in *M. donacium* and *M. mactroides* clams. We focused on 3 key issues that rule the discussions in fisheries nowadays (Defeo & Castilla 2012): (1) the role of climate in fisheries landings, (2) the effects of fishing, and (3) market prices as drivers in the fate of stocks.

MATERIALS AND METHODS

Study area and ecological settings

Mesodesma donacium

The surf clam *Mesodesma donacium* (Lamarck, 1818) is one of the most important bivalves harvested

in Pacific sandy beaches of South America. The species is distributed from Sechura Bay, Peru (5° S; Álamo & Valdivieso 1997) to southern Chile (~42° S; Tarifeño 1980) (Fig. 1). *M. donacium* often exhibits high densities and extremely high annual production, representing >95% of the biomass in the shallow soft-bottom community (Arntz et al. 1987). The across-shore distribution of *M. donacium* is patchy and adult clams are primarily confined to the surf zone, while the vast majority of juveniles occur in the swash zone (Tarifeño 1980, Jaramillo et al. 1994). In Chile, surf clams constitute a sequential fishery (sensu Seijo et al. 1998), with 2 groups of artisanal fishers spatially segregated: (1) fishers who manually collect clams from the intertidal and shallow subtidal beach fringes during low tides, and (2) 'hookah' divers that use small deckless boats with air compressors to extract clams located at the surf zone. In Peru, the macha is extracted both manually in the intertidal by digging with shovels and dredges in the shallow subtidal (Ibarcena et al. 2005).

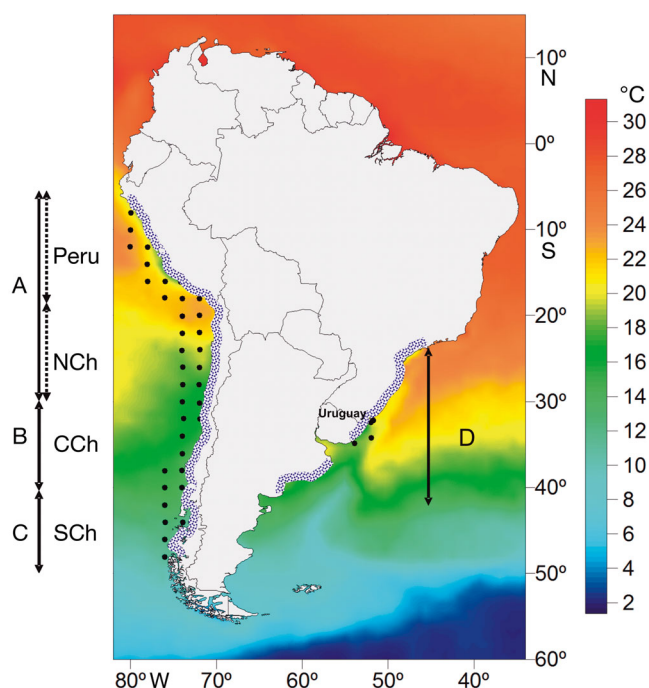


Fig. 1. Geographic distribution of the genus *Mesodesma* along the coasts of South America (purple stipple), highlighting the bioclimatic units: (A) subtropical-temperate, including 2 sub-units, Peru and Northern Chile (NCh); (B) transitional (Central Chile: CCh); (C) subantarctic (Southern Chile: SCh); and (D) the Warm-Temperate Southwestern Atlantic province. •: locations where sea surface temperature anomalies derived from Reynolds et al. (2002) were obtained. The satellite image is an annual composite (1996) of sea surface temperature (color scale in °C) derived from the Moderate-Resolution Imaging Spectroradiometer (MODIS-Aqua)

Environmental conditions in the HCS are broadly characterized by nutrient-rich, cool waters, showing slight seasonal temperature variability compared to those found in other coastal ecosystems at similar latitudes (Camus 2001, Thiel et al. 2007). The influence of the continuous upwelling of cold subsurface waters, mainly at northern Chile and Peru, and seasonal upwelling in southern-central Chile (Thiel et al. 2007), causes an atypical weak north-south temperature gradient and extends the influence of cold environmental conditions northward (Camus 2001). Therefore, many species in the HCS exhibit broad distributional ranges and are adapted to moderately constant low water temperatures (Riascos et al. 2009).

According to Thiel et al. (2007), 3 bioclimatic units can be distinguished within the HCS (Fig. 1): (1) a northern unit, dominated by subtropical and temperate biota, extending from Peru to Northern-Central Chile (4° S to 30° S) (where NCh is Northern Chile); (2) a transitional unit (Central Chile or CCh: 30° S to 40° S), characterized by strong numerical reductions in subantarctic and subtropical species; and (3) a southern unit (Southern Chile or SCh: 40° S to 50° S), dominated by subantarctic and temperate biota, extending from the Chilean archipelago to the Magellan Province.

Mesodesma mactroides

The yellow clam *Mesodesma mactroides* Reeve, 1854, is found in sandy shores of the Warm-Temperate Southwestern Atlantic (WTSa) province of South America (Spalding et al. 2007), from Brazil (24° S) to Argentina (41° S) (Fiori & Defeo 2006; our Fig. 1). This fast-growing, short-lived species (<4 yr) is artisanally exploited (shovels and hand-picking) in the intertidal of sandy beaches from Brazil, Uruguay, and Argentina (Defeo 2003).

The WTSa is characterized by a marked seasonality, with predominance of Subantarctic Water during the cold period (austral winter-spring) and Tropical Water and Subtropical Shelf Water in the warm period (summer-autumn) (Lima et al. 1996, Piola et al. 2000, Ortega & Martínez 2007). The area located over the shelf (27° S to 35° S) is controlled by winter intrusions of Subantarctic Water along with Rio de la Plata and Patos-Mirim discharges, and has large annual sea surface temperature (SST) ranges (7 to 10°C) and an extremely high secular trend toward warming (1.2 to 1.6°C per 100 yr), especially in the proximity of estuaries (Zavialov et al. 1999). In austral winter, the

occurrence of a thermal front separates warm tropical water associated with the Brazil Current and cold Subantarctic Water flowing northward on the shelf with an admixture of coastal freshwater discharges. In summer, shelf break coastal upwellings have been registered along the coast (Podestá 1990), particularly around Cabo Frio (22°S) and Ilha de Sao Sebastiao (24°S), at the northernmost limit of the yellow clam distribution. These upwellings pump up oxygen and nutrient-rich South Atlantic Central Water to the euphotic zones in the inner continental shelf, and weaken considerably during the austral winter (Piola et al. 2000). The southernmost distribution limit of the yellow clam is characterized by a major influence of oceanic cold waters (Guerrero et al. 2010).

Data analysis

SST anomalies (SSTA) for the Pacific and Atlantic coastal regions were estimated by the monthly-average gridded 0.5° latitude by 0.5° longitude recorded by Reynolds et al. (2002). The annual mean SSTA was also determined by biogeographic unit (Fig. 1). Since the northern bioclimatic unit in the Pacific was divided into NCh and Peru (see 'Study area and ecological settings'), the same methodology was applied to estimate mean SSTA for each sub-unit. Long-term biological information for the yellow clam in the Atlantic was available only for the eastern coast of Uruguay, and thus SSTA were estimated for this specific area.

Two broad-scale climate indices were used to represent large-scale processes that may influence clam abundance: the AMO and PDO. PDO and AMO time series were taken from www.esrl.noaa.gov/psd/data/climateindices/list/. Standardized PDO values are derived from monthly SSTA in the North Pacific Ocean, poleward of 20°N. In order to estimate PDO values, monthly mean global SSTA are removed to separate this effect from any 'global warming' signal that may be present in the data (Zhang et al. 1997). The AMO is a climate pattern of long-duration changes in the SST of the North Atlantic Ocean, with identifiable characteristics, specific regional effects, and often oscillatory behavior, which has its principal expression in the SST field (Enfield et al. 2001). As such, the AMO presents cool and warm phases that may last for 20 to 40 yr at a time. A cumulative sum (annual mean values) of the AMO and PDO indices was used to detect sustained shifts in climate, marked by changes in slope of the cumulative sum plot (Fiedler 2002).

Long-term *Mesodesma donacium* landings from Chile (1966 to 2009) and Peru (1970 to 2009) were discriminated by bioclimatic unit. To this end, annual landings (clam catch that is put ashore) from 16 regions in Peru and 12 regions in Chile were assigned to the corresponding unit (no information on fishing effort is available). Peruvian landings were obtained from official sources (e.g. Ministerio de Pesquería del Perú, Ministerio de la Producción de Perú). For Chile, official landings were obtained from the Servicio Nacional de Pesca (SERNAP), and exportation volumes (tons or t) and economic revenues (US\$) were obtained from the Servicio Nacional de Aduanas (Chile). Unit export prices were obtained by the ratio between economic revenues and exportation volumes. Given the marked temporal differences in the development of fishery phases (sensu Castilla & Defeo 2001) and also in SSTA trends (see 'Results') between NCh and Peru (subtropical-temperate bioclimatic unit), data from these 2 sub-units were analyzed separately.

Concerning the yellow clam *Mesodesma mactroides*, a long-term analysis was carried out only for Uruguay. The lack of statistical coverage in Brazil and Argentina precluded a more comprehensive analysis throughout this species' distribution range. In Uruguay, the yellow clam fishery is developed only along a 22 km sandy beach fringe located between La Coronilla and Barra del Chuy (Defeo 2003). Yellow clam abundance, estimated as the number of individuals per strip transect (ind.m⁻¹), were obtained from seasonal surveys carried out during 27 consecutive years (1982 to 2008), according to a systematic design developed to quantify the stock (see Defeo 1996 for details). All clams retained in each sample were measured (maximum valve length) and counted, covering the full range of individual sizes (1 to 76 mm). Annual abundance estimates were obtained by averaging seasonal estimates, which were provided for the whole population and also for the harvestable stock (individuals >50 mm; Defeo 1996). Concerning fishery-dependent statistics, daily information on catch, effective fishing effort (hours), and unit price paid by middlemen to fishers (the product is sold only in the local market) was collected on a per-fisher basis (Defeo 1996).

Generalized additive models (GAM; Hastie & Tibshirani 1990) were used to assess the relationship between landings (surf clam: Peru and Chile) or abundance (yellow clam: Uruguay) and predictor variables: SSTA and unit price were used in the

former, whereas SSTA and effective fishing effort were used in the latter. Taking into account the relatively short time period when the yellow clam fishery was active (see 'Results'), unit price was not considered for modeling purposes. In both cases, time of fishery development (in years) was also included as an independent variable in order to explore long-term trends in partial residuals. Partial residuals remove the effects of all the other variables from the dependent variable and therefore can be used to model the effects against predictors (Xiang 2001). A moving average of landings with a period of 3 yr was performed to model macha landings in the Pacific. All models were estimated using the functions GAM (model building) and mgcv (estimation of smoothing parameters) included in R statistical software (R Development Core Team 2008). Smoothing parameters and degrees of freedom of the functions were estimated using the generalized cross-validation, and penalized cubic regression splines were used as smooth terms (Wood 2006). Different models were evaluated by the significant difference of residual deviance using the *F*-test. The final model was selected according to the level of deviance explained and Akaike's information criterion (AIC). Non-significant terms ($p > 0.05$) were dropped from the model. Additional analyses were performed involving only landings (*Mesodesma donacium* in Chile) or abundance (*M. mactroides* in Uruguay) with price and fishing effort, respectively. The residuals of these models (i.e. the variance not explained by unit price or fishing effort) were modeled against SSTA to test if this climatic variable could account for the variance not explained by the model mentioned before.

RESULTS

Multidecadal basin scale

Mesodesma donacium

The cumulative sum of the PDO showed a marked shift in the ocean-climate regime from a cold to a warm phase in 1977 (Fig. 2A). *Mesodesma donacium* landings in Peru and NCh linearly increased with PDO ($r^2 = 0.28$, $p < 0.05$ and $r^2 = 0.24$, $p < 0.001$, respectively), being low during the cold phase and increasing during the warm phase (Fig. 2B,C). By contrast, landings from CCh and SCh showed no significant correlations with PDO.

Mesodesma mactroides

The cumulative sum of the AMO showed a regime shift between 1994 and 1995 (Fig. 3A). This climatic index was positively correlated with SSTA recorded for the study zone ($r^2 = 0.39$, $p < 0.005$), displaying the best fit with a lag of 4 yr between them (i.e. $SST_{(t+4)}$ vs. $AMO_{(t)}$) (Fig. 3B). Yellow clam abundance was inversely correlated with AMO variations, displaying the best fit with a lag of 4 yr (i.e. $abundance_{(t+4)}$ vs. $AMO_{(t)}$; $r^2 = 0.19$, $p < 0.05$), meaning higher abundance during the cold period and lower during the warm one (Fig. 3C).

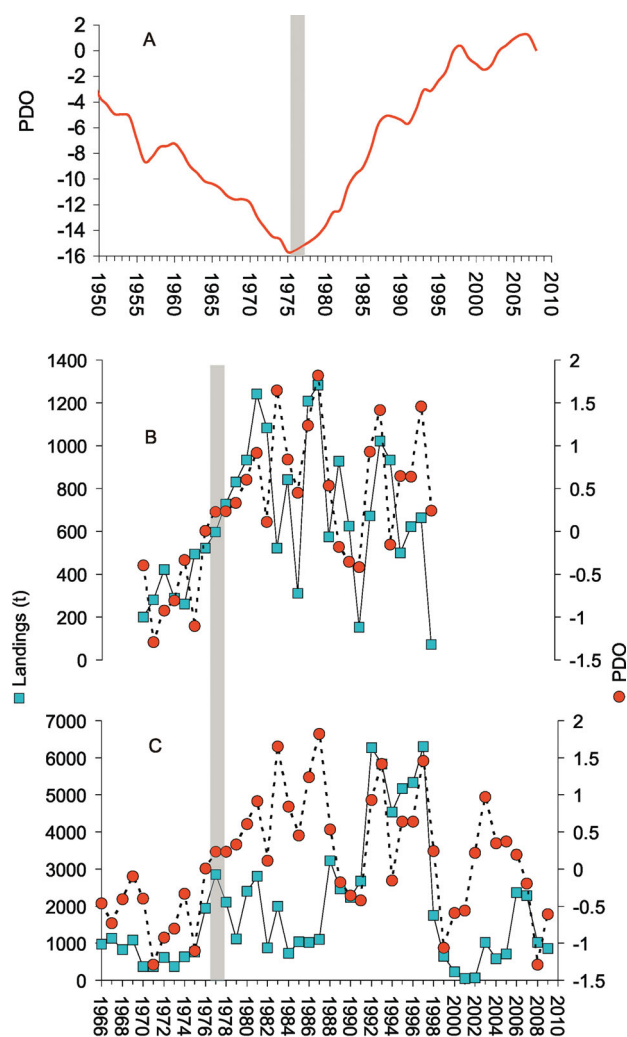


Fig. 2. *Mesodesma donacium*. (A) Cumulative sum of the Pacific Decadal Oscillation (PDO) index; and long-term variations in landings (■) and in the PDO (●) for (B) Peru and (C) Northern Chile. Shaded bar: climate shift in 1977, according to Fiedler (2002) and Chavez et al. (2003). Note the different scales on the x-axes in (A) and (B,C), and in the left-hand y-axes in (B,C)

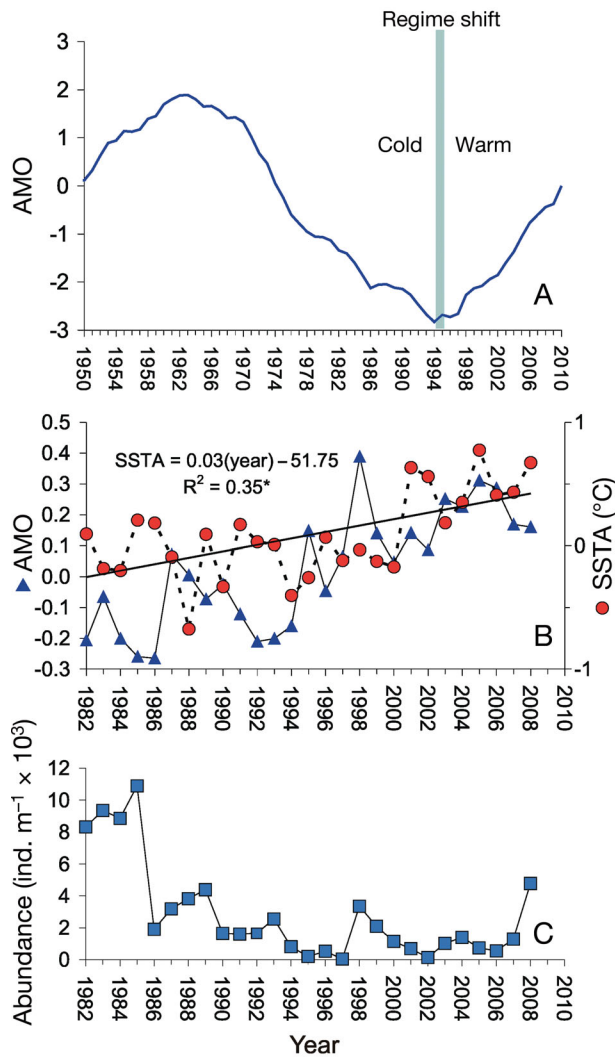


Fig. 3. (A) Cumulative sum of Atlantic Multidecadal Oscillation (AMO) from 1950 to 2008; (B) annual variations in sea surface temperature anomalies (SSTA, ●) and AMO (▲) for the period 1982 to 2008; (C) long-term variations in abundance of *Mesodesma mactroides*, from sampling surveys conducted between 1982 and 2008. The regression equation in (B) corresponds to the models fitted between SSTA and time (years) (* $p < 0.001$). Shaded bar in (A): shift in the ocean-climate regime from a cold to a warm period between 1994 and 1995 (see Goldenberg et al. 2001 for details on this shift)

Interannual coastal scale

Mesodesma donacium

The *Mesodesma donacium* fishery in Peru showed an initial phase characterized by landings ranging between 200 t in 1970 to 521 t in 1976. The expansion phase occurred between 1977 and 1980, when catches reached ca. 4000 t, during the period preceding the strongest ENSO event, which occurred in 1982–83. This event caused mass mortalities, and no

live surf clams were found in shallow waters south of Lima. After another strong warm ENSO event (1997–98), the fishery was closed (1999). This management decision is still in place in Peru (Fig. 4).

The macha fishery in Chile showed an initial fishery phase between 1966 and 1982, characterized by landings ranging between 1000 and 6000 t (Fig. 4). The expansion phase extended approximately between 1983 and 1989 (Fig. 4), as a response to a strong trend toward diversification in the exportation of many Chilean shellfish products. Landings peaked in 1989, reaching ~18 000 t, and drastically declined thereafter (1990 to 2006) down to <4000 t. The reduction in the exported volume from 2329 t (1989) to 1641 t (1992) was compensated by a higher exportation price, reaching the highest export earnings in 1988 (US \$ 9 381 000). Long-term variations in macha unit prices from Chile significantly increased through time, particularly between 1986 and 1988 and from 2002 to 2008 (Fig. 4).

All bioclimatic units showed oscillations in SSTA through time associated with cold and warm periods. With the exception of Peru, SSTA significantly increased through time (Fig. 5), with the highest temperatures observed during the strong ENSO events of 1982–83 and 1997–98 (shaded areas in Fig. 5). Landings in Peru drastically decreased from 4000 t in 1978 to 500 t in 1983 (Fig. 6A). Between 1984 and 1997, landings were ~800 t, and drastically dropped from 700 to 70 t during the 1997–98 ENSO event. Since 1999, the fishery has been closed.

Concerning NCh, the fishery showed a development phase between the 1960s and the mid-1970s, followed by an expansion phase that was interrupted in 1983 (ENSO). The fishery was recovered during the 1990s, reaching the highest historical value in 1997 (6000 t), and dramatically declined 1 yr later (<2000 t), until reaching the lowest value in 2001 (45 t, see Fig. 5B). Concerning CCh, landings showed 2 peaks: the first was observed in the early 1970s, concurrently with a period of negative SSTA, whereas the second occurred in 1986 (7500 t), thereafter decreasing until reaching the lowest values after the 1997–98 ENSO (Fig. 5C). In SCh, landings also showed 2 major peaks (Fig. 5D): the main one in 1988–89 and the second one in 1998, during the ENSO event. A strong increase in landings occurred just after the ENSO of 1982–83, and was followed by an exponential drop during the 1990s (from 9000 to <500 t between 1993 and 1997). Landings increased 8-fold during the 1997–98 ENSO event (4000 t), but this pulse was followed by an exponential decrease, reaching <2000 t yr⁻¹ at the end of the period.

GAM results are shown in Table 1. SSTA was a significant predictor of long-term variations in Peruvian landings (Table 1). Partial residuals showed a linear decrease through time and a nonlinear relationship with SSTA. In the latter, landings were highest at SSTA values close to -1°C , and dramatically declined with positive SSTA values (Fig. 6A). The decline in partial residuals through time suggests that the effect of SSTA alone was insufficient to change the observed trend in landings (Fig. S1A in the supplement at www.int-res.com/articles/suppl/m469p071_supp.pdf). In NCh, unit price was a significant nonlinear predictor of long-term variations in landings (Fig. 6B), but partial residuals showed a similar trend through time to that observed in raw data, particularly from 1976 onwards, when market statistics began, suggesting that the effect of market price was not the only explanatory variable of landing fluctuations (Table 1; Fig. S1B in the supplement).

For CCh, GAM results showed that price and SSTA were the best significant predictors ($p < 0.01$) of macha landings, as evidenced by the consistent increase in r^2 and explained deviance, concurrently with a decrease in AIC (Table 1). Partial residuals followed a nonlinear decreasing relationship with unit price and a negative linear relationship with SSTA (Fig. 7A; Fig. S2A in the supplement). No statistical differences in residual deviance were observed ($p(F)$

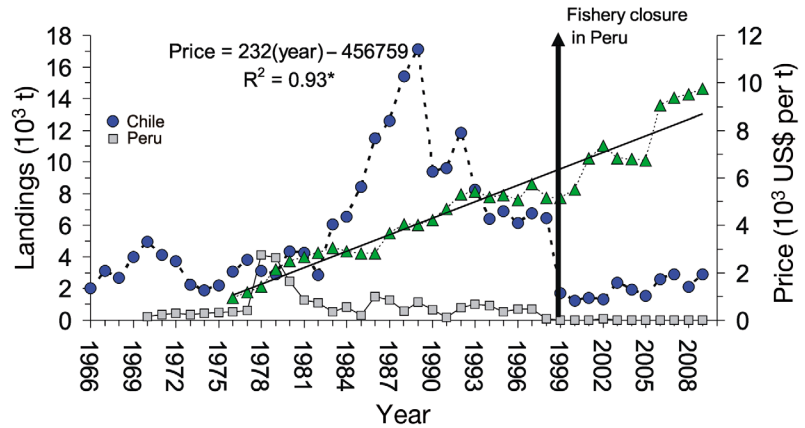


Fig. 4. *Mesodesma donacium*. Long-term trends in landings for Chile (●) and Peru (■), and in unit prices for the Chilean fishery (▲). The regression equation corresponds to the linear model fitted between unit price and time (year) (* $p < 0.001$)

= 0.18) between the model with price (GAM CCh²) and the one with SSTA (GAM CCh³) (Table 1), meaning that both variables have the same importance as predictors of long-term trends. However, the shape of the curve of partial residuals through time did not differ from the one observed with raw data, indicating that market price and SSTA cannot explain entirely the observed trends. The effect of market price is noticeable in partial residuals of the model: removing the effect of market price determined a change in the relationship between landings and SSTA (Fig. S3 in the supplement).

Concerning SCh, unit price and SSTA were also the best significant predictors ($p < 0.01$) of long-term macha landings. Partial residuals showed a nonlinear negative relationship with unit price and, in contrast with the other bioclimatic units, a positive linear relationship with SSTA (Figs. 7B, S2B). The model that included only unit price (GAM SCh²) explained a higher percentage of deviance, and had a lower AIC and lower residual deviance ($p(F) < 0.001$) than the model that only included SSTA (GAM SCh³) (Table 1). Partial residuals showed a similar trend through time to that observed in raw data, indicating that the effect of market price and SSTA cannot explain entirely the observed trend in landings. Further analyses performed by modeling macha landings versus price (only for Chile, for which price information is available) showed that this relationship was significant for all 3

Table 1. *Mesodesma donacium* and *M. mactroides*. Generalized additive model selection, (GAM) for *M. donacium* landings and *M. mactroides* abundance. Non-significant terms ($p > 0.05$) were dropped from the model. Superscripts in the GAM column denote different models for the same region. The best model for each region and species is in **bold**. edf: estimated degrees of freedom; adj.: adjusted; DE: deviance explained; AIC: Akaike information criterion; s: spline smoother; Lan: landings; AB: abundance; f: fishing effort; SSTA: sea surface temperature anomalies; CCh: Central Chile; NCh: Northern Chile; SCh: Southern Chile; Uy: Uruguay

GAM	Terms	edf	Adj. r^2	DE (%)	AIC
Peru	Lan ~ s(Year) + s(SSTA)	3.70	0.36	44.7	463
NCh	Lan ~ s(Year) + s(Price)	8.98	0.91	94.0	494
CCh¹	Lan ~ s(Year) + s(Price) + s(SSTA)	9.01	0.94	95.8	486
CCh ²	Lan ~ s(Year) + s(Price)	8.06	0.92	94.1	495
CCh ³	Lan ~ s(Year) + s(SSTA)	9.34	0.92	94.7	494
SCh¹	Lan ~ (Year) + (Price) + s(SSTA)	11.27	0.82	88.8	537
SCh ²	Lan ~ (Year) + (Price)	10.27	0.77	84.8	545
SCh ³	Lan ~ (Year) + (SSTA)	1.85	0.19	24.2	580
Uy¹	AB ~ s(Year) + s(f) + s(SSTA)	9.01	0.94	96.0	410
Uy ²	AB ~ s(Year) + s(f)	4.57	0.88	90.4	424

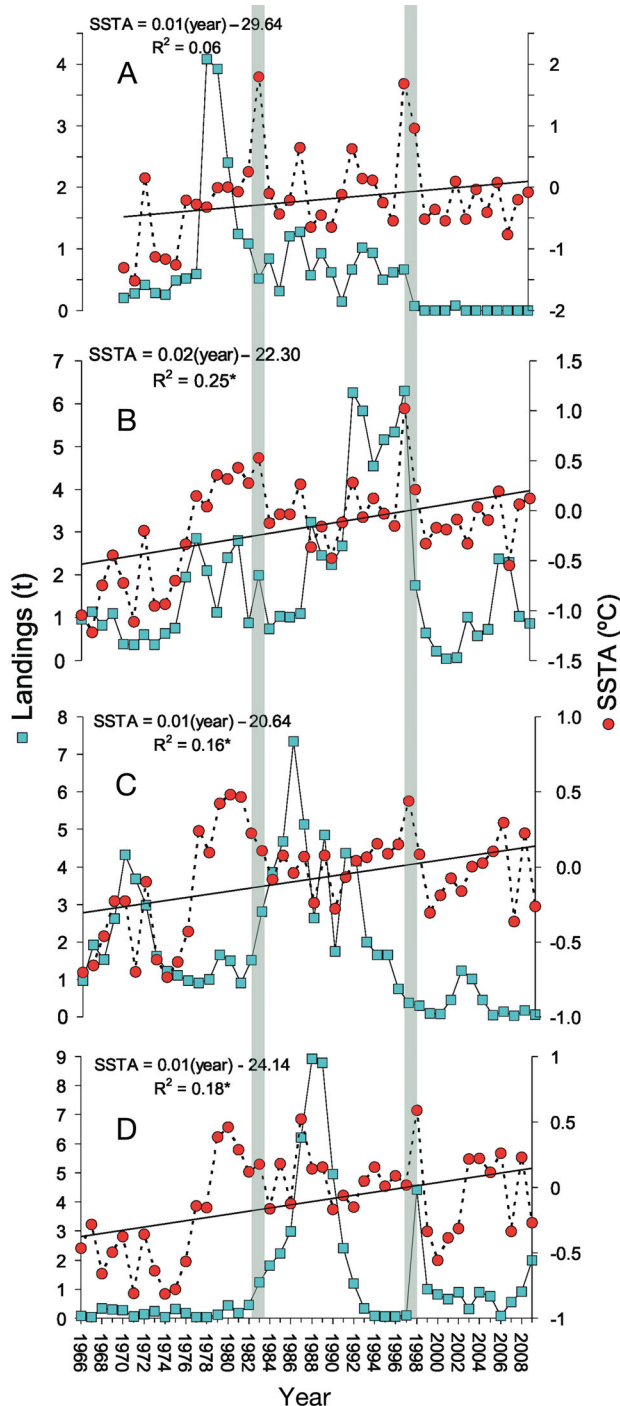


Fig. 5. *Mesodesma donacium*. Annual landings (■) and regional annual mean sea surface temperature anomalies (SSTA) (●) for (A) Peru, (B) Northern Chile, (C) Central Chile, and (D) Southern Chile. Shaded bars: strong El Niño Southern Oscillation (ENSO) events of 1982–83 and 1997–98, which matched with the highest SSTA and a decrease in landings in Peru and Northern Chile. The regression equations correspond to the models fitted between SSTA and time (year) (* $p < 0.001$). Note the different scales for both the right- and left-hand y-axes

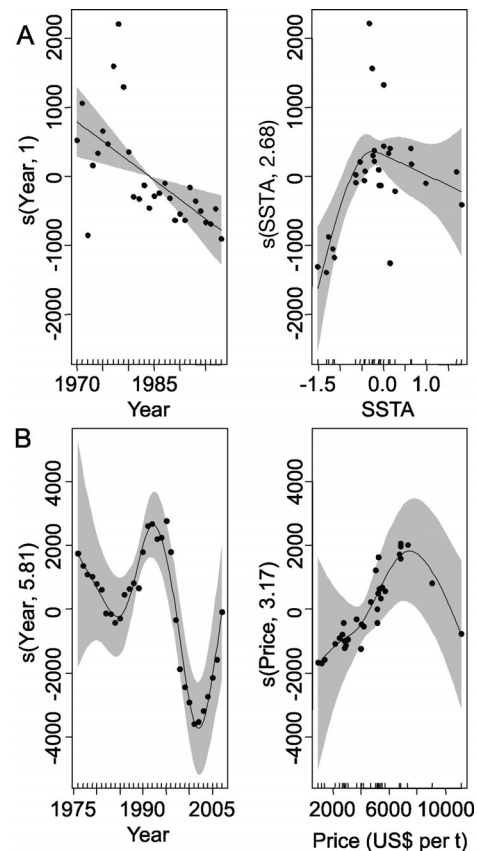


Fig. 6. *Mesodesma donacium*. Estimated generalized additive model (GAM) terms showing the partial residuals (solid lines) of annual landings after fitting against (A) time (year) and sea surface temperature anomalies (SSTA) in Peru; and (B) time (year) and price in Northern Chile. Shaded area: ± 2 SE above and below the estimated smooth curve. Numbers on each y-axis are the estimated degrees of freedom of the plotted terms (partial residuals of landings)

Chilean regions (Table S1 in the supplement). The relationship between model residuals and SSTA was not significant for NCh and SCh, whereas a negative relationship ($r^2 = 0.16$, $p < 0.05$) was found for CCh (Fig. S4A in the supplement).

Mesodesma mactroides

The long-term analysis of the artisanal yellow clam fishery in Uruguay showed a initial phase during early 1980s, followed by an overexploitation phase and the closure of the fishery in 1987 (Fig. 8A). An increase in unit price was observed through time, even at low landing and abundance levels (Fig. 8A). The best unit price-catch relationship followed a function of the form ($r^2 = 0.78$; $p < 0.001$): $\text{Price} = 19.33 \times \text{Catch}^{-0.63}$. The percentage of the harvestable

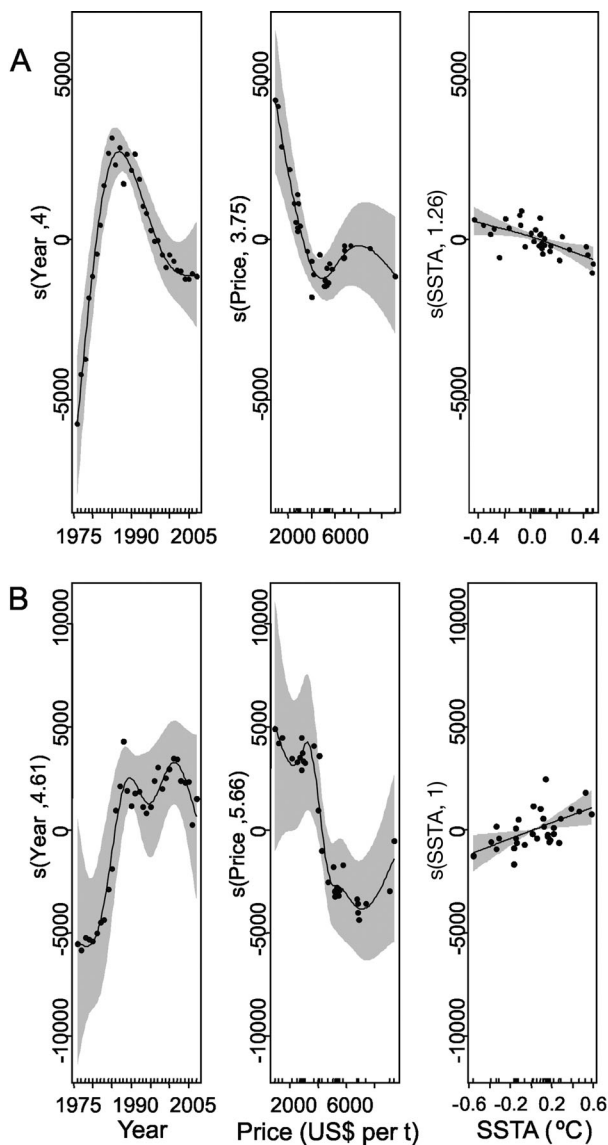


Fig. 7. *Mesodesma donacium*. Estimated generalized additive model (GAM) terms showing the partial residuals of annual landings (solid lines) after fitting against time (years), price, and sea surface temperature anomalies (SSTA) for (A) Central Chile and (B) Southern Chile. Shaded areas: ± 2 SE above and below the estimated smooth curve. Numbers on each y-axis are the estimated degrees of freedom of the plotted terms (partial residuals of landings). Note the different scales

(adult abundance) significantly increased between 1989 and 1994, just after the fishery closure (1987 to 1989). However, the occurrence of several mass mortality events that began in late 1993 determined a new fishery closure until 2008, without showing evidence of stock recovery throughout this period, particularly in the case of the adult (harvestable) stock (Fig. 8B).

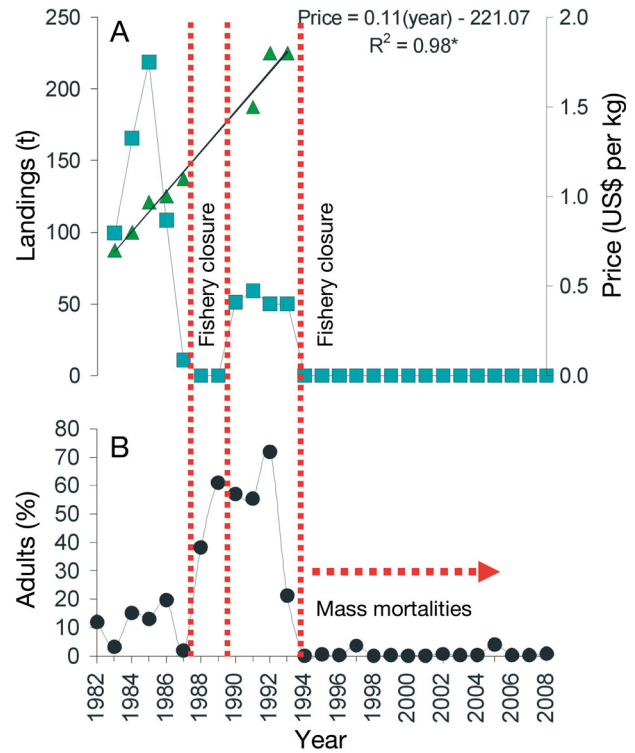


Fig. 8. *Mesodesma mactroides*. Long-term variations in: (A) landings (■) and unit price (▲); and (B) the harvestable stock, as denoted by the percentage of adults (●). The regression equation in (A) corresponds to the linear model fitted between unit price and time (year) ($*p < 0.001$). The red arrow highlights the beginning of mass mortalities since 1993–94 (see Fiori et al. 2004 for details on mass mortalities)

Fishing effort exerted in the previous year and SSTA were the best predictors of yellow clam abundance (Fig. 9, Fig. S5 in the supplement, Table 1). Partial residuals showed a positive relationship with fishing effort and 2 contrasting trends with SSTA: a positive nonlinear relationship with negative SSTA and a negative one with positive SSTA. Partial residuals through time showed the same pattern as for abundance, indicating that the effect of fishing effort and SSTA are insufficient to explain temporal variations in yellow clam abundance. The relationship between abundance and fishing effort was statistically significant (Table S1 in the supplement). The residuals of the model were negatively correlated with SSTA ($r^2 = 0.19$; $p < 0.05$) (Fig. S4B in the supplement).

DISCUSSION

This paper gives evidence of long-term and large-scale effects of fishery bioeconomic factors and climate variability in intertidal sandy beach clams. The

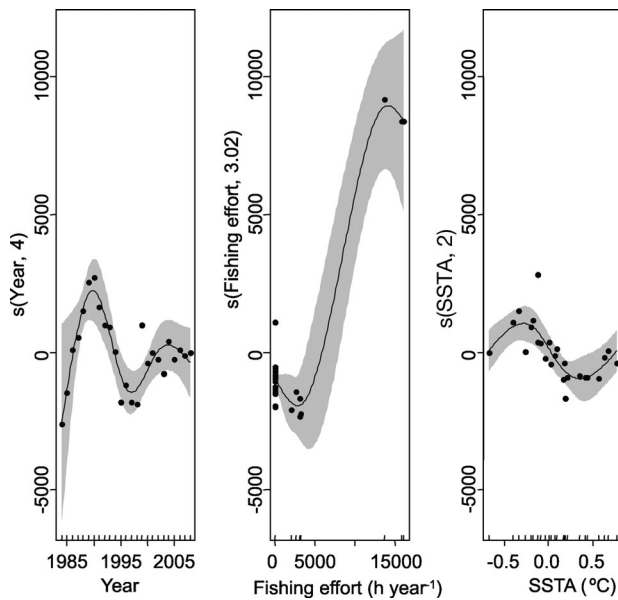


Fig. 9. *Mesodesma mactroides*. Estimated generalized additive model (GAM) terms showing the partial residuals (solid lines) of abundance after fitting against time (year), fishing effort exerted in the previous year, and sea surface temperature anomalies (SSTA). Shaded areas: ± 2 SE above and below the estimate of the smooth curve. Numbers on each y-axis are the estimated degrees of freedom of the plotted term (partial residuals of abundance)

effect of these variables on *Mesodesma donacium* and *M. mactroides* clam fisheries was complex and varied in a differential way according to latitude and the intrinsic characteristics of the oceanographic systems. In this setting, the nature and sign of the relationship between Pacific macha landings and explanatory predictors varied by bioclimatic unit. Indeed, Peruvian landings were negatively correlated with SSTA and appeared to be dramatically affected by ENSO events (particularly 1997–98). By contrast, landings in SCh were positively and significantly correlated with SSTA, suggesting that species abundance could respond positively to slight increases in temperature at its southernmost distribution range. Our findings reinforce the notion that systems can respond in different ways to changes in drivers such as exploitation pressure or temperature rise (Scheffer et al. 2009). Even though our modeling approach was useful to assess the effects of market price, fishing effort, and climate on long-term trends in landings or abundance of sandy beach clams, it is not suitable for predictive purposes. In this vein, modeling catastrophic events (mass mortalities) needs another approach that is far beyond the scope of the present paper.

The dramatic drop in landings at the northernmost edge of the *Mesodesma donacium* range (Peru) and in NCh, observed during or close to strong ENSO events, supports the notion that ENSO constitutes an important natural threat for the macha in the northernmost bioclimatic unit. ENSO is the major intra-decadal and large-scale climate-driven forcing factor in the Chilean–Peruvian coastal upwelling system (Baumgartner & Ortlieb 2002, Chavez et al. 2003, Montecino & Lange 2009), causing dramatic changes in faunal assemblages (e.g. Barber & Chavez 1983, Castilla & Camus 1992, Chavez et al. 1999, Tarazona & Arntz 2001), and affecting the domestic economy of Chile and Peru (Thatje & Heilmayer 2008), including artisanal fisheries (see Castilla & Camus 1992). In addition, the fast boom-and-bust cycle of the fishery in Peru aggravated the situation, suggesting that cumulative impacts of climate and fishing could have prompted the fishery collapse.

The inverse relationship between landings and temperature should be seen as a threshold where other processes took place. The increase in SSTA through time and the occurrence of ENSO events might have challenged *Mesodesma donacium* by distancing populations from optimal environmental conditions, operating directly through physiological processes (metabolism or reproduction) or indirectly through related changes in ecosystem structure (Stenseth et al. 2002). In this vein, mass *M. donacium* mortalities that occurred during strong warm ENSO events have been mainly associated with rising temperatures and increasing susceptibility to parasitism and diseases under anomalous environmental conditions (Arntz et al. 1987, Ibarcena et al. 2005, Riascos et al. 2009, 2011). These mass mortalities, which mainly occurred at the northernmost bioclimatic unit, generated drastic changes in the ecosystem and in the macrofaunal community structure, including increasing densities of subordinate competitors, such as the clam *Donax obesulus* (Arntz et al. 1987, Carstensen et al. 2010).

Mesodesma donacium landings in SCh increased under positive SSTA and during ENSO events, showing an opposite pattern to that observed for the northernmost edge. These trends suggest positive effects of increasing temperatures on clam abundance or fishery activity in this bioclimatic unit, which could be explained by 3 non-mutually exclusive hypotheses: (1) an increase in temperature in an actually cold system, together with a southward weakening of ENSO environmental effects and an improvement in climatic conditions; (2) a ‘mining-shellfish exploitation strategy’ behavior (sensu Defeo

& Castilla 2005), where fishers and divers sequentially move into less-exploited clam beds (i.e. from NCh to SCh); and (3) the existence of a genetic structure along geographic distribution of the species, with 2 groups of haplotypes and a contact zone between 32° and 34° S (CCh), which could explain different responses to climate variability (Peralta 2008). Populations at the edges of a species range could have particular adaptations to extreme conditions, but climate changes make them even more vulnerable to fishing activity. From a management and conservation point of view, this means that special protection should be placed on these populations, where the first adverse environmental impacts are expected to occur (e.g. Peru and NCh). As the rate of change may overwhelm the ability of a species to adapt, a policy of 'managed retreat' (Brander 2010) should be needed. Indeed, a main implication of these trends is that efforts to reduce the risk of unwanted state shifts should address the gradual changes that affect resilience (Scheffer et al. 2001).

Long-term abundance fluctuations in the Atlantic yellow clam clearly showed that environmental effects, reflected by a systematic increase in SSTA, in addition to uncontrolled fishing at the beginning of the study period, have swamped management measures. Indeed, the fishery closure implemented between 1987 and 1989 allowed a fast and strong recovery of the harvestable (adult) stock (Defeo 1996, 1998; our Fig. 8). The fishery was reopened from December 1989 onwards, under a co-management scheme and a precautionary approach that included several management regulations (Defeo 1998). During the co-management phase, harvestable stock abundance increased and catch per unit effort (CPUE) was much higher than in preclosure years (see our Fig. 8B; Castilla & Defeo 2001). However, the occurrence of mass mortalities registered from 1994 onwards decimated the stock, which has not fully recovered since then (see our Fig. 8B; Defeo 2003). A similar situation was observed in Brazil and Argentina (Fiori & Defeo 2006, Herrmann et al. 2011). These mass mortalities sequentially occurred in a north-south direction from 1993 (southern Brazil) to 2002 (Isla del Jabali, Argentina), mainly between late spring and early summer, when these cold-water clams are more sensitive to diseases (Fiori et al. 2004). It is hypothesized that the systematic increase in SSTA, associated with a southward migration of a critical warm isotherm, has exacerbated the negative influence of oceanic warm waters (L. Ortega et al. unpubl.). Concurrently with the systematic increase in SSTA, long-term increasing effects of diseases and

deformities (e.g. foot and gills) have been observed in this clam (Fiori et al. 2004, E. Delgado et al. unpubl.).

Regional warming could also have triggered drastic long-term changes in Atlantic sandy beach communities: mass mortalities of yellow clam promoted an exponential increase of warm-favoring species, such as the wedge clam *Donax hanleyanus* and the mole crab *Emerita brasiliensis*, which are subordinate competitors for space and food in this suspension-feeding guild (Defeo 2003). This shift that occurred in the ecosystem after surpassing a critical threshold or tipping point has been observed in sandy beach ecosystems from southern Brazil, Uruguay (Defeo 2003), and Argentina (Dadón 2005, Herrmann et al. 2009, Thompson & Sánchez De Bock 2009).

We found a significant effect of broad-scale climate variations on both clam fisheries. Tropical SSTA variations are in phase with AMO, which adds support to the evidence that AMO influences South American climate (Seager et al. 2010). In the Uruguayan coast, the positive correlation between SSTA and the AMO suggests that the latter could also affect circulation patterns. In fact, the observed shift from a cold to a warm phase after 1994, the sustained rise in temperature in the SW Atlantic, the southward range shift of tropical species (Segura et al. 2009, Izzo et al. 2010), and the mass mortalities observed since 1993 reinforce the hypothesis of changing of circulation patterns. These effects have been mainly documented in the northern Atlantic (Beaugrand 2004, Gröger & Fogarty 2011), whereas catch fluctuations in the southern Atlantic have been associated with unidentified low-frequency oceanographic anomalies and overfishing (e.g. Brazilian sardine; Matsuura 1996).

In the HCS, biological and non-biological components, ecosystem processes, and fisheries are known to be affected by multidecadal scale variations. In fact, air and ocean temperatures, atmospheric carbon dioxide, landings of pelagic fish, and the productivity of coastal and open ocean ecosystems have varied over periods of about 25 to 50 yr (Montecino & Lange 2009). In the mid-1970s, the Pacific changed from a cold to a warm regime (see Fig. 2A). A shift back to a cold regime occurred in mid to late 1990s (our Fig. 2B,C; Chavez et al. 2003). These basin-scale climate shifts might have influenced NCh and Peru *Mesodesma donacium* landings, with a positive response during the warm phase and a decline during the cold phase, concurrently with the 1997–98 ENSO. The prevailing hypothesis is that the PDO is caused by a 'reddening' (oceanic or other slow components of the climate system outside the domain of

study) of ENSO events, combined with stochastic atmospheric forcing, which goes against the idea that PDO may regulate decadal climate variability (Newman et al. 2003, Pavia 2009, Shakun & Shaman 2009). Consequently, the PDO could be seen as a consequence of past accumulated ENSO events that produce mild ENSO-like conditions in southern tropical Pacific coastal zones (i.e. deeper thermocline, positive SSTA, higher sea level). In contrast, high-frequency climate variations like ENSO, especially strong events, had dramatic negative effects on *M. donacium* at the northern Pacific bioclimatic units.

Unit price significantly increased through time in both *Mesodesma* clam fisheries. The steady increase in prices at low landing levels accelerated changes in resource use motivated by profit, suggesting that this variable constitutes a key economic driver that could lead to stock depletion. The growing demand associated with high export prices in *M. donacium* triggered an increase in fishing effort, which in turn affected stock sustainability. This response to market forcing was clearly shown in NCh, where landings dropped after reaching a certain unit export price, probably masking the relationship with SSTA. A similar pattern was observed in the artisanal Peruvian bay scallop *Argopecten purpuratus* fishery (Badjeck et al. 2009). In Peru, the negative effects of ENSO (1982–83) on *M. donacium* were exacerbated by a high fishing intensity (1980 to 1981) and a sustained increase in global market demand (i.e. the southern Peru production of macha was exported to Chile; Ibarcena et al. 2005). In addition, the opening of *M. donacium* foreign markets (i.e. Spain) towards the selection of clam sizes lower than the legal marketable size has been observed (Defeo et al. 1993). Thus, overexploitation trends were aggravated by globalization of markets. The increase of prices even at low landing and abundance levels, observed in both Pacific and Atlantic *Mesodesma* fisheries, resemble the anthropogenic Allee effect, in which exploitation rates increase with decreasing population size or density (Courchamp et al. 2006, Berec et al. 2007). This phenomenon is particularly noticeable in coastal stocks artisanally harvested, such as the intertidal clams analyzed here, because price values of the exploited species largely exceed the negligible exploitation costs in easily and readily accessible fishing grounds (Defeo & Castilla 2012). This highlights the need to consolidate institutional management responses, supported by integrative science, as a means to develop solid governance fishery systems to promote resilience under uncertainty (Thatje et al. 2008, Miller et al. 2010, Gutiérrez et al. 2011, Perry et al. 2011).

In summary, a complex combination of intensive exploitation, bioeconomic factors, and climate variability explained large-scale and long-term trends in landings and abundance of sandy beach clams. These factors acting together may accelerate the decline in the clams' abundance, leading them to population levels close to extinction. The lack of response of the stocks to drastic management measures (i.e. long-term closures) suggests that these complex social-ecological systems have exceeded critical thresholds (tipping points), shifting abruptly from one state to another through a catastrophic bifurcation that propels the system through a phase of directional change towards a contrasting state (Scheffer et al. 2009). Early warnings of climate tipping points (Lenton et al. 2008, Scheffer et al. 2009, Lenton 2011) could provide information to help manage sandy beach ecosystems that are increasingly threatened by long-lasting and large-scale stressors (Defeo & McLachlan 2005, Schlacher et al. 2007, Defeo et al. 2009).

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Effects of fishing, market price, and climate on two South American clam species

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Supplement. Residual analysis of Generalized Additive Models.

Table S1. *Mesodesma donacium* and *M. mactroides*. Generalized additive model (GAM) for *M. donacium* landings with price and *M. mactroides* abundance with fishing effort. Percent of deviance explained, adjusted r^2 (* $p < 0.001$), Akaike information criterion (AIC), and estimated degrees of freedom (edf) are given. s: spline smoothers; Lan: landings; CCh: Central Chile; NCh: Northern Chile; SCh: Southern Chile; Uy: Uruguay. All models showed a strong relationship between landings (*M. donacium*) or abundance (*M. mactroides*) with price or fishing effort respectively, meaning that they are not independent

Model	Terms	edf	r^2	Deviance explained (%)	AIC
GAM NCh	Lan ~s(Price)	4.15	0.24*	34.6	561
GAM CCh	Lan ~s(Price)	5.87	0.66*	72.9	539
GAM SCh	Lan ~s(Price)	5.74	0.62*	69.5	558
GAM Uy	Lan ~s(Fishing effort)	3.32	0.84*	86.4	430

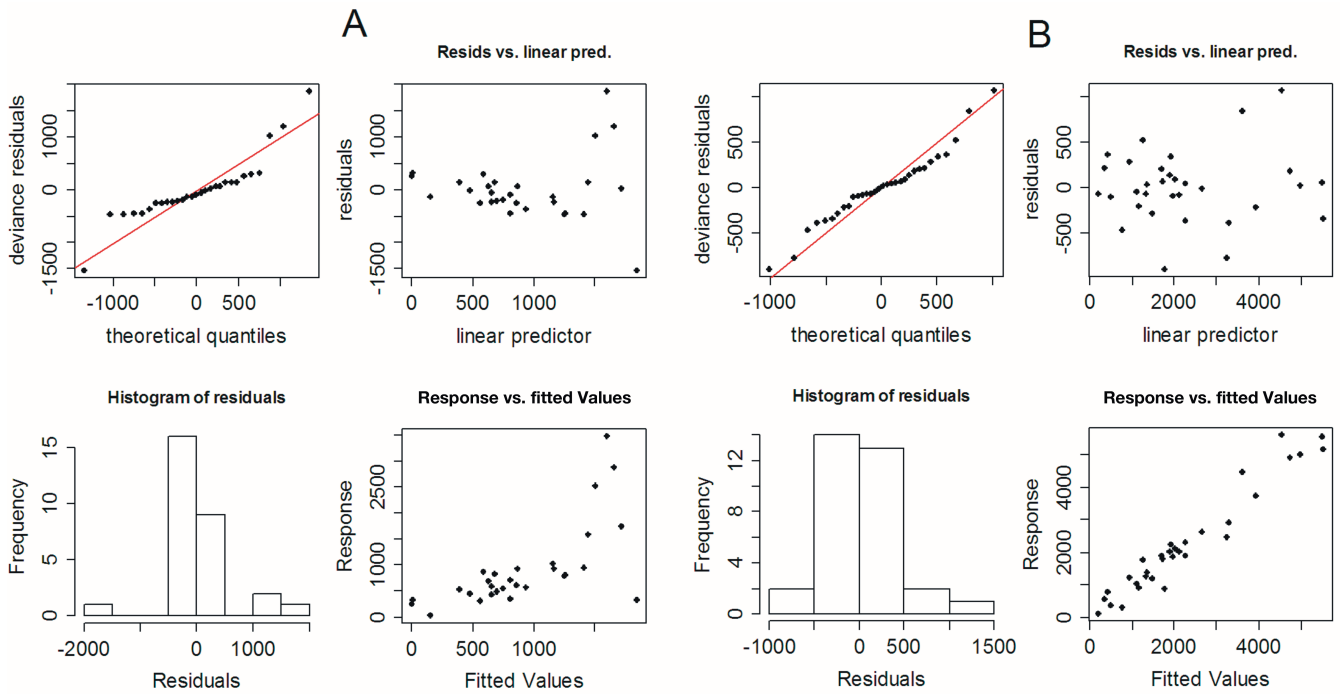


Fig. S1. *Mesodesma donacium*. Residual analysis plot of Peru generalized additive model (GAM) (A) and Northern Chile (NCh) GAM (B). The basic model checking plots of residuals for the Peru GAM (A) shows in the upper left normal theoretical quantiles (Q-Q plot) a clear deviation from the normal assumption in the distribution of the residuals. The upper right plot of residuals versus fitted values (linear predictor) shows that the assumption of constant variance is untenable, confirmed by the lower left histogram of residuals that shows the pattern described in the Q-Q plot: there are too many residuals at the center of the distribution relative to the sides. The response variable against fitted values, shown in the lower right panel, stresses the failure of the constant variance assumption. The observed trend in model residuals suggests that the lack of other predictors preclude model efficiency. The model checking plot of residuals for NCh GAM (B) shows the upper left Q-Q plot close to the straight line, suggesting that the normal distribution assumption of the residuals is reasonable. The upper right plot suggests that variance is roughly constant as the mean increases but some residuals tend to be overspread. The histogram of residuals at the lower left appears quite consistent with normality and the lower right plot of response against fitted values shows a positive linear relationship with a good deal of scatter

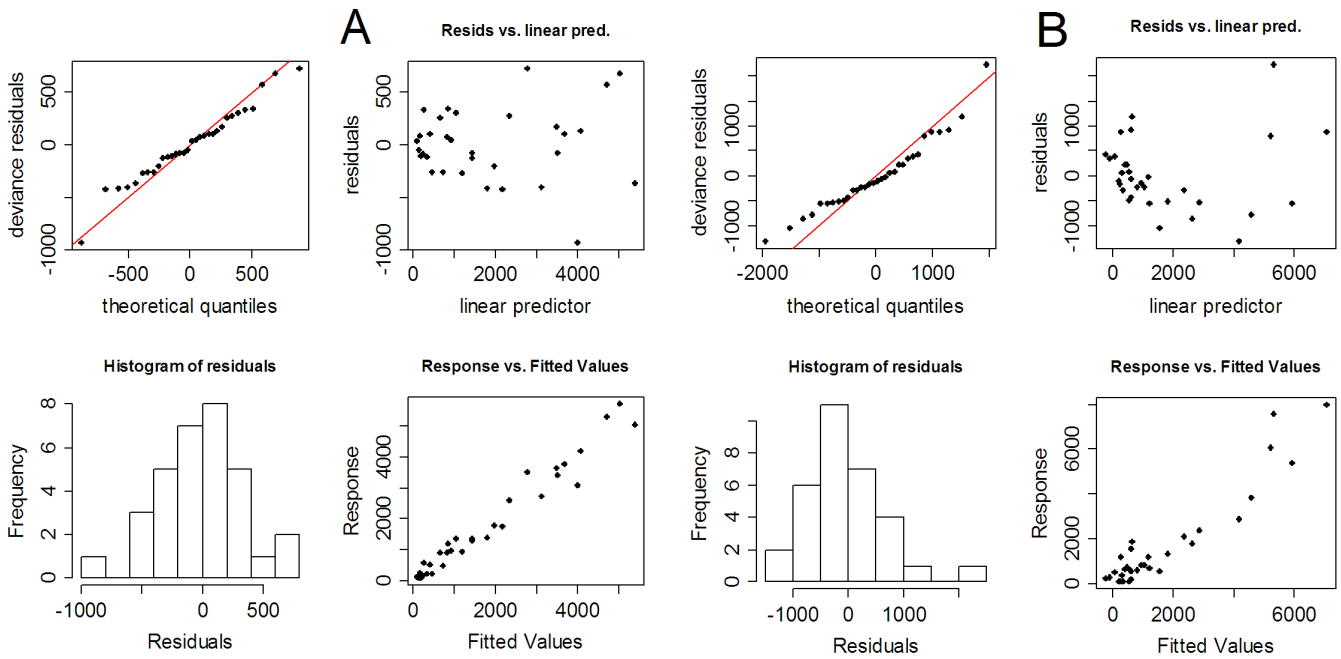


Fig. S2. *Mesodesma donacium*. Residual analysis plots of Central Chile (CCh¹) generalized additive model (GAM) (A) and Southern Chile (SCh¹) GAM (B). The basic residual plots for CCh¹ (A) GAM shows the upper left Q-Q plot reasonably close to the straight line, suggesting that the normal distribution assumption of the residuals is reasonable. The upper right plot suggests that variance is nearly constant as the mean increases, showing few high values. The histogram of residuals at the lower left appears quite consistent with normality and the lower right plot of response against fitted values shows an acceptable positive linear relationship with scarce dispersion. The plots of residuals for SCh¹ (B) GAM show the upper left Q-Q plot close to the straight line but some residuals diverge at the tails. The upper right plot shows that the variance of the residuals is not constant. The histogram of residuals at the lower left appears quite consistent with normality and lower right plot of response against fitted values shows a quite acceptable linear relationship

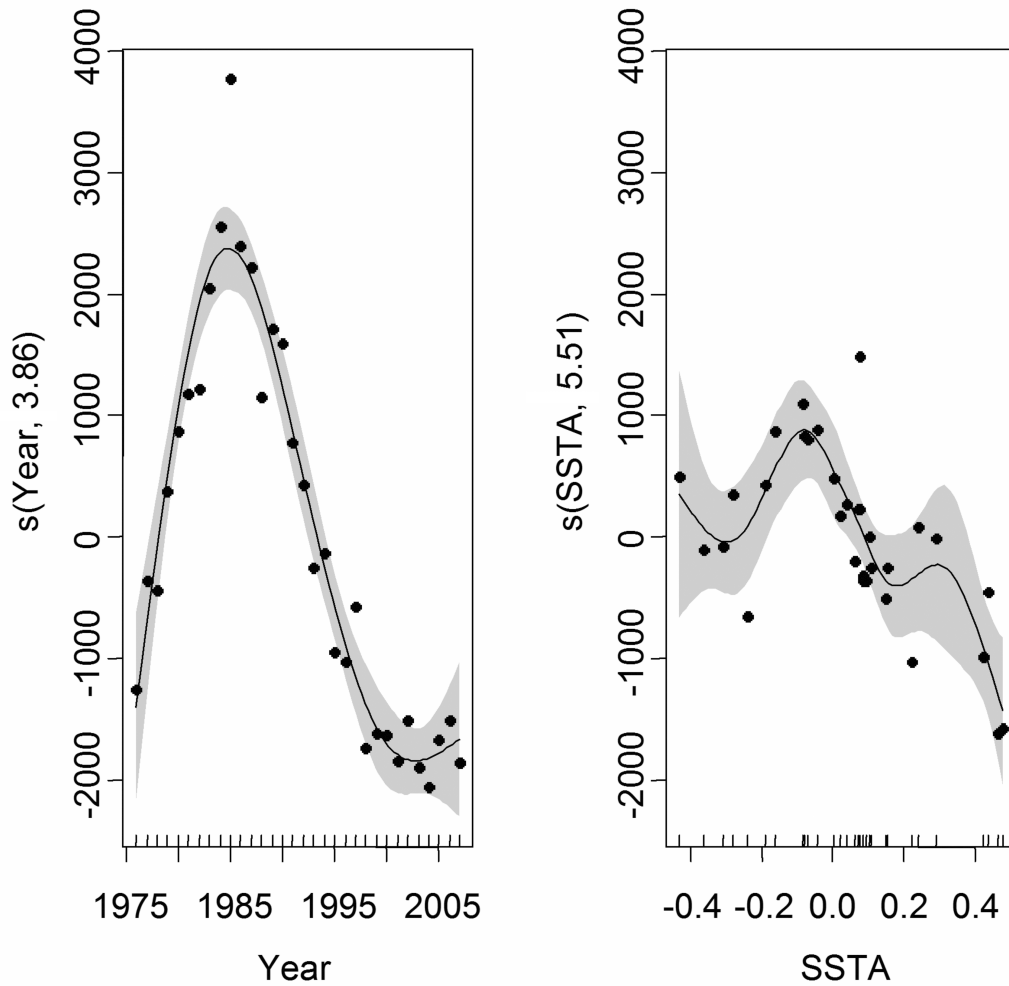


Fig. S3. *Mesodesma donacium*. Estimated model terms showing the partial residuals of landings (solid lines) through time (year), and sea surface temperature anomalies (SSTA) for Central Chile (CCh³; see Table 1 in the main paper). Shaded areas indicate ± 2 SE above and below the estimated smooth curve. Numbers on each y-axis are the estimated degrees of freedom of the plotted term (partial residuals of landings). Even though the effect of SSTA was insufficient to change the observed trend in landings, the elimination of market price effect determined a different relationship between partial residuals of landing and SSTA. Partial residuals showed 2 contrasting trends with SSTA: a positive nonlinear relationship with negative SSTA ($SSTA > -0.3$) and a negative one with positive SSTA

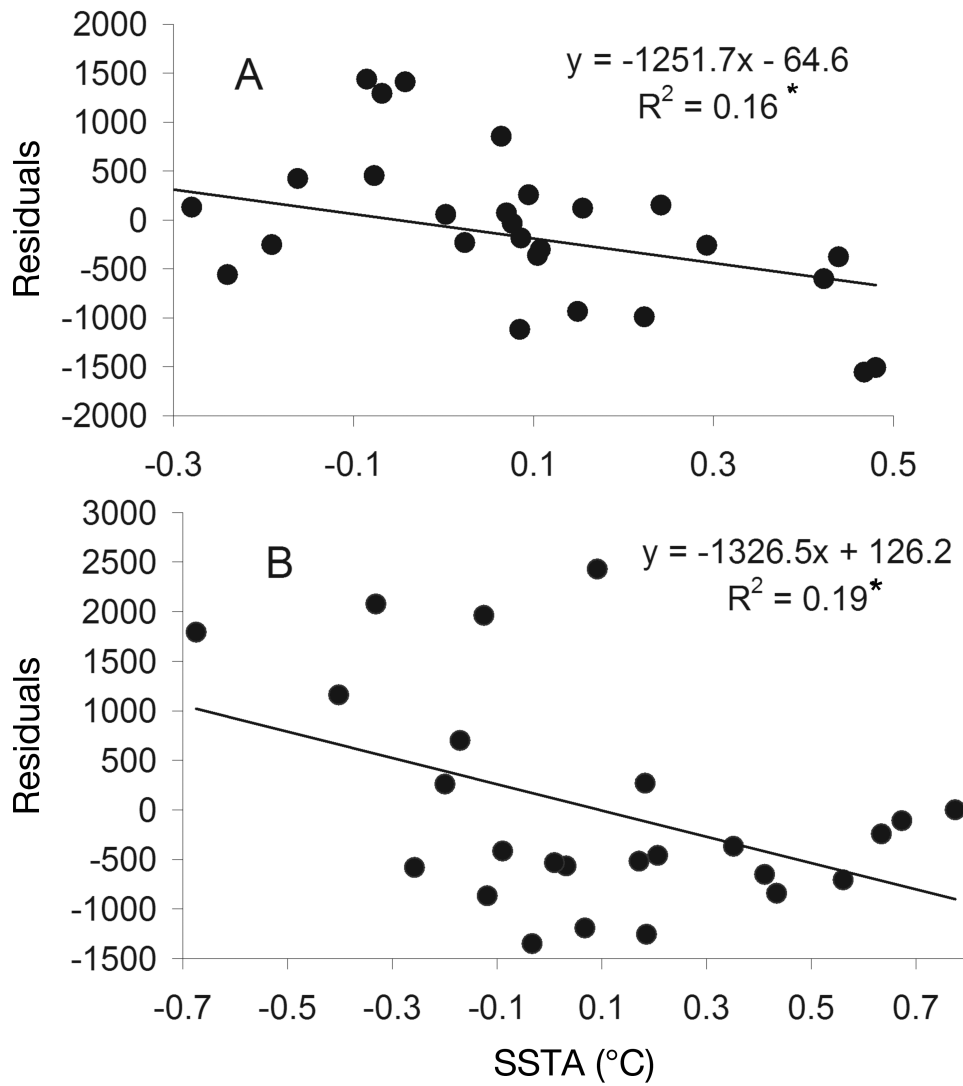


Fig. S4. (A) *Mesodesma donacium*. Central Chile model residuals (with price) relationship with sea surface temperature anomalies (SSTA) and (B) *Mesodesma mactroides*. Uruguay model residuals (with fishing effort) relationship with SSTA. The regression equations correspond to the models fitted between model residuals and SSTA (* $p < 0.05$). These results highlight that the variance not explained by the market price or fishing effort could be explained by the SSTA

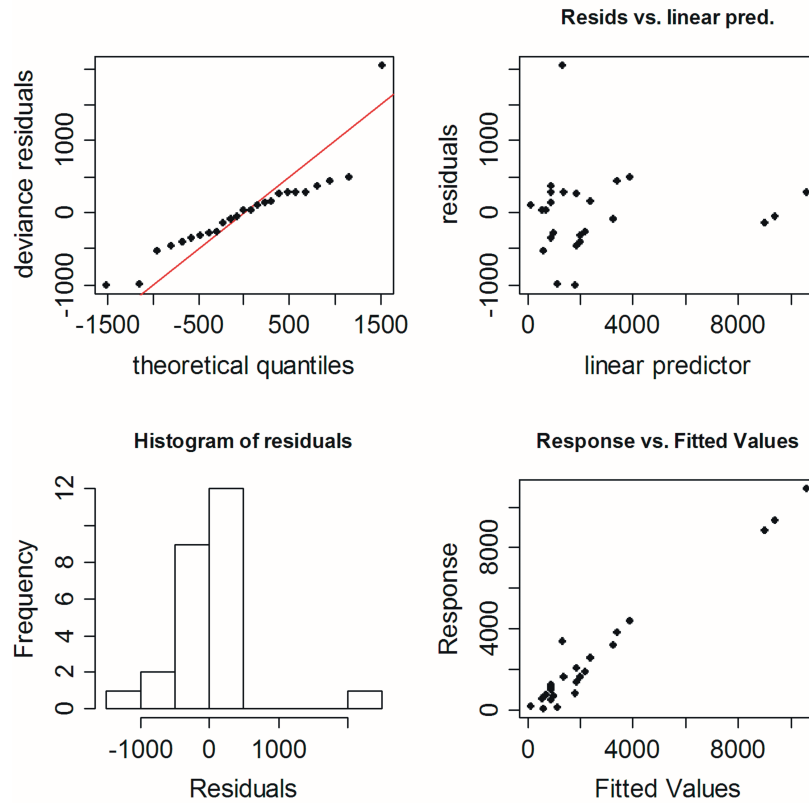


Fig. S5. *Mesodesma mactroides*. Basic model checking plot for the residual analysis of Uruguay generalized additive model (GAM). The model checking plots of residuals for the Rocha GAM shows in the upper left Q-Q plot a clear deviation from the normal assumption in the distribution of the residuals. The upper right plot of residuals versus fitted values (linear predictor) shows that the assumption of constant variance is untenable, confirmed by the lower left histogram of residuals that shows the pattern described in the Q-Q plot: there are too many residuals at the center and left of the distribution relative to the right side. The response variable against fitted values, shown in the lower right panel, displays an acceptable linear relationship with a gap in residuals distribution highlighted before in the frequency distribution of residuals

Generalidades sobre los modelos aditivos generalizados

Los modelos aditivos generalizados, GAM, se utilizan cuando se espera que la relación entre las variables sea compleja y por lo tanto difícil de ajustar con otros modelos o cuando no existe una razón a priori que determine la utilización de un modelo en particular. Brindan además, una excelente forma de interpretar los datos de manera gráfica.

Una de las principales razones para el uso GAM es que éstos no asumen supuestos como aquellos implícitos en modelos como por ejemplo la regresión paramétrica estándar. De hecho los GAM son una generalización de los modelos lineales.

Un modelo lineal se representa como:

$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_d X_d + \varepsilon$ donde se asume que $\varepsilon \sim N(0, \sigma^2)$. Si se llama $\mu = E(Y)$ se obtiene

$$\mu = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_d X_d$$

En un modelo lineal generalizado, GLM, el predictor lineal y la variable dependiente están relacionadas por una función de enlace o "link" g .

$$g(\mu) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_d X_d$$

Finalmente un modelo aditivo generalizado, GAM, se representa como

$$g(\mu) = \beta_0 + f_1(X_1) + f_2(X_2) + \dots + f_d(X_d)$$

donde las funciones $f_i(X_i)$ son funciones no paramétricas definidas por los datos denominadas *smoothers*.

Los modelos aditivos generalizados y modelos lineales generalizados se pueden aplicar en situaciones similares, pero sirven para diferentes propósitos analíticos. Los modelos lineales generalizados enfatizan la estimación y la inferencia de los parámetros del modelo, mientras que los modelos aditivos generalizados se centran en la exploración de los datos no paramétricamente. Los modelos aditivos generalizados son más adecuados para explorar el conjunto de datos y la visualización de la relación entre la variable dependiente y las variables independientes.

Si consideramos los "smoothing terms" como: $\beta_0, s_1(\cdot), s_2(\cdot), \dots, s_d(\cdot)$ en el modelo aditivo. Existen muchas maneras para acercarse a la formulación y la estimación de modelos aditivos. El algoritmo de "backfitting" es un algoritmo general que puede adaptarse a un modelo aditivo.

Definimos el residual parcial j th como:

$$R_j = Y - \beta_0 - \sum_{k \neq j} s_k(X_k)$$

Los residuales parciales eliminan los efectos de todas las otras variables de Y , por lo que se pueden utilizar para modelar los efectos contra x_j (Xiang 2001).

CAPÍTULO 4

Effects of climate variability on the morphodynamics of Uruguayan sandy beaches

Effects of Climate Variability on the Morphodynamics of Uruguayan Sandy Beaches

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ABSTRACT

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Effects of long-term trends in climatic variability on the morphodynamics of a reflective and a dissipative sandy beach in Uruguay (SW Atlantic Ocean) were analyzed. The Atlantic Multidecadal Oscillation (AMO) alternates between warm and cold cycles with a periodicity of roughly 70 years, with a shift toward a warm phase since 1995, resulting in an increase of sea surface temperature in the study area. Wind speed anomalies (WSA) also increased through time and were associated with an increasing speed of southerly winds, particularly after 1997. Beach morphodynamics showed no statistically significant trends in grain size, but long-term morphodynamic patterns differed between beaches: the dissipative beach showed an increase in swash and beach width, Dean's parameter, and the Beach Index (a measure of beach morphodynamic state). At the same time, the slope decreased, augmenting the beach's dissipative characteristics. The reflective beach showed an increase in slope and swash width through time, and a decrease in the Beach Index, indicating an intensification of reflective characteristics. Long-term morphodynamic changes were more evident in the dissipative beach and related to climate forcing (*e.g.* WSA). A higher resilience was observed in the reflective beach, even though an increasing frequency of storms is affecting both beaches. Accelerating erosion, rising sea levels, and expanding urban development in the Uruguayan coast could affect biodiversity and critical habitats. Multidisciplinary investigation programs and conservation strategies are needed to mitigate negative anthropogenic effects on these ecosystems.

ADDITIONAL INDEX WORDS: *Climate variability, Atlantic Multidecadal Oscillation (AMO), beach morphodynamics, Atlantic Ocean, storms.*

INTRODUCTION

Human impacts on sandy shores have a long history (Nordstrom, 2000) and are predicted to intensify exponentially over the next few decades (Brown *et al.*, 2008). Effects of climate change may be most immediately and profoundly felt in sandy beaches, a critically important coastal ecosystem worldwide (Defeo *et al.*, 2009; Schlacher *et al.*, 2007) that is at risk of habitat loss and ecological impacts from warming, erosion caused by sea-level rise (SLR), and intensification of storms (Dugan *et al.*, 2010).

The positive long-term relationship between global mean temperatures and SLR (Rahmstorf, 2007), along with the fact that warmer air and sea temperatures translate into more frequent and severe storms (IPCC, 2007), will probably modify

morphodynamic characteristics of sandy beaches. SLR poses a threat to shorelines in general, and sandy beaches in particular (Aiello-Lammens *et al.*, 2011; Defeo *et al.*, 2009; Schlacher *et al.*, 2007). Global SLR rose at a rate of 1.7 ± 0.3 mm/y from 1950 to 2009 and at a satellite-measured rate of 3.3 ± 0.4 mm/y from 1993 to 2009 (Nicholls and Cazenave, 2010). Because of the high spatial variability in crustal subsidence rates, wave climates, and tidal regimes, it is the set of local conditions (especially the relative SLR), rather than a single global mean sea-level trend, that determines each locality's vulnerability (Gornitz, 1995; see Houston and Dean, 2012 for a recent discussion).

Marine regressions and transgressions are natural geological processes, as shown by fossil records and drill core data. The impacts of SLR on sandy beaches, notably beach squeeze, erosion, and habitat loss, are modulated by geologic factors such as isostatic adjustment (Brown and Fisher, 1977; Courtillot, 1999; Hallam and Wignall, 1999; Monroe and Wicander, 2005). In addition, oceanic temperature is influ-

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enced by climatic conditions such as the Atlantic Multidecadal Oscillation (AMO; ESRL/NOAA 2013), which modulates the climate in both North and South America (McCabe, Palecki, and Betancourt, 2004; Seager *et al.*, 2007). The AMO, an index of detrended sea surface temperature anomalies (SSTA) averaged over the North Atlantic from 0–70° N, is a natural climate oscillation linked to internal ocean–atmosphere variability and has existed throughout the Holocene (Knudsen *et al.*, 2011). Warm phases occurred during 1860–1880 and 1930–1960, and cold phases occurred during 1905–1925 and 1970–1990. Since 1995, the AMO has been positive, in a new warm phase. These swings in North Atlantic SSTs are probably caused by natural internal variations in the strength of ocean thermohaline circulation and the associated meridional heat transport (Collins and Sinha, 2003; Sutton and Hodson, 2003) that could affect the circulation of the Atlantic basin. Anthropogenic interventions are additional threats to coastal margins, including the construction of harbors, groins, jetties, and seawalls; dredging; interception of silt and sand by upstream reservoirs; interruption of littoral drift by breakwaters; pollution of groundwater; and extraction of beach sand, and they are increasing erosion and environmental degradation (Defeo *et al.*, 2009 and references therein; Esteves and Finkl, 1998; Finkl, 1993; Finkl and Krupa, 2003).

In the SW Atlantic Ocean (SAO), a significant increase in frequency and height of the waves propagating from the E and ESE has been observed (Codignotto *et al.*, 2012). This is important for Uruguayan sandy beaches, which are exposed to the swell coming from the SE. Here we assess interannual changes in the morphodynamics of two Uruguayan sandy beaches and their relationship with climate forcing, mainly wind speed, over the last 30 years. We also analyze the potential connection between SSTA trends in the SAO (shelf and adjacent oceanic region) and the AMO broad scale climate index. We hypothesize that increasing SSTA values lead to changes in wind speed, affecting sandy beach morphodynamics.

METHODS

Study Area

The study was conducted in two exposed microtidal (tidal range = 0.5 m) oceanic sandy beaches of Uruguay 100 km apart (Figure 1a), oriented to the NE (Goso Aguilar, Mesa, and Alvez, 2011): (1) Arachania (34°36' S, 53°44' W), a reflective beach with a steep slope and coarse sediments (Figure 1b); and (2) Barra del Chuy (33°45' S, 53°27' W), a wide dissipative beach with a gentle slope, fine to very fine well-sorted sands, exposed to strong wave action, and having a wide surf zone of a longshore-bar-trough type, which is particularly vulnerable to SLR (Figure 1c).

We sampled physical parameters from 1988 to 2010 at Barra del Chuy (120 sampling events), and from 1996 to 2010 at Arachania (75 sampling events). Additional information was obtained for 1982 from Defeo, Jaramillo, and Lyonnet (1992). Beach slope was estimated by the profiling technique of Emery (1961), and beach width was measured as the distance from the base of the dunes to the lower limit of the swash zone, where water moves over the beach surface after a broken wave has

collapsed (Defeo and McLachlan, 2005). Swash width was measured as the distance between the upper and lower swash limits at sampling time. Breaker height (m) was determined visually, and wave period (s) was estimated as the time interval (using a stopwatch) between breakers during 5 minutes. Sediment samples were taken at 4-m intervals with a 6.5-cm diameter corer to 10–15 cm depth to estimate grain size. To this end, samples were passed through a series of sieves (interval = 0.5 phi) in a mechanical shaker for 15 minutes, and grain size was determined by the method of Folk (1980). An overall estimate of grain size for each beach in each sampling event was obtained by averaging individual estimates.

Estimates of breaker height, wave period, and sand particle size were used to calculate two compound indices of beach state: (1) Dean's parameter (Ω ; Short, 1996):

$$\Omega = \frac{Hb \times 100}{Ws \times T} \quad (1)$$

where Hb is breaker height (m), Ws is sand fall velocity (m/s), T is wave period (s), and (2) a modified version of the Beach Index (BI) originally developed by McLachlan and Dörvlo (2005), as follows

$$BI = \frac{\text{Tide}}{BS \times \text{Sand}} \quad (2)$$

where Tide is maximum spring tide range (m), BS is the beach slope, and Sand is mean grain size (cm). Tables from Gibbs, Mathews, and Link (1971) were used to calculate settling velocities based on particle size. $\Omega < 2$ characterizes reflective beaches, $\Omega > 5$ defines dissipative ones, and $2 < \Omega < 5$ characterizes intermediate beaches.

Sea Surface Temperature Anomalies and Wind Speed

SSTA were calculated based on the data series in Reynolds *et al.* (2002) by averaging SSTA from $4^\circ \times 3^\circ$ grid cells of the SW Atlantic shelf and the adjacent oceanic region (SAO) (Figure 1a). The AMO was used to represent large-scale processes that may influence climatic conditions. AMO time series were taken from National Oceanic and Atmospheric Administration (NOAA, 2013). SSTA data for empirical orthogonal function analysis were obtained from the Extended Reconstructed Sea Surface Temperature, version 3 (ERSST_V3) dataset based on IRI/LDEO Climate Data Library (IRI/LDEO, 2013). Monthly wind speed anomalies (WSA) and meridional (v) and zonal (u) wind components for a fixed point (35° S; 52.5° W at 1000 mb pressure level) were downloaded from the IRI/LDEO Climate Data Library (IRI/LDEO, 2013; Kalnay *et al.*, 1996).

Data Analysis

Long-term variations of sandy beach physical descriptors, WSA, and SSTA were modeled by linear and nonlinear fitting procedures, and the model that maximized the goodness of fit (r^2) was selected. Bivariate relationships between climate and physical variables were also modeled by linear or nonlinear fitting. To this end, climate (SSTA and WSA) and beach physical data were smoothed by performing a running mean with a period of 4 years and 3 years, respectively.

Wind speed and direction were calculated from the meridional or north–south direction (v) and zonal or west–east direction (u) components. The wind speed from the S,

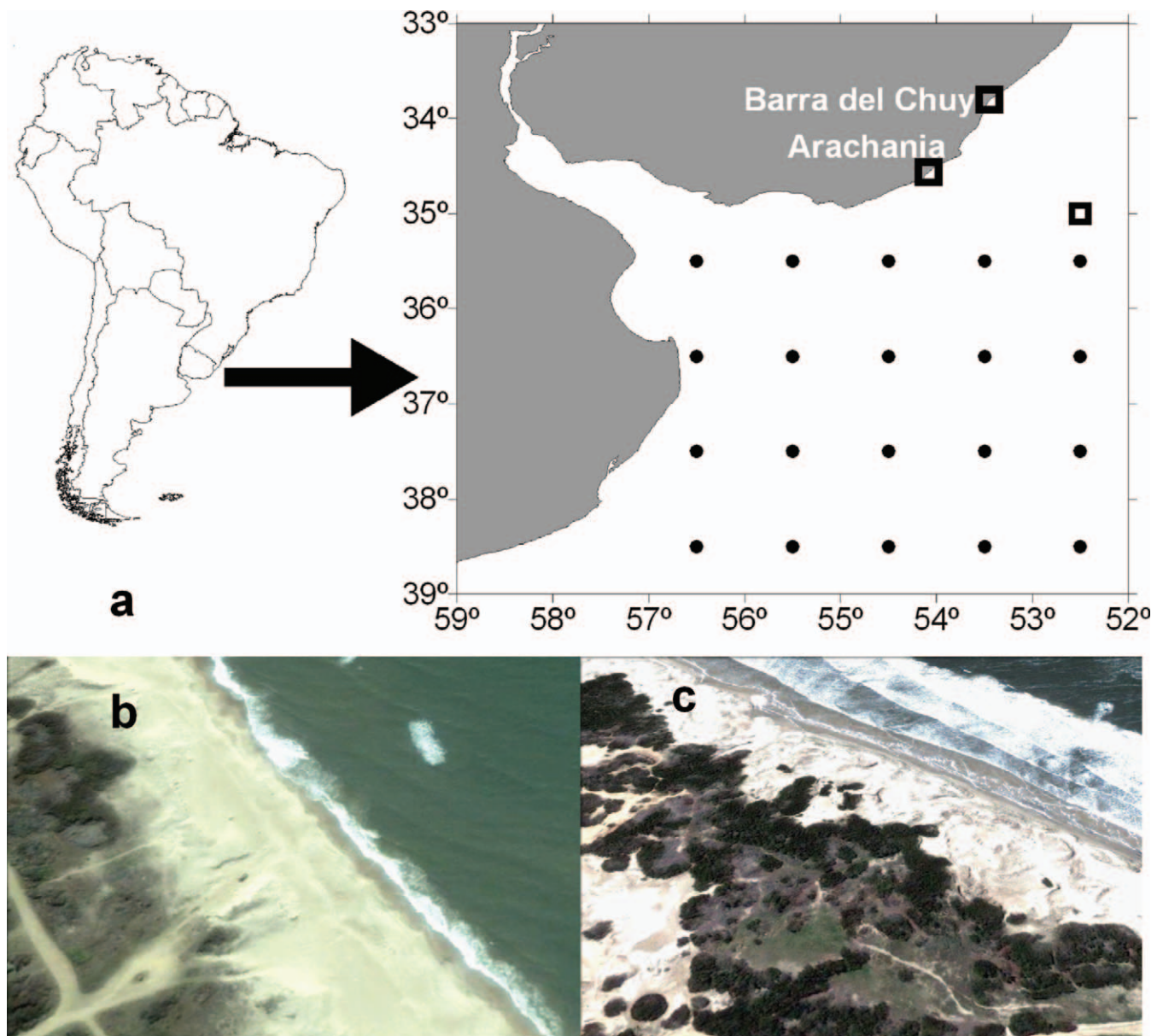


Figure 1. (a) Study area, showing the geographical location of Arachania and Barra del Chuy beaches in Uruguay, and the data points where information of sea surface temperature anomalies (SSTA) (circles) and wind speed and direction (squares) was gathered; (b) Arachania; and (c) Barra del Chuy. (Color for this figure is available in the online version of this paper.)

SSE, and SE was extracted by filtering wind directions from a long-term (from 1982 to 2010) monthly wind database. Since winds from the southern component are less frequent than others (*e.g.* from the north), gaps in the monthly mean of wind speed series from this sector (south) are expected when the average of u and v components were performed. Cumulative sums of the annual AMO index (AMOCs) and SSTA (SSTAcS) were used to detect sustained shifts in climate, marked by changes in slope of the cumulative sum

plot (Fiedler, 2002 and references therein). Empirical orthogonal function (EOF) analysis of detrended and standardized SSTA from North Atlantic and SAO time series was used to investigate potential correlations between the leading modes of variability (EOF1). The analyses were performed using a PostScript-based language provided by the IRI Data Library. The correlation between EOF1 (North Atlantic and SAO) and AMO were performed with the annual means.

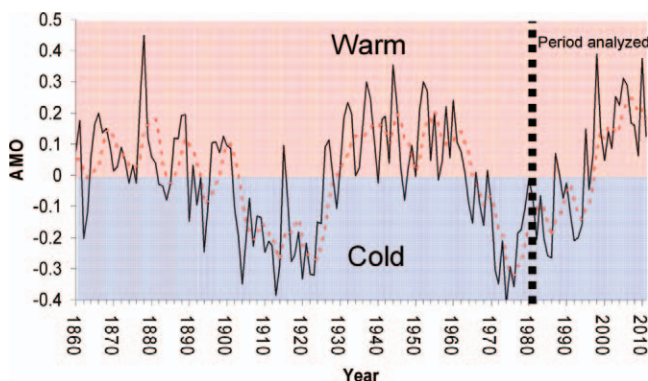


Figure 2. Atlantic Multidecadal Oscillation (AMO) index (solid line) and 5-year running mean (dashed line). The time period analyzed in this paper is highlighted. (Color for this figure is available in the online version of this paper.)

RESULTS

Climate Variability

The AMO has increased since the 1970s, shifting to a warm phase in the late 1990s (Figure 2), in agreement with the increasing trend in SSTA in the study area. SSTA and AMO were positively correlated ($r^2 = 0.55$, $p < 0.001$), displaying the best fit with a 3-year lag (*i.e.* $SSTA_{(t+3)}$ vs. $AMO_{(t)}$) that was noticeable in AMOCs and SSTAcS as well (Figure 3).

The first leading EOF mode (EOF1) of the SAO (Table 1) was positively correlated with the AMO, displaying the best fit with a 4-year lag ($r^2 = 0.25$; $p < 0.05$). The SAO EOF1 was also positively correlated with the EOF1 of the North Atlantic, displaying the best fit with a 4-year lag ($r^2 = 0.21$; $p < 0.05$).

Wind Speed

Both SSTA and annual mean WSA increased through time ($SSTA = 0.05(\text{year}) - 93.60$, $r^2 = 0.79$, $p < 0.001$; $WSA =$

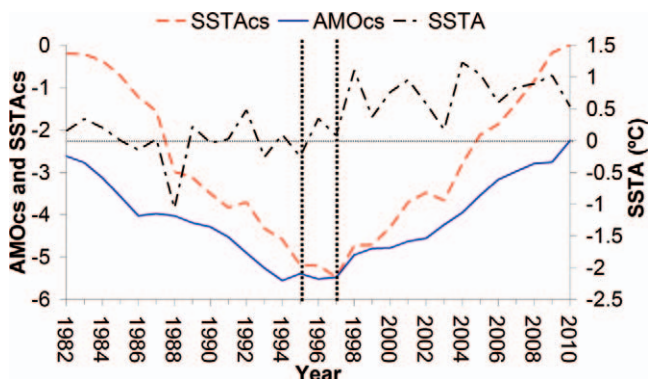


Figure 3. Long-term variations in SSTA and in the cumulative sums of AMO (AMOCs) and SSTA (SSTAcS) in the study area. Dashed bars indicate a regime shift from a cold to a warm period since 1995 (AMOCs) and after 1997, in the SW Atlantic shelf and the adjacent oceanic region. (Color for this figure is available in the online version of this paper.)

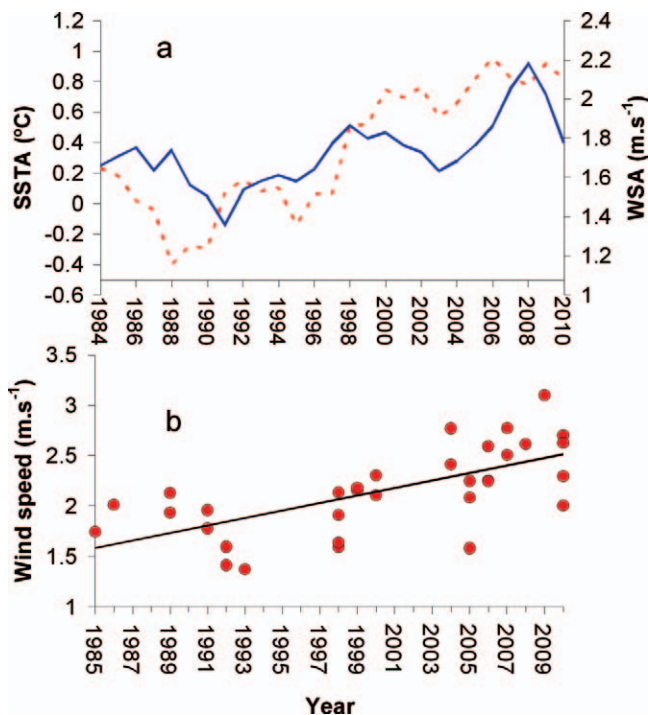


Figure 4. Long-term variation in the SW Atlantic Ocean during 1982–2010: (a) SSTA (dashed line) and WSA (solid line), which were positively correlated ($WSA = 0.31 \times SSTA + 1.61$; $r^2 = 0.60$, $p < 0.001$); (b) southerly wind speed components (S, SSE, and SE) derived from monthly mean values. Early years of the time series were in computation of the moving average. (Color for this figure is available in the online version of this paper.)

$0.01(\text{year}) - 29.32$, $r^2 = 0.53$, $p < 0.001$) and were positively correlated (Figure 4a). This trend was associated with an increasing speed of southern winds through time ($\text{Wind speed} = 0.04(\text{year}) - 72.20$, $r^2 = 0.44$, $p < 0.001$), particularly from the S, SSE, and SE sectors, showing annual fluctuations both in speed and in monthly frequency. An increasing frequency of these winds was observed after 1997 (Figure 4b).

Beach Morphodynamics

Arachania had a mean ($\pm$ standard error) beach width of 41 ± 7 m, a swash zone width of 11.7 ± 4.7 m, coarse sediments (grain size = 0.45 ± 0.08 mm), a steep slope (6.5 ± 1.6 cm/m), a narrow surf zone, and a relatively well-developed foredune (Figure 1b). Barra del Chuy had a beach width of 69 ± 12 m, a swash zone width of 16.3 ± 6.3 m, fine to very fine (0.20 ± 0.03 mm) well-sorted sands, a gentle slope (2.9 ± 0.5 cm/m), a wide

Table 1. General characteristics of the climate index and the empirical orthogonal function leading modes.

Climate Index	Coordinates	EOF1 % Variance Explained
AMO	70° N–0°	
EOF1 North Atlantic	70° N–0°; 85° W–20° W	23
EOF1 SAO	34° S–40° S; 56.5° W–52.5° W	84

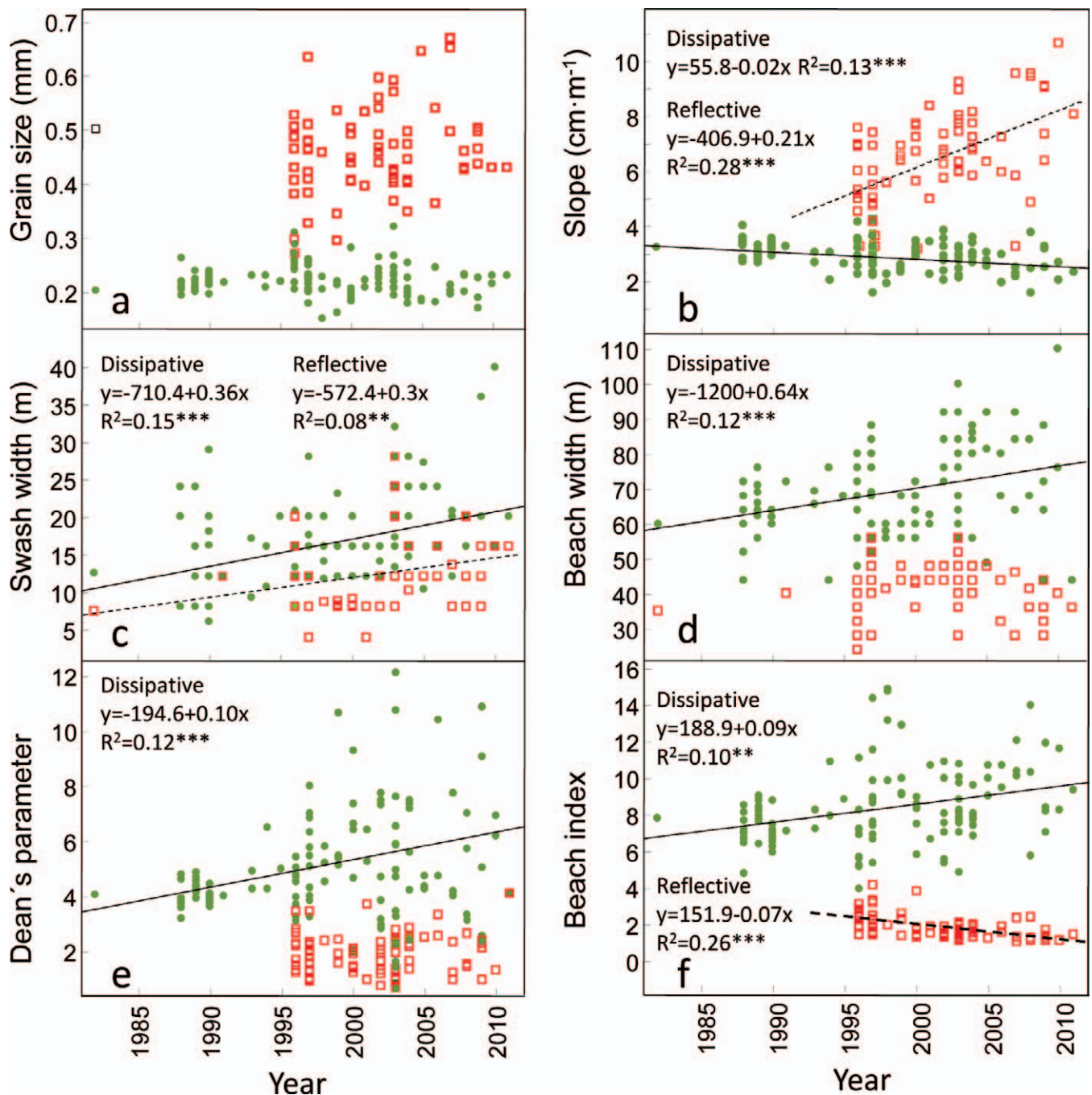


Figure 5. Long-term variations in physical parameters and composite indices of beach state at Arachania (squares) and Barra del Chuy (circles): (a) grain size; (b) beach slope; (c) swash width; (d) beach width; (e) Dean's parameter Ω ; and (f) Beach Index (BI). Only statistically significant correlations are shown. $**p < 0.01$; $***p < 0.001$. (Color for this figure is available in the online version of this paper.)

surf zone with up to five lines of breakers, and large transgressive and vegetated dunes (Figure 1c).

At Barra del Chuy, the following morphodynamic patterns were found: (1) grain size showed no evident trend through time (Figure 5a); (2) beach slope decreased linearly through time (Figure 5b); and (3) swash width (Figure 5c), beach width

(Figure 5d), Dean's parameter Ω (Figure 5e), and the BI (Figure 5f) increased. With the exception of grain size, the trends were highly significant. At Arachania, the following temporal patterns were observed: (1) grain size (Figure 5a), beach width (Figure 5d), and Dean's parameter Ω (Figure 5e) showed no significant trends; (2) beach slope (Figure 5b) and swash width

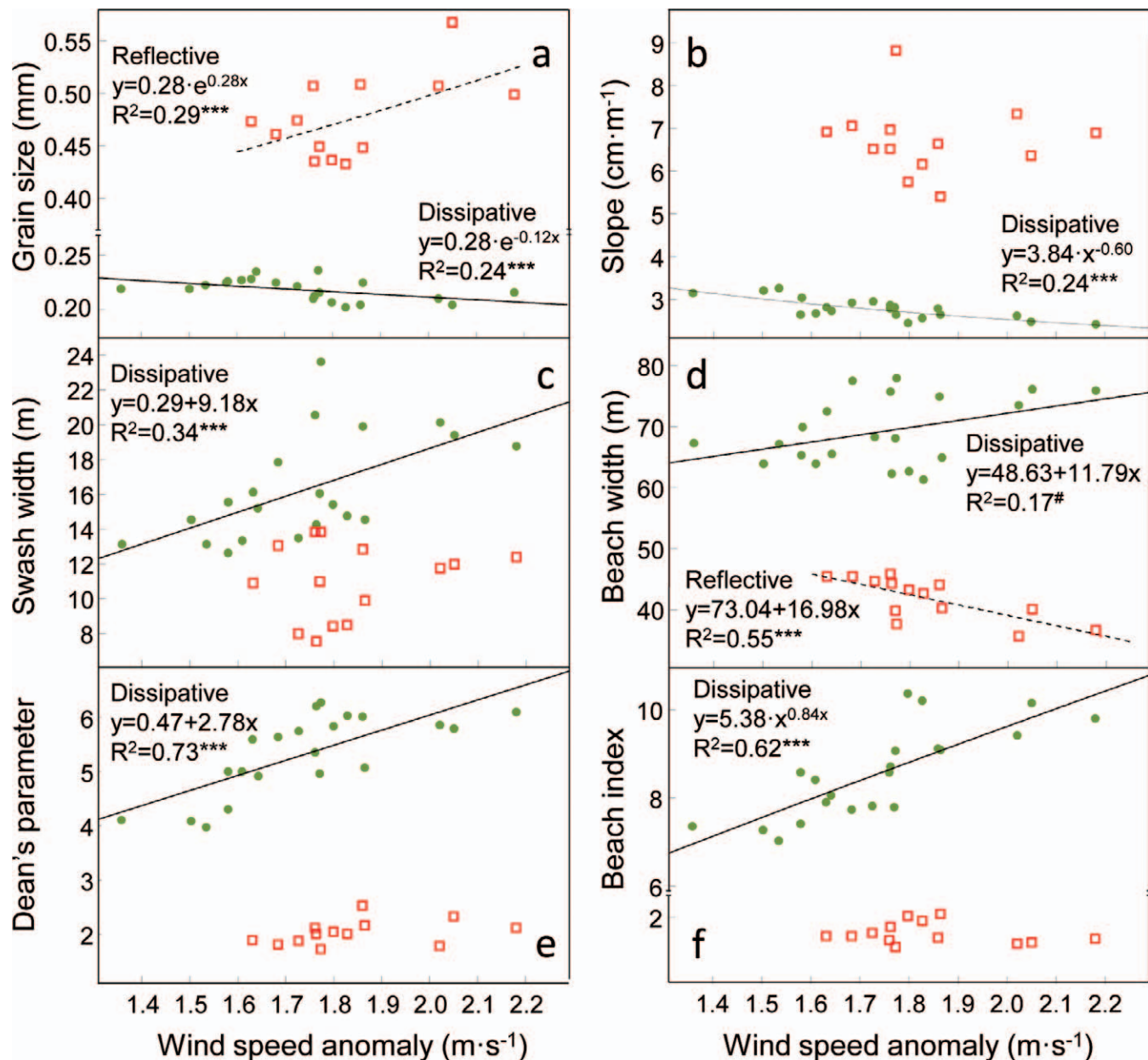


Figure 6. Best models fitted for the relationship between wind speed anomaly and beach physical variables at Arachania (squares) and Barra del Chuy (circles). A 3-year moving average was used for fitting. (a) grain size; (b) beach slope; (c) swash width; (d) beach width; (e) Dean's parameter Ω ; and (f) Beach Index (BI). Only statistically significant correlations are shown. *** $p < 0.001$; $p < 0.05$. (Color for this figure is available in the online version of this paper.)

(Figure 5c) increased significantly; and (3) BI decreased significantly (Figure 5f).

Long-term trends in grain size, beach width, swash width, and slope in the dissipative beach were significantly correlated with WSA (Figures 6a–d). In the reflective beach, grain size (Figure 6a) and beach width (Figure 6d) followed opposite patterns from those depicted in the dissipative beach. Only in the dissipative beach did the compound

indices of beach state, Dean's parameter, and BI increase significantly with WSA (Figures 6e and f).

DISCUSSION

Climatic Variability

The positive correlation between SSTa and the SAO EOF1 with the AMO, as well with the North Atlantic EOF1, suggests that the North Atlantic variability induces changes in SAO

temperature fields. Indeed, the AMO variability is linked with the Atlantic meridional overturning circulation (Wei and Lohmann, 2012), so changes in ocean circulation could determine the observed trend in SSTA in the SAO. Poleward propagation of SSTA by boundary currents, reinforced by regional atmospheric warming (Reid and Beaugrand, 2012), matches with the observed trends in the region, *i.e.* a shift to a warm phase after 1997 and the plausible connection with an enhanced advection of the waters transported by the Brazil Current.

The increase in storm frequency in the study area could be associated with positive SSTA and was confirmed by a significant increase in WSA and wind speed from the southern quadrant, especially after 1997. SE storms in the region constitute significant anomalies on average levels, in a region dominated by N winds. SE storms showed a minimum in the decades 1951/1960 and 1961/1970, increasing thereafter (Bischoff, 2005). Escobar, Vargas, and Bischoff (2004) observed a positive trend in the absolute frequency of the SE storms during the last decades, rising from 44 cases in the 1960s to 79 in the 1990s. D'Onofrio, Fiore, and Pousa (2008) also revealed that the frequency and duration of positive storm surges have increased during the last 30 years. A same pattern has been observed in the southern Brazilian coast, where cold fronts with strong southern winds produce high-energy waves that induce morphological changes on Southern Brazilian sandy beaches (Alves and Pezzuto, 2009; Calliari, Tozzi, and Klein, 1998; Klein and Menezes, 2001).

Physical Variability in Sandy Beaches, and Socio-Ecological Implications

The reflective beach showed an increase in slope and swash width through time and a decrease in the BI; as well a decrease in beach width and an increase in grain size with increasing WSA (see Figure 6). Taken together, these long-term trends indicate an intensification of reflective characteristics, resulting in coastal squeeze. This increases the risk of erosion, because narrow beaches provide less protection from storms (Benedet, Finkl, and Klein, 2004). Reflective beaches are more susceptible to higher waves and experience rapid and intense erosive processes. Any elevation in wave energy in these beaches can induce erosion because of the direct dissipation of the wave energy on the beach face (Short, 1999). Alves and Pezzuto (2009) observed intense erosive processes in a reflective beach of Southern Brazil during storms and a rapid restoration of the beach profile. In our study, the marked variability in beach slope and swash width observed in the reflective beach contrasted with a lack of evident changes in grain size. In this context, our long-term study demonstrated that mean grain size could be defined as an enduring sandy beach variable (Valesini *et al.*, 2010) because it does not undergo substantial changes over time when compared with other variables of the habitat, such as beach slope, wave climate, and swash processes. However, this characterization of grain size could not be applied elsewhere because the rate of sediment supply to the beach, the sediment source, and degree of connectivity between beach embayments could alter these patterns.

The dissipative beach showed an increasing trend through time in swash and beach width, Ω and BI, concurrently with a decrease in slope, indicating an intensification of dissipative characteristics. Again in this case, grain size did not show substantial changes over time, reinforcing its role as an enduring variable of the habitat. Beach profiles could be modified by wind action, when sand is blown along or across the beach, lowering some parts and building up others. This is in agreement with the inverse correlation observed between WSA and beach slope, indicating accentuated dissipative characteristics with increasing wind speed. The increasing trend in southern wind speed is directly associated with wave climate, and its impact on the beach face and the magnitude of erosive processes depends on the beach morphodynamic state (Short, 1999). Storm-related erosive processes in a dissipative beach could alter the subaerial profile. The morphological changes resulting from this erosive process tend to persist, indicating that this type of beach is characterized by a reduced capacity for recovery of its subaerial profile (Alves and Pezzuto, 2009). Changes in swash width, Ω , slope, beach width, and BI, and the significant correlations found between these variables and the increase in WSA, suggest that climate forcing is shaping the morphodynamics of the dissipative beach. The dissimilar long-term trends in both beaches with contrasting morphodynamics suggest a greater susceptibility of the dissipative beach to climate forcing, as reflected by the long-term increase in Ω , BI, and swash width and the correlation between several physical variables and WSA. The observed between-beach difference is probably enhanced by the isostatic adjustment during the Holocene, with a lifting of the continents and retreat of the sea. Indeed, a higher relative lifting of the continental block was found at the location of the reflective beach than at that of the dissipative beach (Bossi and Ortiz, 2011).

Sediment accretion/erosion cycles and resulting signals in sand thickness and beach widths could also be magnified by climate forcing, strongly affecting coastal dynamics (Barnard, Hubbard, and Dugan, 2012), beach habitat functions (biodiversity, food webs, nutrient cycling, dune building), and economic and recreational values (Defeo *et al.*, 2009; Schlacher *et al.*, 2007). Dissipative beaches host significantly greater biodiversity than reflective ones (Defeo and McLachlan, 2005, 2011; Lercari and Defeo, 2006; Lock *et al.*, 2011; McLachlan and Dorvlo, 2005; Munilla and San Vicente, 2005). The exclusion of intertidal species toward the reflective end was explained by a combination of coarse sand, high swash frequency and velocity, and an increase in erosion–accretion dynamics (Brazeiro, 2001; McArdle and McLachlan, 1991). In our study, the slope of the reflective beach increased through time (reaching 10 cm/m in 2010) and BI decreased, *i.e.* it became more reflective. These trends could cause biodiversity loss in the ecosystem structure and functioning (Bergamino, Lercari, and Defeo, 2011; Yamanaka, Raffaelli, and White, 2010). In the dissipative beach, the significant increase in swash width over time and its positive relationship with WSA suggest an unstable erosive environment with a potential habitat loss for intertidal species (especially filter feeding clams and crustaceans), which usually dominate these macrofaunal communities (Barboza *et al.*, 2012; McLachlan and Brown, 2006). Our results emphasize the value of baseline information

on coastal ecosystems and illustrate the long-term differential responses of reflective and dissipative beaches to climate forcing. Multidisciplinary investigation and conservation strategies need to be implemented in order to mitigate negative climatic and anthropogenic effects on this ecosystem.

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CAPÍTULO 5

Impacts of climate variability on Latin American small-scale fisheries

Research, part of a Special Feature on [Cooperation, Local Communities, and Marine Social-ecological Systems: New Findings from Latin America](#)

Impacts of Climate Variability on Latin American Small-scale Fisheries

Omar Defeo^{1,2}, Mauricio Castrejón³, Leonardo Ortega², Angela M. Kuhn⁴, Nicolás L. Gutiérrez⁵ and Juan Carlos Castilla⁶

ABSTRACT. Small-scale fisheries (SSFs) are social-ecological systems that play a critical role in terms of food security and poverty alleviation in Latin America. These fisheries are increasingly threatened by anthropogenic and climatic drivers acting at multiple scales. We review the effects of climate variability on Latin American SSFs, and discuss the combined effects of two additional human drivers: globalization of markets and governance. We show drastic long-term and large-scale effects of climate variability, e.g., sea surface temperature anomalies, wind intensity, sea level, and climatic indices, on SSFs. These variables, acting in concert with economic drivers, have exacerbated stock depletion rates in Latin American SSFs. The impact of these drivers varied according to the life cycle and latitudinal distribution of the target species, the characteristics of the oceanographic systems, and the inherent features of the social systems. Our review highlights the urgent need to improve management and governance systems to promote resilience as a way to cope with the increasing uncertainty about the impacts of climate and globalization of markets on Latin American SSFs.

RESUMEN. Las pesquerías artesanales son sistemas sociales-ecológicos que desempeñan un papel clave en términos de seguridad alimentaria y la mitigación de la pobreza en América Latina. Estas pesquerías se encuentran cada vez más amenazadas por las presiones antropogénicas y climáticas que actúan a múltiples escalas temporales y espaciales. En este trabajo se ha evaluado la relación entre la variabilidad climática y los recursos pesqueros como una aproximación para comprender los posibles efectos a corto y largo plazo del cambio climático sobre las pesquerías artesanales en América Latina, teniendo en cuenta el efecto combinado de dos factores de estrés humanos adicionales: la globalización de los mercados y la gobernanza. En base al análisis cuantitativo de las extensas bases de datos utilizadas y empleando el enfoque de casos de estudio, este trabajo demuestra que se están produciendo efectos dramáticos a largo plazo y a gran escala de la variabilidad climática, que actuando de manera concertada con factores bioeconómicos, han exacerbado las tasas de depleción de los stocks en América Latina. En particular, hemos identificado dos principales factores del cambio global: (1) la variabilidad del clima a través de las anomalías de temperatura superficial del mar, de la intensidad del viento, del incremento del nivel del mar y del uso de índices climáticos, y (2) el aumento en los precios unitarios en las pesquerías artesanales que se encuentran altamente integradas en el mercado mundial de productos de la pesca. Los resultados también indican que el impacto de estos factores varía según el ciclo de vida y la distribución latitudinal de las especies objetivo, las características intrínsecas de los sistemas oceanográficos y las particularidades inherentes de los sistemas sociales. Nuestros resultados ponen de manifiesto la necesidad urgente de desarrollar instituciones sólidas, mejores sistemas de gobernanza y regulaciones de gestión eficaces para promover la resiliencia como una manera de hacer frente a la creciente incertidumbre sobre el impacto futuro del cambio climático y la globalización de los mercados internacionales sobre las pesquerías artesanales de América Latina.

Key Words: *climate variability; ENSO; global change; Latin America; resilience; small-scale fisheries*
América Latina, cambio global; ENSO; pesquerías artesanales; resiliencia; variabilidad climática

INTRODUCTION

Small-scale fisheries (SSFs) are embedded in social-ecological systems (SES) that include biophysical and social subsystems operating through interdependent feedback relationships (Ostrom 2009, Perry et al. 2010, Hall 2011). SSFs play critical roles in developing countries, in the context of food security and poverty alleviation (Berkes et al. 2001, Chuenpagdee et al. 2006, Jentoft and Eide 2011), accounting for 90% of some 120 million direct and indirect fisheries livelihoods that support more than 500 million people (FAO 2012). The resilience of SSFs is frequently low (Pauly 2006, Bueno and Basurto 2009) given their vulnerability to local and

global external drivers that affect the resources per se and/or the social structure of the system (Hall 2011, Jentoft and Eide 2011). Indeed, the coastal systems in which SSFs are developed exhibit high climatic and oceanographic variability (Chavez et al. 2003) and are particularly vulnerable to perturbations produced by extreme natural events and climate change trends.

In Latin America, about 2500 small-scale fishing communities and several million people are directly or indirectly engaged in the activity (Defeo and Castilla 2005, Salas et al. 2011). These SSFs are developed in inshore coastal waters, aimed for sale and/or subsistence, by one fisher or a small group of fishers

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that employ different fishing gears to extract a wide diversity of coastal resources (Defeo and Castilla 2005). Management tools and institutional arrangements also differ among fisheries (Begossi 2010, Salas et al. 2011). Latin American SSFs are increasingly threatened by human and climatic drivers acting at multiple temporal and spatial scales, including uncontrolled fishing intensity, interdependencies with industrial fisheries, sea-level rise, hurricanes, and other climatic events (Bovarnick et al. 2010, Defeo and Castilla 2012). Consequently, SSFs are being degraded rapidly, suffering underemployment, income reduction, and reduced access to marine food (Defeo and Castilla 2012).

As the number and magnitude of global change drivers increase over time, there is an urgent need to understand how the performance of SSFs is being affected by climate variability and human drivers. Even though climate change is currently receiving most attention, others are acting simultaneously, and their combined effects should be analyzed (Perry et al. 2010, McCay et al. 2011). In this paper we review the effects of climate variability on SSFs in Latin America, considering also the combined effects of two additional human drivers: globalization of markets and governance. To show potential combined effects of these drivers, emphasis is placed on case studies for which long-term information is available for both the biophysical and social subsystems of SSF.

EFFECTS OF CLIMATE VARIABILITY ON LATIN AMERICAN SSFs

Shellfisheries

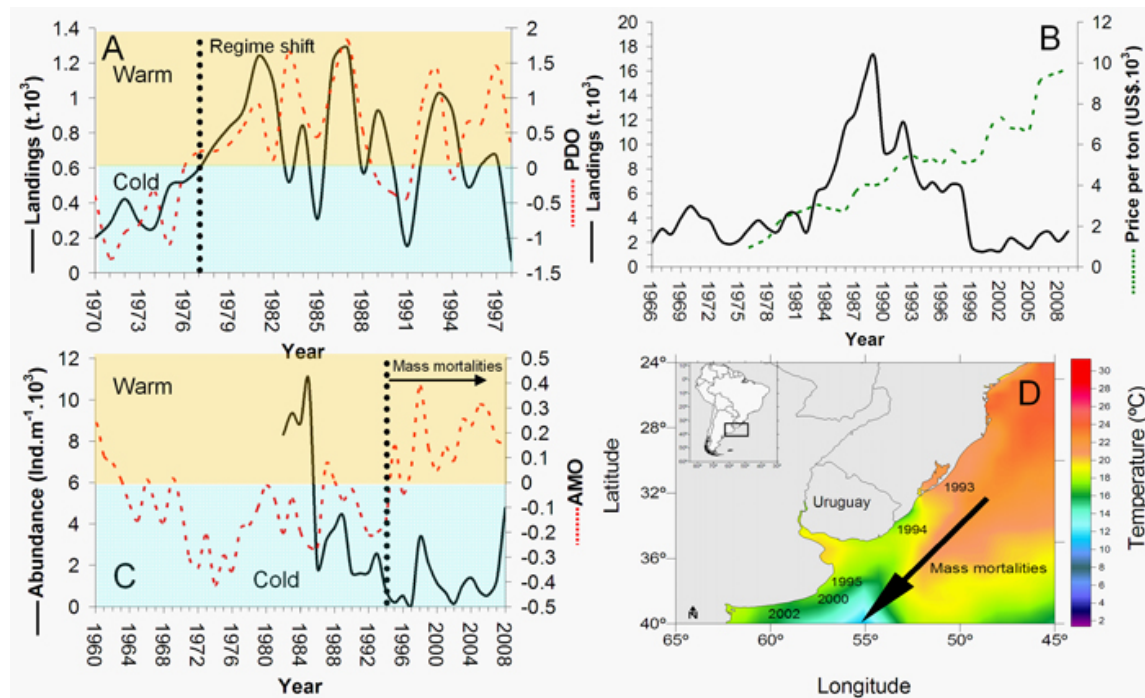
Sedentary and sessile shellfishes are susceptible to rapid environmental changes. Owing to their strict association with sedimentological variables (Defeo and McLachlan 2011), several shellfishes are unable to adapt their distribution to compensate for warming temperatures and other climate change consequences, such as ocean acidification and sea level rise (Defeo et al. 2009, Heath et al. 2012, Narita et al. 2012). These drivers could affect habitats and biophysical processes and thus could alter shellfish demography, dispersal patterns, life history traits, and interaction strength with other species (Stenseth et al. 2002, Rouyer et al. 2008, Mellin et al. 2012). Potential impacts resulting from climatic drivers can be related to the Atlantic Multidecadal Oscillation (AMO), the Pacific Decadal Oscillation (PDO), and the El Niño Southern Oscillation (ENSO), which account for major variations in weather and climate around the world (Stenseth et al. 2002). This variability influences currents and water mass properties (Delworth and Mann 2000) and affects ecosystems, including species targeted by SSFs (Montecino and Lange 2009).

Changes in climatic drivers might directly favor certain species over others, based on their latitudinal distribution and the oceanographic features of the area (Badjeck et al. 2009). Indeed, a recent evaluation of the surf clam (*Mesodesma donacium*) in the Pacific (distribution range from 5°S to 42°

S) suggested that warm ENSO (El Niño) events negatively affected landings in Peru and northern Chile (Fig. 1A), but favored landings in southern Chile (southernmost edge of the species distribution), showing a positive correlation with increasing sea surface temperature anomalies (SSTA; Ortega et al. 2012). Particularly in Peruvian beaches, the strong 1982/1983 and 1997/1998 El Niño events caused mass mortalities of surf clam (Arntz et al. 1987). The same differential response to extreme events was observed for the artisanally harvested Peruvian bay scallop (*Argopecten purpuratus*): in the north of Peru, strong El Niño events drastically increased floods and river discharges, causing a decrease in scallop biomass, whereas increasing temperatures in the south produced a positive effect on stock size (Badjeck et al. 2009). During the 1997/1998 El Niño event, Independence Bay (14°S, Peru) showed a 10°C increase in sea surface temperature (SST), high oxygen concentrations, and diminished phytoplankton concentrations. Many benthic species were affected, e.g., macroalgae, portunid crabs, and polychaetes, whereas others benefited, e.g., scallop, sea stars, and sea urchins, particularly *A. purpuratus*, whose biomass increased 50-fold (Taylor et al. 2008). Castilla and Camus (1992) also showed declining shellfish landings in northern Chile after the 1982/1983 El Niño, in concurrence with high exploitation levels of the gastropod *Concholepas concholepas* and the kelp *Lessonia nigrescens*. Nevertheless, Defeo and Castilla (1998) described a dramatic increase in *Octopus mimus* landings and density, by a factor of 100, in northern Chile, during and after the 1982/1983 El Niño. Increasing SST enhanced recruitment and availability of octopus prey items (Castilla and Camus 1992).

In the southwestern Atlantic Ocean, long-term trends in abundance of the yellow clam (*Mesodesma mactroides*) were negatively affected by a combined effect of increasing SSTA and fishing intensity (Ortega et al. 2012). SSTA was positively correlated with AMO variations and both indices were inversely correlated with yellow clam abundance (Fig. 1C), meaning higher abundance during cold periods. The AMO shifted after 1994 from a cold to a warm period (Goldenberg et al. 2001), probably triggering yellow clam mass mortalities. Indeed, mass mortalities that decimated populations of *M. mactroides* (Atlantic) and *M. donacium* (Pacific) along their geographic ranges had been associated with increasing temperatures (Arntz et al. 1987, Fiori et al. 2004, Riascos et al. 2009). In *M. mactroides*, mass mortalities sequentially has occurred in a north-south direction since 1993 (southern Brazil) to 2002 (Argentina; Fig. 1D). These mortalities were mainly observed between late spring and early summer, when these cold-water clams are more sensitive to diseases (Fiori et al. 2004, Herrmann et al. 2011). The systematic increase in SSTA, associated with a southward migration of a critical warm isotherm, has exacerbated the negative influence of warm waters.

Fig. 1. (A) Long-term variations in the surf clam (*Mesodesma donacium*) landings and Pacific Decadal Oscillation (PDO) index for northern Chile. The shaded bar indicates a climate shift that occurred in 1977, according to Fiedler (2002) and Chavez et al. (2003). See the drastic decline in landings and PDO during the 1997/1998 El Niño. (B) Long-term trends in landings and unit prices for the surf clam fishery in Chile. (C) Long-term trends in abundance of the yellow clam (*Mesodesma mactroides*) in a Uruguayan beach and Atlantic Multidecadal Oscillation (AMO) index. See the match in the regime shift from a cold to a warm period that took place between 1994 and 1995 (Goldenberg et al. 2001) and the occurrence of mass mortalities. (D) At a large scale, these mortalities sequentially occurred in a north-south direction from 1993 (southern Brazil) to 2002 (Argentina). For illustration purposes, sea surface temperature for the year 2006 is shown. Data source: Ortega et al. (2012).



The effects of climate variability, in addition to unregulated fishing, have swamped management measures directed to rebuild stocks. In Peru, adverse climate effects on clams were exacerbated by unsustainable harvest levels and weak governance, i.e., open access. After the 1997/1998 El Niño event, the surf clam almost disappeared and the fishery was closed in 1999. The species has not recovered, and the fishery is still closed (Ortega et al. 2012). On Atlantic coasts, mass mortalities have determined fishery closures for almost two decades, without evidence of recovery of the harvestable stock (Fiori and Defeo 2006). The lack of response of stocks to long-term fishery closures suggests that these systems exceeded critical thresholds or tipping points (Scheffer et al. 2009), shifting from one state to another that included drastic variations in community composition. Indeed, *Mesodesma* clams, formerly dominant in terms of biomass, were replaced by their subordinate competitors for food and space, the bivalves *Donax* spp and sand crabs *Emerita* spp in Pacific

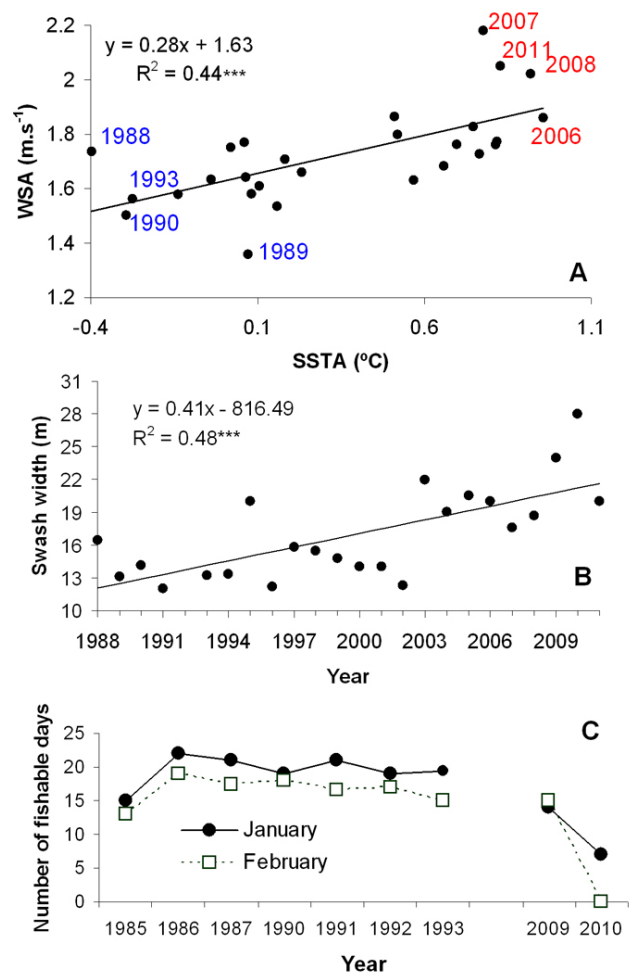
(Arntz et al. 1987) and Atlantic (Defeo 2003) sandy beach ecosystems. Mass mortalities were also observed in intertidal and shallow subtidal shellfish, e.g., oysters, pen shells, clams, spiny lobsters, of the Gulf of California, where coastal fisheries comprise some 70 species, for an annual catch of nearly 200,000 tons (Lluch-Cota et al. 2007). ENSO events (El Niño and La Niña) and associated climate-driven hypoxia affected the abundance and distribution of these resources in a differential way (Micheli et al. 2012).

The sustained increase in SST could accelerate sea level rise rates, inundating many low-lying coastal and intertidal areas. In addition, changes in the global heat balance could lead to extreme weather events, including more frequent and severe storms (IPCC 2007). These events could affect coastal ecosystems, resulting in coastal squeeze, which leaves ecosystems trapped between erosion and rising sea level on the wet side and encroaching development from expanding human populations on land (Defeo et al. 2009, Revell et al.

2011). This could affect the quality and availability of species' habitats targeted by SSFs and therefore the abundance of, and accessibility to, fish stocks targeted by fishing-dependent coastal communities. An example is provided by a 29-yr study for the yellow clam *M. mactroides*, which is harvested by hand-picking methods in the intertidal zone. There is a strong correlation between SSTA and wind speed anomalies (Ortega et al. 2013), which reach their highest values toward the end of the study period (Fig. 2A). The increasing wind speed anomalies are associated with faster and more frequent onshore winds, which explain the linear increasing pattern in swash width through time (Fig. 2B). These changes in the intertidal habitat could negatively affect clams' recruitment and survival, as well as the accessibility by fishers to the resource. Thus, economic income from fishing could be diminished because of a decrease in the number of fishable days through time (Fig. 2C). Consequently, unemployment and disruption and relocation of fishing villages could be generated. This hypothesis should be subject to future research.

Humans are a major force in global change, shaping ecosystem dynamics from local environments to the biosphere as a whole (Folke et al. 2011). Thus, managing SSFs should take into account the interactions between drivers affecting biophysical and social subsystems (Perry et al. 2011). In this context, the combination of weak governance, globalization of markets, fishing pressure, and climate change has exacerbated resource depletion in Latin American shellfisheries, impinging on resource sustainability and the well-being of SSF communities (Defeo and Castilla 2012). Notably, shellfish unit price significantly increased since the early 1980s, particularly as a result of (Defeo and Castilla 2005, 2012, Ortega et al. 2012): (1) incentives generated by market globalization and an exponential increase in demand, mostly coming from developed countries where shellfish have been previously overexploited; (2) weak and unstable governance regimes, which lack structures and processes needed to shape collective actions leading to sharing power and making decisions; and (3) uncontrolled and unsustainable harvest levels. Indeed, deficit of supply relative to demand, coupled with low harvesting costs and open access regimes, pushed the price up (see Fig. 1B and Defeo and Castilla 2012) and triggered an exponential increase in fishing effort, even under diminishing catch rates, which have driven several shellfishes artisanally harvested in Latin America to levels close to extinction, i.e., the anthropogenic Allee effect (see Courchamp et al. 2006 for concept development). Depletion patterns of high-value species caused a shift of fishing effort onto formerly low-value species, causing a sequential depletion of shellfisheries during the last three decades. Open access systems do not work, and a way to approach this problem is by rewarding local management with formal cross-scale governance recognition and support. Unfortunately, Latin American regulatory

Fig. 2. (A) Long-term variations in sea surface temperature anomalies and wind speed anomalies for the southwestern Atlantic Ocean. Values corresponding to the beginning and end of the time series are highlighted. (B) Long-term linear increase in the swash width at Barra del Chuy beach, Uruguay, where the yellow clam (*Mesodesma mactroides*) is harvested. (C) Variations in the number of fishable days for January and February (austral summer), which constitute the months with the highest fishing activity. *** $P < 0.001$. A and B: data source from Ortega et al. (2013). C: original information.



agencies tend to respond late to the problems at hand, once they are more difficult or even impossible to resolve. This situation commonly occurs because many countries lack long-term strategic planning and accountability mechanisms (reviewed in Defeo and Castilla 2012). As SSFs in Latin America tend to be strongly influenced by short-term economic and political interests, they are less resilient and

more vulnerable to the long-term challenges associated with climate variability.

Negative and positive effects of El Niño: Galápagos as a case study

The Galápagos Islands, Ecuador, represent a unique place to assess the potential impacts of climate variability on marine species because of their location on the Equatorial Pacific Ocean, the main influence area of ENSO. Long-term analysis indicates that shallow reef habitats across the central Galápagos archipelago experienced major transformations during the 1982/1983 El Niño event (Edgar et al. 2010 and references therein). The removal of large lobsters and fish predators by SSFs probably magnified 1982/1983 El Niño impacts through a cascade of indirect effects involving population expansion of grazing sea urchins. Thus, heavily grazed reefs with crustose coralline algae, “urchin barrens,” replaced former macroalgal and coral habitats, resulting in declines in biodiversity (Edgar et al. 2010). Wolff et al. (2012a) evaluated the dynamics of subtidal communities and marine vertebrates during the period 1994–2009, based on a trophic mass balance model of the Bolívar Channel ecosystem, the most productive area of the archipelago. These authors showed that SST increased by 7°C during the 1997/1998 El Niño, when phytoplankton concentration decreased by 46% and 33%, respectively, and the ecosystem size (total energy throughput) was reduced by 70%. This was reflected in the reduction of pelagic and demersal fish, seabirds, reptiles, and marine mammals. Wolff et al. (2012a) suggested that bottom-up effects largely control the system during El Niño events.

Not all species are affected negatively by El Niño events. For example, the biomass of spiny lobsters (*Panulirus penicillatus* and *P. gracilis*) and sea cucumbers (*Isostichopus fuscus*) increased after the 1997/1998 El Niño. The production (landings) of these two iconic Galápagos shellfisheries could be related to variations in SST in general (Fig. 3A, C), and particularly during El Niño events (Fig. 3B, D). The strongest impact is associated with the 1997/1998 El Niño event, which represents the most intense climatic event recorded in the last 30 years. Two and five years after this event, the spiny lobster and sea cucumber registered maximum historic production levels (85 tons of tail and 8.3 million individuals, respectively). The significant linear relationship between the lagged production (catch series linearly detrended from 1994 to 2011 to account for the effect of fishing) and SST explained 36% and 49% of the annual production registered for the spiny lobster and sea cucumber fisheries, respectively (Fig. 3B, D).

The high production levels registered for the sea cucumber SSF in 2002 have been the combined result of two main factors (Hearn et al. 2005, Castrejón 2011, Wolff et al. 2012a): (1) a strong recruitment pulse triggered by the 1997/1998 El Niño that led to unusually high stock densities during years 2000–

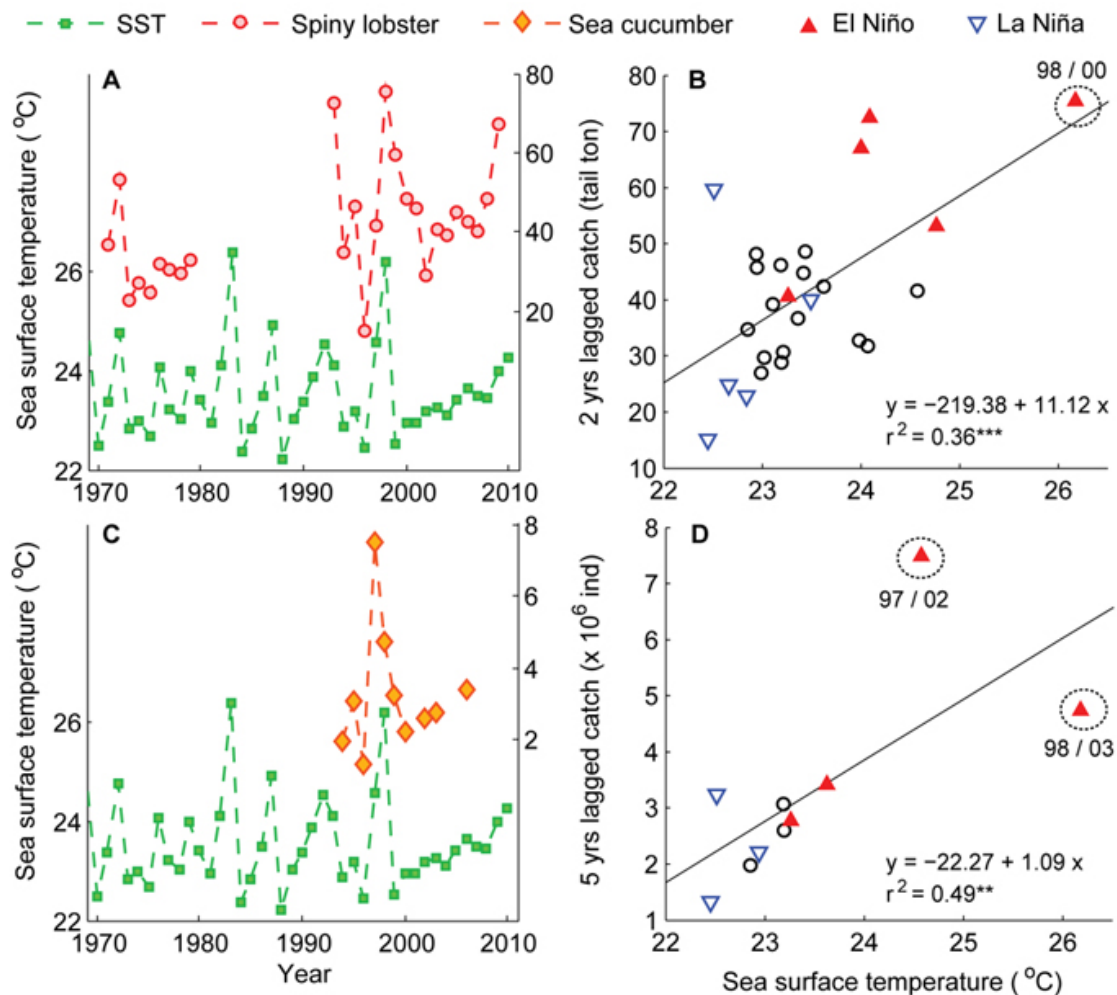
2003; and (2) an increase in fishing effort that resulted from the opening of the sea cucumber artisanal fishery in 1999. Sea cucumber recruits increased in density by a factor of 20 in the west part of the archipelago (Hearn et al. 2005). Such pulse was reflected in the catch composition, where the proportion of juveniles increased from 9% in 1999 to 56% in 2002 (Murillo et al. 2002). The same factors, combined with a low predator abundance, e.g., demersal fish, and high prey abundance, e.g., sea urchins, after the 1997/1998 El Niño, could explain the high production of spiny lobsters in 2000 (Bustamante et al. 2002, Hearn and Murillo 2008, Wolff et al. 2012b). However, conclusive scientific evidence is still needed to support this hypothesis. After 1998, warm anomalies associated with ENSO have been mostly confined to the central Pacific Ocean (Lee and McPhaden 2010). Thus, Galápagos experienced an extended cool regime during the last decade, which together with overfishing might be responsible for the low levels of sea cucumber recruitment (Wolff et al. 2012a). The combined effects of poor recruitment and high fishing levels have severely affected this SSF, leading to its closure in 2006, 2009, 2010, and 2012.

Impacts of climate variability in freshwater and estuarine SSFs

The effects of climate variability in freshwater and estuarine systems will likely result in an increased temperature, decreased dissolved oxygen levels, eutrophication, water level changes, stratification, and salinization (Jeppesen et al. 2012). The response of freshwater fish to warmer waters has been strong and fast in recent decades, including changes in assemblage composition, shifts toward dominance of eurythermal species (Jeppesen et al. 2012), loss of spawning habitats, and changes in spawning and recruitment of fish stocks exploited by SSFs (Ficke et al. 2007). A remarkable interannual variation in abundance and yield of freshwater and coastal lagoon fishes targeted by SSFs has been attributed to ENSO variability (Ficke et al. 2007) and concurrent changes in salinity, as observed in the introduced tilapia *Oreochromis niloticus* SSF in northern Colombia (Blanco et al. 2007). In this case, favorable climate-hydrological changes during La Niña years 1996, 1999, and 2000, promoted an increase in fishery yields, whereas tilapia disappeared from the coastal lagoon between 2001 and 2005, partially because of salinity concentrations > 10 PSU. River discharge variations associated with climatic signals (ENSO and others) could affect ichthyoplankton retention of the whitemouth croaker (*Micropogonias furnieri*), the main resource targeted by artisanal and industrial fisheries in the Rio de la Plata estuary. These events could regulate fish recruitment by promoting high (low) recruitment during low (high) discharge periods (Acha et al. 2012).

Nonindigenous species (NIS) are extending their southern range of distribution in Latin America (Orensanz et al. 2002, Castilla and Neill 2009), and their abundance increased

Fig. 3. Time series and linear regressions between mean annual sea surface temperature (SST in situ, Santa Cruz Island) and lagged annual catch of spiny lobster (*Panulirus penicillatus* and *P. gracilis*; A, B) and sea cucumber (*Isostichopus fuscus*; C, D) in the Galápagos Islands, Ecuador. Catch series from 1995 to 2011 were linearly detrended and the residuals added to the mean, to account for the effect of fishing. Encircled triangles in B and D indicate the positive effect of 1997/1998 El Niño over spiny lobster (2000) and sea cucumber (2002–2003) catches. El Niño and La Niña events were defined based on the Oceanic Niño Index (ONI) estimated by the National Oceanic and Atmospheric Administration (NOAA). **: $P < 0.05$; ***, $P < 0.001$. Catch and SST time series were provided by Galápagos National Park and Charles Darwin Foundation (2012).



exponentially during the last 20 years, partly because of the combination of rising temperature and strong El Niño events (Castilla et al. 2005). Particularly, NIS invasions have altered community structure and diversity in freshwater and estuarine ecosystems of Latin America, and negatively affected SSFs. For example, the sustained increase of the Asiatic clams (*Corbicula fluminea* and *Limnoperna fortunei*) and the invasive whelk (*Rapana venosa*) in coastal/inshore ecosystems of South America generated drastic ecosystem

effects that included the depletion of native species exploited by SSFs, such as the blue mussel (*Mytilus edulis platensis*; Lercari and Bergamino 2011).

DISCUSSION

Our review provides growing evidence of long-term and large-scale effects of climate variability, and their synergy with bioeconomic drivers, on Latin American SSFs. The impact of different drivers varies according to the life cycle of the species, oceanographic characteristics, and the inherent

features of the social systems. Interactions between multiple human-induced drivers exacerbated nonlinear responses of ecosystems to climate change and restricted their adaptive capacity (Ling et al. 2009). Our long-term case studies showed that there is not a single response of SSFs to different climatic and human drivers. In some cases the responses were only temporary, e.g., in Galápagos ENSO triggered successful recruitments, but weak governance led to overexploitation in the short term. Therefore, it is difficult to isolate natural and human-induced, e.g., market, factors that jointly alter these SES. Methods directed to quantify the impacts of climate change on marine ecosystems are generally hard to test, partially because of uncertainties about the magnitude of specific impacts on several ecosystem components (Barange et al. 2010, Grafton 2010). It is worth highlighting that our review is focused on Latin American SSFs, but all three drivers analyzed here, i.e., climate variability, weak governance, and market globalization, affect other SSFs, and also industrial fisheries, throughout the world. Given that global fisheries catches have already changed in a manner associated with global warming trends (Cheung et al. 2013), the need to consider environmental conditions when formulating management strategies has acquired more importance than ever. This is particularly relevant for SES threatened by multiple drivers acting in a nonlinear manner through time and space (Perry et al. 2010).

Long-term Latin America shellfish data series reviewed here showed drastic effects of climate variability on SSFs. Most shellfishes are structured as metapopulations defined by a planktonic larvae and a benthic adult phase decoupled in space and time. Large fluctuations in abundance, highly driven by climatic drivers, have led to their description as “resurgent populations” (McLachlan et al. 1996). In addition, most of these stocks appear to be quasi-pulse age-class dominated populations, where contractions/expansions in their geographic range and changes in their population structure vary according to environmental settings, notably SST. Recruitment tends to occur regularly in source areas and to be irregular or spasmodic in sink areas or marginal portions of the habitat, i.e., the habitat favorability hypothesis (Caddy and Defeo 2003). Successful recruitment linked to favorable climate conditions could give rise to a fishery for one, or a very few, age groups occupying areas where the species was not previously abundant. These features of coastal shellfish make them particularly susceptible to the combined effects of fishing and climate fluctuations, going through a “boom and bust” cycle in which landings are initially high in concurrence with successful recruitments, and then decline to low levels when unfavorable climatic situations lead to poor recruitment. Thus, management of SSFs with harvest controls alone will be ineffective if these environmentally driven variations in abundance and habitat quality are not taken into account (Caddy 2007). An appropriate exploitation strategy seems to

be to harvest sink areas, with populations made up of one or two year classes, but avoiding overexploiting the “core or source,” which could be identified by the presence of multiple year classes that survived previous anomalous climatic episodes (Caddy and Defeo 2003). These source areas should be closed to fishing during favorable years that could include El Niño events (see Fig. 3B, D), to trigger the recovery of the stocks. However, there are no examples in which the “source-sink” metapopulation theory has been applied to manage Latin American shellfisheries in the context of climate variability. Solid SSF management should also be able to recognize early-warning signals of climate tipping points (Scheffer et al. 2009, Lenton 2011) before populations go into rapid decline. As overfishing reduces resilience of stocks to climate-driven catastrophic phase shifts (Ling et al. 2009), detection capabilities of early-warning signals previous to such shifts are of critical importance. However, the detection of these signals remains a challenge because (Boettiger and Hastings 2013): (1) vast amounts of data should be collected well before the system nears a tipping point; and (2) long-term trends could be subject to undocumented changes in data-collection procedures, a switch in management practice, or a shift in environmental conditions.

The recognition of spatial patterns in population demography and dynamics is of utmost importance for marine spatial planning and management of stocks exploited by SSFs in Latin America (Defeo and Castilla 2005, Castrejón and Charles 2013). In this context, matching spatial property rights and size of the management units with scales of dispersal is urgently needed to achieve management success (Castilla and Defeo 2001, McCay and Jones 2011, White and Costello 2011). If this requirement is fulfilled, a combination of spatially-oriented tools that include spatial property rights (TURFs) and Marine Protected Areas (MPAs) strategically sited could increase both fishery profits and abundance (Costello and Kaffine 2010) and, at the same time, could respond more effectively to climate change (McCay and Jones 2011). These tools could be complemented by cooperation arrangements and quota regulations (Gutiérrez et al. 2011, White and Costello 2011) and, if strategically sited and distributed, could ameliorate ecosystem impacts caused by increasing SSTA associated with global warming (Edgar et al. 2010). Micheli et al. (2012) showed that, despite high and widespread mass mortality events of benthic invertebrates in Baja California, Mexico, juvenile replenishment of the pink abalone (*Haliotis corrugata*) remained stable within MPAs, because of large body size and high egg production of the protected adults.

A species’ vulnerability to climate change depends on its exposure and sensitivity to climate variability, its resilience to recover from perturbations, and its potential to adapt to change (Williams et al. 2008). These vulnerability criteria require behavioral, physiological, and genetic data (Doney et al. 2012,

Huey et al. 2012), which is needed for species targeted by SSFs in Latin America. This is particularly important for coastal shellfisheries, where exploitation is increasingly constrained by the accumulation of toxins associated to harmful algal blooms, which can render them unsafe for human consumption (Defeo et al. 2009). The budget for real-time monitoring, control, and surveillance of these events is insufficient in Latin American countries, and the risk of diseases for consumers is high. Vulnerability assessment to climate change requires a multidisciplinary effort to develop adaptive management frameworks directed to mitigate the effects of climatic drivers on species and on coastal communities' well-being. Decision-making processes on SSFs should also focus on implementing adaptation responses to cope with potential bioeconomic losses (Grafton 2010, Cinner et al. 2012a), such as the reduction in the number of fishing days and economic revenues resulting from habitat loss (see Fig. 2).

Weak governance, e.g., open access, and a problematic governability, i.e., governance capacity, have exacerbated climate-induced changes on SSFs in Latin America. Both issues represent major threats to the social security of Latin American fishers (Kalikoski et al. 2010, Defeo and Castilla 2012). Governance institutions (*sensu* Chuenpagdee and Song 2012) have been unable to adopt proactive and effective governing actions to deal with the combined impact of fishing and climate variability on communities' well-being. Weak governance, in conjunction with erosion of traditional resource use systems, open-access regimes, poverty, lack of alternative employment, and easy access to stocks with low investment and operating costs, has promoted overfishing and increased the vulnerability of SSF communities to climate change in Latin America (Kalikoski et al. 2010). Defeo and Castilla (2012) recently categorized the issues highlighted above as "wicked fishery problems" (*sensu* Jentoft and Chuenpagdee 2009) that undermine SSF governance systems. Some local-scale solutions to these governance and governability problems include self-imposed governance with spatial property rights, internal rules, and comanagement (Basurto 2005, Defeo and Castilla 2005, 2012, Gelcich et al. 2010). Adaptive comanagement in self-organized communities is able to create ways to develop mechanisms to cope with the influence of climate variability on resource abundance and availability (Kalikoski et al. 2010), promoting flexible adaptation responses and strengthening adaptive capacities to different drivers (Grafton 2010, Cinner et al. 2012a). Finally, ecolabelling programs created additional incentives for improved management systems and stronger governance structures (Gutiérrez et al. 2012). For example, the Baja California rock lobster Marine Stewardship Council (MSC) certification empowered cooperatives, promoting their autonomy and ultimately improving the resilience of the system (Pérez-Ramírez et al. 2012).

At larger scales, sea-zoning for artisanal and industrial fleets, including allocation of exclusive spatial rights to SSF communities, mitigated governance problems in some countries, including Chile (Castilla 2010) and Uruguay (Horta and Defeo 2012). However, local institutions generally lack cross-scale linkages with higher governance levels (Cinner et al. 2012b), suggesting that formal cross-scale governance recognition and support through the institutionalization of fishery rights is still needed in Latin American SSFs (Defeo and Castilla 2005, Chakalall et al. 2007). This is of the utmost importance in highly valued transboundary resources, e.g., spiny lobsters, which require regional institutional arrangements to be properly managed in Latin America.

Unit price constitutes a key economic driver that could lead to stock depletion in Latin American SSFs (reviewed in Defeo and Castilla 2012). Deficit of supply relative to an exponentially growing demand, associated with high export prices, triggered an increase in fishing effort, which in turn affected stock sustainability. This phenomenon is particularly noticeable in coastal SSFs, because price values of the exploited species largely exceed the low investment and operating costs. In addition, illegal trade accelerated depletion rates, taking advantage of the high intertemporal preferences in resource use and the inadequate enforcement of management measures (Defeo and Castilla 2012). This highlights the need to develop solid governance fishery systems by the consolidation of strong institutions that promote resilience under uncertainty scenarios of biophysical and social issues (Gutiérrez et al. 2011). Therefore, to cope with the increasing uncertainty on the long-term impact of climate change and globalization of international markets, we urgently need solid institutions, better governance systems, and effective management regulations to ensure successful, safe, and sustainable SSFs in Latin America.

Responses to this article can be read online at:

<http://www.ecologyandsociety.org/issues/responses.php/5971>

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CAPÍTULO 6 – DISCUSIÓN GENERAL

En esta Tesis se demostraron los efectos conjuntos de la pesca y de la variabilidad climática en sistemas sociales-ecológicos (SES) pesqueros de pequeña escala de América Latina. Para ello se abordaron investigaciones a diferentes escalas espacio-temporales y se analizaron los impactos y respuestas locales de los SES a dichos agentes externos (Figura 6.1). La respuesta de los SES a dichos agentes dependió de las interconexiones entre los diferentes subsistemas que los componen. Los indicadores de abundancia de las pesquerías del género *Mesodesma* variaron en el largo plazo en función de las anomalías de temperatura y de variables económicas y pesqueras. Asimismo, se observó que muchas pesquerías de pequeña escala de América Latina se encuentran altamente moduladas por la variabilidad climática, afectando tanto al subsistema biofísico (e.g., hábitat de las especies explotadas) como al socio-económico (esfuerzo de pesca y precios de los productos).

6.1 Clima

Los impactos de la variabilidad climática global en los ecosistemas marinos son a menudo propagados a través de grandes distancias por teleconexiones atmosféricas y modificados por procesos oceánicos locales y regionales (Schwing et al. 2010). Los eventos climáticos, particularmente los interanuales como el ENSO y otras oscilaciones climáticas a escalas decadales o mayores, determinan cambios en la producción, distribución y biomasa de las poblaciones marinas así como en los niveles organizacionales del sistema. De esta manera, si poblaciones distintas que no están conectadas experimentan cambios concurrentes, probablemente estén respondiendo a cambios a nivel de la cuenca oceánica o del clima global (Alheit & Bakun 2010). Las variaciones climáticas son transmitidas a través de los flujos de calor, humedad, la circulación atmosférica y de la circulación oceánica a gran escala y ésta se presenta como patrones reconocibles de la variabilidad que producen señales a nivel regional, determinando procesos

que modifican las características de los ecosistemas, sus funciones y productividad (Horel & Wallace 1981).

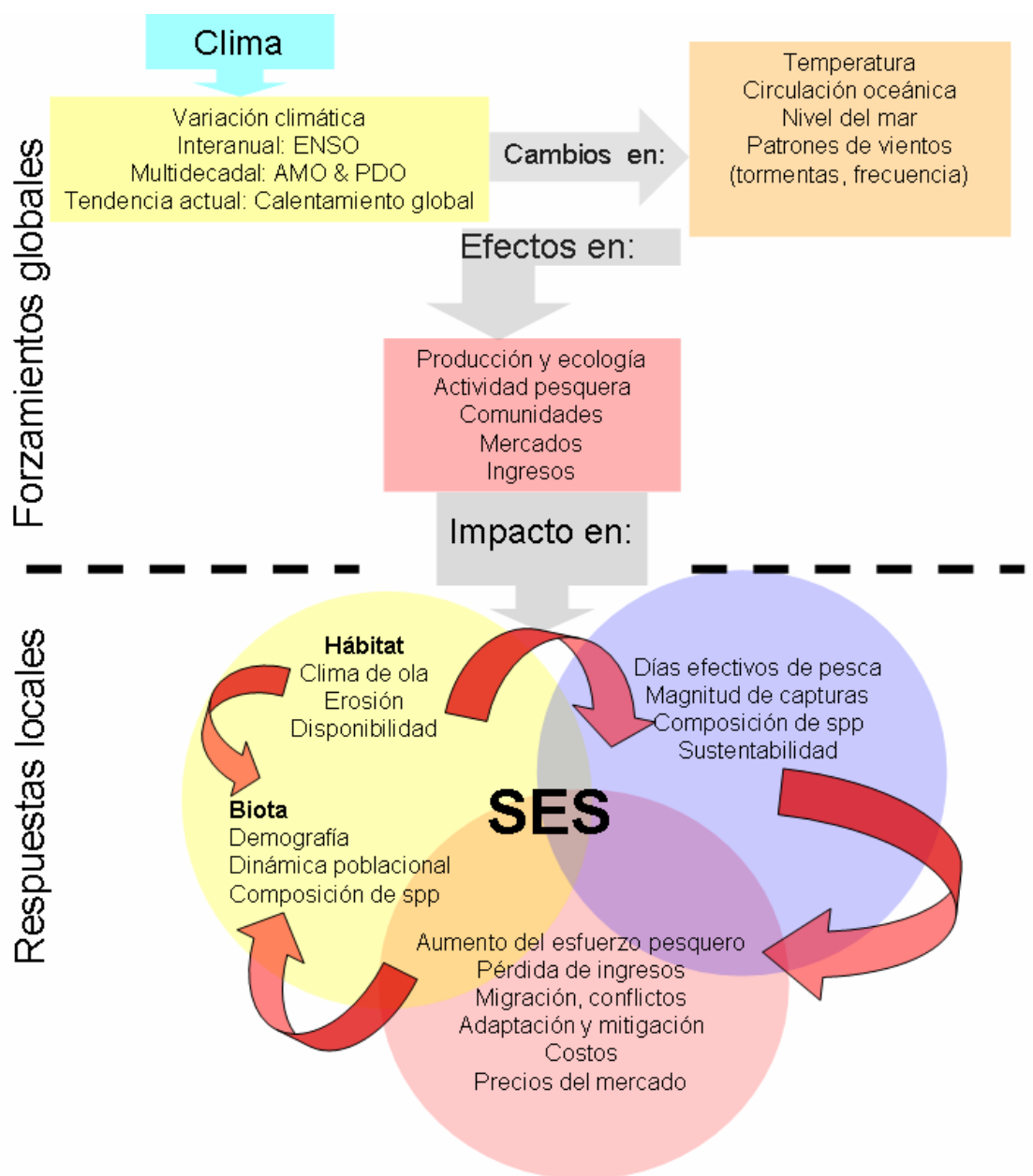


Figura 6.1. Diagrama conceptual de la variabilidad climática y la pesca: efectos, impactos e interconexiones a diferentes escalas detectados en esta Tesis. Esta figura no pretende abarcar toda la complejidad del SES sino esquematizar las diferentes interconexiones abordadas en la Tesis.

En esta Tesis se demostró que la temperatura es un forzamiento físico importante en la demografía del género *Mesodesma* en América del sur (Capítulos 2, 3 y 5; Figura 6.1). Las variaciones interanuales en la temperatura influyen en las fluctuaciones de los índices de abundancia de ambas especies. En particular se observó que la abundancia de *M. mactroides* fue alta durante un período frío (i.e. predominio de anomalías negativas de temperatura) y disminuyó drásticamente en el período cálido donde predominan las anomalías positivas de temperatura. En el caso de *M. donacium* del centro de Chile se observó una respuesta similar cuando se quitó el efecto de los precios del mercado (Capítulo 3, Figura S3). Los eventos ENSO cálidos, en particular los eventos extremos, mostraron un efecto devastador en *M. donacium* de la costa del Pacífico tropical que incluyen Perú y el norte de Chile. Este efecto se diluyó en dirección sur, e incluso se sugiere en esta Tesis que la ocurrencia de eventos ENSO podría influir positivamente en las capturas de esta especie en el sur de su área de distribución. En el caso del Atlántico, si bien no se analizó información de la almeja amarilla en toda su área de distribución, los eventos de mortandades masivas consecutivas en el tiempo con una secuencia latitudinal creciente (Capítulo 5, Figura 1D) sugieren un proceso oceanográfico-climático como desencadenante, aunque resta aún evaluar esta hipótesis mediante análisis a macroescala.

Los índices climáticos de gran escala (PDO y AMO) influyeron en los índices de abundancia de estas especies y en las características ambientales de su hábitat. La relación entre el PDO y la abundancia de recursos pesqueros ya había sido estudiada en el Pacífico (e.g., Chavez et al. 2003, Lercari & Chavez 2007, Montecino & Lange 2009), en particular con peces. En el caso de *M. donacium* se constató que durante los períodos en los cuales el PDO era positivo las capturas fueron mayores. Sin embargo, no había antecedentes de la influencia del AMO para el Atlántico sur, donde se observó mayor abundancia durante la fase negativa y menor en la positiva. Teniendo en cuenta la interconexión entre los océanos del sur y su potencial influencia en el clima mundial, es factible que el Atlántico Norte esté siendo afectado por algún proceso climático oceánico-atmosférico

proveniente del sur y que esta señal sea transmitida a posteriori a otras zonas. Otra posibilidad es que las variaciones térmicas del Atlántico Norte estén relacionadas con las variaciones del Atlántico tropical, en particular con El Niño del Atlántico (Zebiak 1996). Esto sucedería de la misma manera que se postula que el PDO es el producto de los forzamientos provocados por los eventos ENSO del Pacífico, que luego resurgen como anomalías de temperatura en el Pacífico Norte (Newman et al. 2003). El AMO podría estar relacionado con los procesos oceánicos y atmosféricos que ocurren en el Atlántico tropical. En este sentido, se ha observado la propagación de anomalías positivas de temperatura desde los trópicos, transportadas por las corrientes de contorno luego de los eventos ENSO cálidos (Reid & Beaugrand 2012). Además, el clima, en particular el régimen de precipitaciones de América del Sur, es modulado por los eventos ENSO del Pacífico y el AMO (Seager et al. 2010) y las anomalías de temperatura del Atlántico ecuatorial (Barreiro & Tippmann 2008), por lo que existe una gran cantidad de interconexiones que no se abordaron en esta Tesis pero que deben ser estudiadas en el futuro.

Las tendencias observadas en los patrones de vientos en la costa Atlántica de Uruguay i.e. un aumento en la velocidad de los mismos, en particular los de componente sur, influye sobre el clima de olas. El fuerte oleaje erosiona la línea de costa y puede determinar la pérdida de hábitat para las especies que habitan zonas costeras, en particular playas arenosas. Los vientos de componente sur, en particular los del sureste, constituyen una anomalía para el área de estudio. Estos eventos estarían básicamente asociados a un sistema de alta presión al sur de esta área y otro de baja al norte. Estos procesos atmosféricos no fueron abordados en esta Tesis.

6.2 Hábitat

Las playas arenosas han sido vistas erróneamente como desiertos ecológicos y han atraído poca atención para su investigación ecológica. Sin embargo, son

habitadas por numerosas especies de valor intrínseco, tienen importantes vínculos con los ecosistemas adyacentes y tienen gran valor socioeconómico (Defeo et al. 2009). Al mismo tiempo, son vulnerables a las crecientes presiones humanas, incluyendo el cambio climático. A pesar de la gran incertidumbre respecto a la magnitud de los cambios que puede producir el clima en los ecosistemas costeros y las consecuencias ecológicas del cambio climático, se estima que las especies adaptadas al frío disminuirán en abundancia y la composición de las comunidades cambiará (FAO 2010).

Esta Tesis aportó una serie de evidencias acerca de los efectos del clima sobre las poblaciones de almejas del género *Mesodesma* en América del Sur, que sumadas a otros efectos de origen humano, provocan grandes fluctuaciones en su abundancia. Asimismo, se constató que el incremento en las anomalías de velocidad de viento influye en las características morfodinámicas de las playas arenosas de Uruguay (Capítulo 3). Esto tuvo particular efecto en la playa disipativa donde habita *M. mactroides*, lo cual podría ser otro factor físico, sumado al aumento de la temperatura oceánica, que estaría actuando sobre el hábitat y perjudicando a la población de almejas. Además, esta tendencia climática podría influir negativamente en la actividad pesquera, determinando mayor frecuencia de eventos climáticos extremos y crecidas del mar que disminuirían los días efectivos de pesca (Capítulo 5). Por otra parte, estos eventos climáticos extremos podrían generar varamientos masivos, incrementando la mortalidad de esta especie.

El tamaño de grano del sedimento de las playas estudiadas fue detectado como una variable perdurable (sensu Valesini et al 2010) que resistió a los cambios producidos por los forzamientos climáticos. Asimismo, se pudo constatar una mayor resiliencia a los forzamientos climáticos de la playa reflectiva respecto a la disipativa, en concordancia con los estudios de otros autores de la región (e.g. Alves & Pezzuto 2009). En este caso particular, esa mayor resiliencia estaría potenciada por procesos isostáticos ocurridos durante el Holoceno, donde la zona oeste de Rocha donde se encuentra la playa reflectiva se elevó relativamente más

que la zona este, donde se encuentra la disipativa, lo que la hace más susceptible al incremento del nivel del mar.

Las tendencias observadas en el largo plazo en los otros parámetros (pendiente, ancho del swash, ancho de la playa) podrían causar pérdida en la biodiversidad y cambios en la estructura del ecosistema (Bergamino et al. 2011). En la playa disipativa de Barra del Chuy, el aumento significativo en el ancho del swash en el tiempo y su relación positiva con las anomalías de viento sugieren un entorno erosivo inestable y una virtual pérdida de hábitat para las especies intermareales (bivalvos y crustáceos), que suelen dominar la macrofauna de estas comunidades. Asimismo, la acentuación de las características morfodinámicas reflectivas en Arachania podría determinar una disminución del número de especies (Barboza et al. 2012).

El aumento de la temperatura en la zona de estudio (i.e. Atlántico) suele estar acompañado de la incursión de especies que habitan aguas tropicales, tanto costeras como oceánicas (e.g. Demicheli et al. 2006, Segura et al. 2009, Izzo et al. 2010), lo cual sugiere mayor influencia de aguas cálidas advectadas por la Corriente de Brasil. Las aguas cálidas tienen menor carga de nutrientes que las aguas frías advectadas por la Corriente de Malvinas (Ciotti et al. 1995, Martínez & Ortega 2007), lo cual puede determinar una potencial disminución de la productividad primaria de la zona (control bottom-up o ascendente) que impactaría directamente en los consumidores como el zooplancton y, en el caso de las playas arenosas, en los suspensívoros que se alimentan directamente de éstos. Los cambios asociados con el aumento de temperatura también pueden promover una mayor estratificación de la columna de agua y una eventual oportunidad para organismos que tienen la posibilidad de migrar para obtener los nutrientes necesarios (e.g. dinoflagelados: Peperzak 2003, Cloren & Dufford 2005). Estos organismos responsables de la producción de mareas rojas han incrementado la frecuencia de sus floraciones, lo cual puede estar relacionado al aumento de la temperatura marina (Peperzak 2003, Moore et al. 2008). Estas floraciones pueden

ocasionar mortandades masivas, pero en general se asocian a su toxicidad y amenaza a la salud humana (Moore et al. 2008) y al cierre de pesquerías. De esta manera, las floraciones algales pueden afectar negativamente las pesquerías de moluscos de playas arenosas y otras zonas costeras (McLachlan et al. 1996), generando significativas pérdidas económicas a los pescadores y una amenaza para la salud.

Los eventos ENSO son un fenómeno climático global que afecta fundamentalmente las características térmicas de la zona de influencia de la Corriente de Humboldt (Thiel et al. 2007). Dichos eventos se relacionan con cambios en la circulación oceánica, y aumentos significativos de la temperatura del océano en las costas del Pacífico, de la concentración de oxígeno y del nivel del mar, así como anomalías positivas de precipitación e inundaciones que afectan a las zonas costeras con agua dulce cargada de sedimentos (Thatje 2008). Producto de estos cambios en el hábitat se observan variaciones significativas en la abundancia de los organismos que habitan estas zonas, incluyendo la parcial desaparición de algunos (e.g. *M. donacium*) y el aumento de otras especies simpátricas, que en el caso de las playas arenosas del Pacífico peruano se reflejó en aumentos de *Donax obesulus* y *Emerita analoga* (Arntz et al. 1987). Estas variaciones climáticas y oceánicas interanuales afectan las pesquerías no solo del Pacífico sino incluso de otras zonas del Atlántico, debido a su impacto sobre las precipitaciones en América del Sur (Capítulo 5). De esta manera pueden afectar mayormente a las especies estuarinas, disminuyendo su reclutamiento debido a la dispersión y transporte de sus huevos y larvas a zonas no favorables para su sobrevivencia durante anomalías positivas de descarga fluvial (Acha et al. 2008) o eventuales cambios en la salinidad.

Como se mencionó anteriormente, el aumento de la temperatura en la región parece estar asociado a una mayor advección de aguas cálidas. Este fenómeno favorece los cambios en rangos de distribución de organismos tropicales, ampliando los límites de distribución a latitudes más altas, lo que posibilita

potenciales interacciones nuevas (e.g. competencia, predación) con las especies nativas. Incluso, puede favorecer a otros competidores simpátricos como se ha observado con *Donax hanleyanus* y *Emerita brasiliensis* en la Barra del Chuy, Uruguay (Defeo 2003). Dado que en general las variaciones climáticas decadales presentan ciclos (e.g. Chavez et al. 2003), los organismos tienen a presentar patrones de variación asociados a los mismos, por lo que los pescadores artesanales suelen adaptarse a esa variabilidad y explotar los recursos más abundantes (Capítulo 5).

6.3 Pesquerías artesanales y variabilidad climática

Las comunidades pesqueras artesanales presentan estrategias bien desarrolladas para adaptarse a la variabilidad climática normal de los sistemas marinos. Éstas incluyen, por ejemplo, migración estacional a otras zonas de pesca, cambio de especies objetivo y aumento de la presión pesquera sobre determinados recursos (Perry et al. 2010). En los Capítulos 3 y 5 de esta Tesis se abordaron estos temas y en particular en el Capítulo 3 se discutió el incremento de las capturas de *M. donacium* en la zona sur de Chile. Ésta podría estar asociada a un mayor reclutamiento producto de un leve incremento en la temperatura o la mejora de las condiciones climáticas, lo que permitiría una mayor accesibilidad a las zonas de pesca y en consecuencia a un aumento de los días efectivos de pesca y en las capturas. Alternativamente, puede estar asociado con la migración de los pescadores de otras zonas sobreexplotadas y/o afectadas por el aumento de la temperatura, redundando en un significativo aumento de la presión pesquera y el colapso de la misma. En el caso del norte de Chile y Perú, donde los efectos del ENSO son más intensos, se observó que la presión pesquera, sumada a los efectos negativos del aumento de la temperatura, llevó al colapso de la pesquería.

En teoría se piensa que la extinción de especies raras no puede deberse a la acción del hombre pues, al ser escasas, los costos de su explotación superan a

los posibles beneficios (Clark 1990). Sin embargo, es precisamente su rareza la que contribuye a su extinción por acción antropogénica (Courchamp et al. 2006). Usualmente en el contexto de dinámica poblacional, el efecto Allee describe una situación en la cual la tasa de crecimiento poblacional decrece bajo alguna densidad mínima crítica. Dicho efecto fue detectado por Warder Clyde Allee, zoólogo y ecologista conocido por sus investigaciones sobre el comportamiento animal, proto-cooperación, y por identificar el efecto de depensación o denso-dependencia inversa que lleva su nombre (Allee, 1931, 1938, Allee et al. 1949). El concepto de efecto Allee antropogénico se refiere a la extinción de una especie potenciada por factores económicos incluso cuando la densidad de población es extremadamente baja (Defeo & Castilla 2012). En general, se podría esperar que el aumento de los costos de explotación conduzca al aumento de los precios, que a su vez se traduce en una caída de la demanda. Sin embargo, otros factores actúan para reforzar la demanda, por ejemplo, cuando se convierte en un artículopreciado o raro (Courchamp et al. 2006). Este efecto es aplicable a la pesquería de moluscos costeros (Defeo & Castilla 2012). Por tanto, las comunidades pesqueras costeras no son independientes de la globalización y demanda de los mercados internacionales. Éstos pueden incidir en una mayor presión pesquera, sobre todo en la explotación de recursos que no requieren mayor inversión de capital, lo cual conlleva a un aumento de la presión pesquera incluso cuando las abundancias son bajas debido a que la tendencia creciente de los precios del mercado motiva a que se sumen más pescadores o aumente el esfuerzo con el subsiguiente colapso de la pesquería.

La tendencia observada en el clima y su efecto en las playas arenosas, en particular la disipativa de Barra del Chuy en la costa Atlántica, podría tener efectos adversos en la comunidad pesquera local (Figura 6.1). Las crecidas del nivel del mar, producto del aumento en la frecuencia y velocidad de los vientos de componente sur, limitarían la cantidad de días efectivos de pesca, determinando una disminución de ingresos, desempleo y migración, afectando la actividad local (Hall 2011). Sin embargo, los pescadores muestran una capacidad de reacción y

adaptación a los cambios ocasionados por el clima que supera ampliamente la de las instituciones que regulan las pesquerías (Badjeck et al. 2009). En el Capítulo 5 de esta tesis se examinaron casos donde los pescadores cambiaban de especie asociados a la disminución de especies objetivo debido a la sobreexplotación, combinado con el efecto negativo de los eventos ENSO cálidos externos. El aumento de la temperatura durante estos eventos favoreció el reclutamiento de algunas especies (e.g. pepinos de mar y langostas), aumentando su abundancia. Esto fue seguido de un aumento significativo de las capturas y la sobreexplotación de los recursos producto de una débil gobernanza. En este sentido, la evaluación de la vulnerabilidad al cambio climático requiere un esfuerzo multidisciplinario para el desarrollo de marcos de gestión adaptativos encaminados a mitigar los efectos del clima sobre las especies y el bienestar de las comunidades costeras. Los procesos de toma de decisiones también deben centrarse en la aplicación de las medidas de adaptación para hacer frente a posibles pérdidas bioeconómicas (Grafton 2010, Cinner et al. 2012), como la reducción del número de días de pesca y de los ingresos económicos derivados de la pérdida de hábitat (Figura 6.1).

La débil gobernanza ha exacerbado los cambios inducidos por el clima en las pesquerías artesanales de América Latina. Una gobernanza débil, junto con la erosión de los sistemas tradicionales de uso de recursos, los regímenes de libre acceso, la pobreza, la falta de alternativas de empleo, y el fácil acceso a los recursos pesqueros con bajos costos de inversión y operación, han promovido la sobrepesca y el aumento de la vulnerabilidad de las comunidades pesqueras artesanales al cambio climático en América Latina (Kalikoski et al. 2010). Algunas soluciones a estos problemas de gobernanza y gobernabilidad a nivel local incluyen la combinación de esquemas de autogestión con derechos de propiedad espacial, la existencia de reglamentos internos de las comunidades locales y el desarrollo de estrategias de co-manejo (Defeo & Castilla 2005, 2012), aunque son escasos los ejemplos donde se han advertido tendencias positivas al respecto.

Basado en lo expuesto anteriormente, sería conveniente incluir en las políticas públicas, y en particular en las medidas de manejo pesquero, pronósticos climáticos con el objetivo de prever los potenciales efectos en los patrones de abundancia de las especies objetivo. De esta manera se lograría mayor resiliencia en los sistemas marinos y se evitarían o mitigarían las consecuencias negativas tanto de los forzamientos climáticos, de la sobreexplotación de recursos y las pérdidas de ingreso por parte de los pescadores. Esto implica grandes inversiones en investigación para generar información que permita modelar las respuestas de los recursos a la explotación pesquera, la variabilidad climática e incluso las tendencias del mercado. No obstante, la detección de esas señales tempranas que determinan un cambio de régimen o el pasaje de un estado a otro no son triviales (Boettiger & Hastings 2013), son fáciles de señalar una vez que pasaron pero muy complejas de pronosticar.

Los impactos negativos de la variabilidad climática en el sector pesquero son los más ampliamente documentados en la literatura, mientras que los impactos positivos no son los más citados (Badjeck et al. 2010). En esta Tesis se mostraron ejemplos de los efectos de la variabilidad climática en diferentes pesquerías, con claros casos donde los efectos fueron negativos (e.g. Perú y Norte de Chile, Uruguay) y otros donde podrían señalarse como positivos (e.g. sur de Chile e Islas Galápagos). En consecuencia, la variabilidad climática no impacta de manera homogénea a todas las comunidades. Sin embargo, en todos los colapsos pesqueros se advierte como denominador común la falta de políticas adecuadas de adaptación que permitan identificar anticipadamente las oportunidades que brinda una determinada coyuntura climática. En todos los casos descritos se observó un fuerte componente de sobreexplotación (en algún momento del desarrollo pesquero), al que se le suma el componente ambiental. Por tanto, no se le debe atribuir solo al clima las oscilaciones en los índices de abundancia sino también a la falta de eficacia, calidad y adecuada orientación en las intervenciones de los Estados en el manejo de las pesquerías (i.e. gobernanza).

6.4 Conclusiones y recomendaciones generales

Las tendencias climáticas observadas en los marcos temporales estudiados mostraron dependencia de *M. donacium* y *M. mactroides* a variaciones de la temperatura.

En el caso de *M. mactroides* en Uruguay, se constató que las capturas fueron altas durante los períodos fríos y bajas en los cálidos. El pasaje de período frío al cálido, sumado a una previa sobreexplotación y eventos de mortandades masivas, diezmó a la población e impidió implementar las herramientas de manejo pesquero con éxito. En este contexto, se mostró que la variación en la abundancia no explicada por es esfuerzo pesquero estaba significativamente relacionada con la temperatura.

En el caso de *M. donacium*, la sobreexplotación, sumada a un posterior evento ENSO cálido de 1982-83, determinó el colapso de la pesquería en Perú y en el norte de Chile, en este caso después el ENSO de 1997-98. No obstante, se detectó una respuesta latitudinal diferencial, incrementándose las capturas en el sur de Chile luego de estos eventos cálidos. Las variaciones en el precio unitario tuvieron un papel sustancial en la explicación de los patrones de largo plazo en el caso de Chile.

Las variaciones de largo plazo en los precios de los productos tuvieron un impacto importante en el desarrollo de las pesquerías artesanales, pudiendo influir negativamente en los casos de sobreexplotación, sobre todo cuando se requiere una inversión mínima para acceder al recurso y explotarlo y cuando existe demanda del producto, tanto a nivel local como internacional.

El incremento de la frecuencia de vientos de componente sur a partir de 1998 afectó las características morfodinámicas de las playas arenosas de la costa uruguaya, tendiendo a acentuar las características reflectivas de *Arachania* y las

disipativas de Barra del Chuy. Estas tendencias climáticas y sus efectos en la costa pueden determinar pérdida de biodiversidad y afectar las actividades pesqueras locales. En consecuencia, esta tendencia climática puede afectar negativamente tanto al recurso como a los pescadores, debido a que modifica el hábitat de la especie, limita la accesibilidad al recurso y por tanto el tiempo efectivo de pesca. Estos cambios podrían afectar no solo a las especies explotadas sino también en forma global a la biodiversidad de los sistemas arenosos costeros.

La falta de interacción entre los distintos niveles de toma de decisiones en el manejo de recursos naturales y la ausencia de aplicación del conocimiento producido por la investigación científica es un problema que debe ser abordado en el futuro. Se necesita mayor participación de las instituciones que manejan los recursos pesqueros para mitigar los efectos de los eventos climáticos extremos y la sobrepesca en las comunidades pesqueras. Para ello es indispensable invertir en investigación para afrontar los futuros desafíos donde se conjunta una mayor presión humana sobre los recursos pesqueros y degradación del medio ambiente, sumado a escenarios climáticos adversos. El trabajo en modelización climática para prever cambios en el clima es de vital importancia a la hora de emprender cualquier proyecto que presente dependencia con el clima.

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