Identifying environmental constraints at the edge of a species' range: scallop *Psychrochlamys patagonica* in the SW Atlantic Ocean

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ABSTRACT: Recognizing the relationships between oceanographic variables and population descriptors has been a major step in understanding geographical range limits. In the present study, we investigate which oceanographic features are responsible for the decrease in fitness and consequent northern limit of the scallop *Psychrochlamys patagonica* distribution in Uruguayan waters of the SW Atlantic Ocean (SAO), based on information compiled from fishing and oceanographic surveys. *P. patagonica* showed clear population responses to physical variables, including a marked decrease in abundance, individual size and muscle weight towards the northern edge of the range. A generalized additive model (GAM) significantly explained 78.7% of the deviance in scallop abundance and retained all 4 descriptors in the model as significant, showing a decrease in abundance at lower latitudes with higher temperature and at lower values of chl *a* and water depth. The performance of GAMs was compared with that of the equivalent generalized linear models (GLMs) and it was concluded that the extended flexibility offered by GAMs resulted in better overall fits. Spatial variations in scallop abundance were accurately predicted by the GAM, including the 2 peaks at latitudes 36° 20' S and 36° 50' S. These spatial variations were closely related to the shelf break front around the 100 m isobath, where abundance was higher. The northern range limit of the species in the SAO may be caused by a sharp decrease in habitat quality, indicated by temperatures higher than 9°C (above species tolerance limit) associated with the influence of the Subtropical Water. Whereas physiological tolerance to temperature appears to be an important mechanism driving the range boundary of *P. patagonica*, food availability (reflected by the highest concentrations in chl *a*) is a key explanatory factor of the spatial variations in scallop abundance.

KEY WORDS: *Psychrochlamys patagonica* · Species borders · Environmental constraints · Generalized additive model · GAM · Southwestern Atlantic · Uruguay

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INTRODUCTION

The distribution range of sedentary invertebrates is strongly influenced by their oceanic and benthic environment. Although such relationships are inherently dynamic, distributions have been related to a range of environmental features, including sea surface and bottom temperature (Jensen et al. 2005), salinity (Christophersen & Strand 2003), water depth (Katsanevakis 2005), and food availability (Cusson & Bourget 2005).

However, the importance of these factors appears to differ among regions and species, highlighting the importance of studying the role of oceanographic features in the distribution of benthic invertebrates on a regional basis (Portner 2002, Jensen et al. 2005, Kater et al. 2006).

Discontinuities in population density often correlate to abiotic boundaries; range limits may be hard (e.g. coastline) or soft (e.g. hydrographic gradient), and may be caused by single or multiple factors, both at single

points and along the entire range margin (Sagarin et al. 2006). Given that environmental factors potentially involved in range limitation are frequently interrelated (Freeman & Rogers 2003) and generally show complex patterns of variation across the environment, their analysis is sometimes not straightforward (Sagarin et al. 2006).

Scallops commonly have recurrent spatial distribution patterns that have been attributed mainly to dispersal and larval retention mechanisms associated with hydrographic features (Caddy 1989, Arnold et al. 1998). Therefore, many scallop fishing grounds are recurrent in location (Sinclair et al. 1985) and have been harvested for several decades (Stokesbury 2002). Those aggregations are spatially discontinuous (i.e. several km apart) and tend to be spatially coincidental with oceanographic (e.g. frontal systems) and habitat (e.g. substrate type) features that facilitate larval retention, food supply and maximize species fitness (Bogazzi et al. 2005). Oceanographic characteristics are also responsible for abrupt changes in scallop abundance, particularly close to geographical range limits (Heilmayer 2003).

The scallop *Psychrochlamys*[1] *patagonica* is distributed along the SW Atlantic Ocean (SAO), between 35° 50′ S and 48° 00′ S. Large associations or beds have been related to frontal zones (Bogazzi et al. 2005). In Uruguayan waters, *P. patagonica* occurs between 35° 50′ S and 37° 00′ S and between 70 and 120 m depth (Defeo & Brazeiro 1994, Gutiérrez & Defeo 2003). This area is strongly affected by the confluence of the Brazil (warm and salty) and Malvinas/Falkland (cold) currents. The convergence between the northward Subantarctic Water (SAW) (Sverdrup et al. 1942, Thomsen 1962) and the southward Subtropical Water (STW) (Emilsson 1961, Thomsen 1962) defines a frontal zone with a prominent variation in temperature (Ortega & Martínez 2007). This front, also known as the shelf break front (Acha et al. 2004), is characterized by high productivity (Carreto et al. 1995) and phytoplankton abundance (Brandini et al. 2000).

Previous studies in Uruguayan waters, which constitute the northern limit of *Psychrochlamys patagonica* distribution, showed marked spatial patterns in life

history traits (Defeo & Gutiérrez 2003, Gutiérrez & Defeo 2003) and population dynamics (Gutiérrez & Defeo 2005), notably a decrease in abundance, growth and survival towards its northern limit (i.e. 35° 50′ S). These patterns have been attributed to less favorable environmental conditions, but hypotheses about which oceanographic features are actually responsible for the decrease in fitness and consequent northern limit of the species distribution have never been tested. The present study investigates spatial patterns in abundance, individual size and muscle yield of the scallop *P. patagonica* in relation to oceanographic characteristics. To this end, a model-building technique was applied to determine and predict the potential sensitivity of scallop abundance to spatial variations in environmental change, particularly in the northern limit of its distribution range.

MATERIALS AND METHODS

Study area. The study focuses on the SAO between latitudes 35° 50′ and 37° 00′ S and the 75 and 135 m isobaths. The total study area encompasses approximately 5100 km^2 over the Uruguayan shelf (Fig. 1) and is characterized by an even bottom topography and water
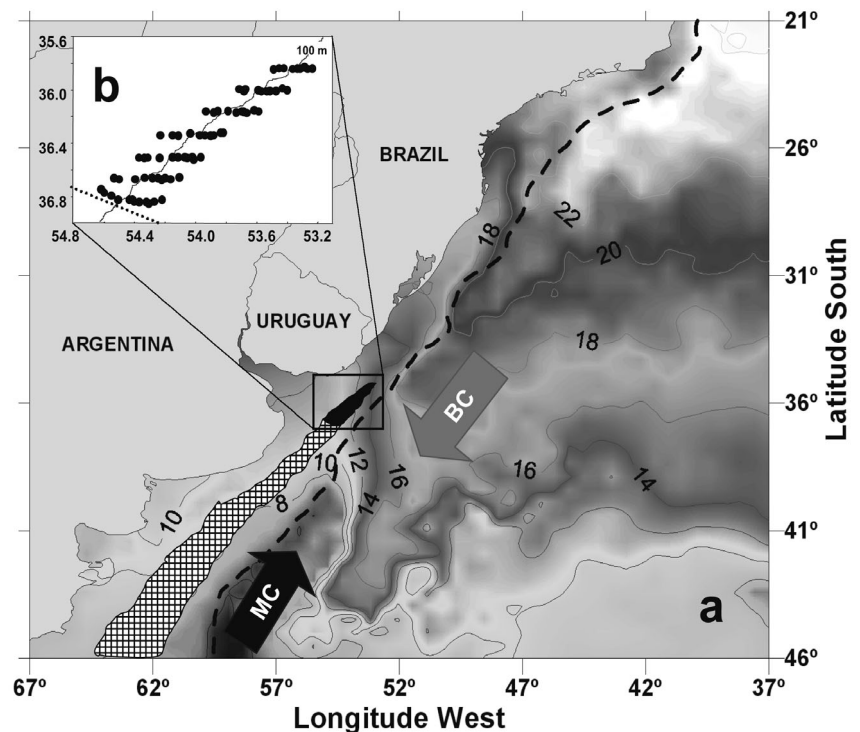

Fig. 1. *Psychrochlamys patagonica*. Study area in Uruguayan waters of the SW Atlantic Ocean: (a) cross-hatched area: species distribution in Argentinean waters; dashed line: 200 m isobath; sea surface temperature (SST) isotherms are also shown, highlighting confluence between Malvinas/Falkland (MC) and Brazil (BC) currents; (b) sampling stations

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[1]We follow the recent generic re-allocation of *Zygochlamys* by Jonkers (2003)

masses with contrasting thermohaline properties. The Tropical Water (TW) carried by the Brazil Current (Sverdrup et al. 1942) is restricted to the northern shelf and mixes with the STW in the water column during their southward flow. The water of the southern shelf, cold and relatively fresh, corresponds to the SAW which, during its northward flow, is mixed with the STW between the 100 and 200 m isobaths at latitudes lower than 36° 30′ S and 35° 40′ S during autumn and spring, respectively (Ortega & Martínez 2007). Therefore, the Uruguayan shelf has a high degree of horizontal and vertical heterogeneity, with oceanographic processes affecting water column stability (i.e. shelf convergences) and providing favorable environmental conditions for spawning, nursery and breeding of fish and invertebrate populations (Bakun & Parrish 1991).

Biological and oceanographic data. Data used to assess the stock of the scallop *Psychrochlamys patagonica* were collected during July 2001. Survey operations were conducted from the Uruguayan RV 'Aldebarán' in a strip of the continental slope 139 km long and 37 km wide (total area surveyed: 5100 km^2). A total of 67 sampling stations were located systematically (by GPS) on parallel transects along the latitudinal gradient at 10 nautical miles (18 km) intervals between 35° 50′ S and 36° 50′ S and at 5 m intervals within the depth range 75 to 135 m, until at least 1 sampling station without organisms was recorded. Thus, the survey covered the entire species distribution in Uruguayan waters. Each tow was carried out with an otter trawl directly attached to the doors (otter boards), a net opening of 9.5 m and a mesh size of 5 cm, with a mean trawling speed of 3.2 knots over a 15 min towing time (Gutiérrez & Defeo 2003). Some 11 080 scallops were measured on board with callipers (1 mm accuracy) from the umbo to the ventral border of the shell (valve height *H*), representing the entire range of sizes typical for this scallop found throughout the study area. Laboratory measurements of total weight without epibionts and adductor muscle weight were made on an electronic balance with 0.01 g accuracy. Latitudinal variations in muscle weight of 60 mm scallops (W_{60}) were estimated (except for 35° 50′ S, where individuals were <60 mm).

Long-term oceanographic data were obtained from 10 annual surveys conducted from 1991 to 2001 with the RV 'Aldebarán,' where selected stations exactly matched all those of the scallop survey. Long-term information was averaged for each of the 7 latitudes and 12 depths (5 m intervals between 75 and 135 m depth) in order to model the relationship between oceanographic and biological data. During these surveys, CTD (SBE-19, Sea-Bird Electronics) casts profiled the water column from the surface to about 5 m above the bottom. Water samples for biological analy-

ses were taken with Niskin bottles. Immediately after collection, 1000 ml samples were filtered through 47 mm diameter glass fiber filters (Whatman GF/C) for assessment of total chlorophyll. Filters were stored dried and frozen for subsequent analysis in the laboratory. Chlorophyll was extracted with 90 % acetone and analyzed with a Shimadzu UV-2101 PC, UV-VIS Scanning spectrophotometer (Parsons et al. 1984). Total chl *a* was calculated according to Jeffrey & Humphrey (1975). The mean chl *a* (mg m^{-3}) at each station was estimated by graphical integration of the discrete values and then divided by the integration depth.

Data analyses. Information on biomass (*B*: kg m^{-2}) at each station was calculated by the swept area method (Caddy 1979) as $B = c/(ae)$, where *c* is the total catch in each haul, *a* is the area swept by the gear (mean ± SD: 5141 ± 344 m^2) and *e* is gear efficiency, defined as the fraction of scallops in the path of the gear that are actually caught. This parameter was set at 0.35, according to precautionary estimates provided by Lasta & Iribarne (1997).

Single relationships between population and oceanographic variables (mean estimates for each latitude and depth) were modeled by linear or nonlinear fitting, and the model that best explained the relationship between biological and physical variables was selected according to the coefficient of determination (r^2).

The relationship between scallop biomass and oceanographic variables was examined within both a generalized linear model (GLM) and a generalized additive model (GAM) framework for comparative purposes (Hastie & Tibshirani 1990, Guisan & Thuiller 2005). To this end, biomass estimates and oceanographic variables from the 67 sampling stations were used. Due to overdispersion in abundance data, negative binomial models were used for both GLMs and GAMs; additionally, for the latter, thin plate splines were considered for multidimensional smoothing (Wood 2006). An offset parameter equal to the natural logarithm of the effective swept area sampled was found to be an adequate model for abundance data. All the environmental variables measured were included for model fitting: latitude, longitude, depth, bottom temperature, bottom salinity (hereafter temperature and salinity, respectively), sigma-t (σ_T) and mean chl *a*. GAMs fit non-parametric functions to estimate the relationships between response and predictor variables without imposing limitations on the form of the underlying relationships. Smoothing parameters, as well as the degrees of freedom (the degree of non-linearity) of the functions from the data, were estimated using the generalized cross-validation (GCV) criterion. An explanatory variable or term in the model was removed (as per Wood 2006) if (1) the estimated degrees of freedom (EDF) for the term were close to 1; (2) the plotted

confidence band for the term included zero every-where; and (3) the GCV score decreased and the deviance explained increased when the term was dropped. Because of correlations among covariates, terms were dropped one at a time, starting with the term for which the zero line was most within the confidence band (Wood 2006). Each model fit was analyzed with respect to the level of deviance explained (0 to 100%; the higher the better), the GCV score (the lower the better), and the confidence region for the smooth function (which should not include zeroes throughout the range of the predictor). Akaike's information criterion (AIC), also used to evaluate each model fit and parsimony, accounts for degrees of freedom used and the goodness of fit, such that more parsimonious models have lower AIC (Chambers & Hastie 1992). The AIC was calculated in R (http://cran.r-project.org/) as –2 log likelihood + 2*npar*, where *npar* represents the number of parameters in the fitted model. Residual plots were evaluated for violations of model assumptions. In order to assess whether the non-parametric smooth terms should be simplified to linear terms, we built negative binomial GLMs using the same variables selected by GAMs. Both approaches were then compared by AIC and significances of differences in deviance were checked using approximate χ^2 tests (Hastie & Tibshirani 1990). Finally, spatial GAM biomass predictions were plotted and a polynomial interpolation-extrapolation approach was used to estimate biomass at points not sampled (Wood 2006). Observed (*O*) and predicted (*P*) biomasses were plotted and fitted to a linear regression $O = \alpha + \beta P$. Departures from a one-to-one line through the origin indicate model inadequacy, and thus the significance of α and β was tested (*t*-test) under the null hypotheses $\alpha = 0$ and $\beta = 1$ (Power 1993). All models were estimated by the GAM function in the mgcv and MASS libraries of R.

RESULTS

Oceanographic patterns

Latitudinal variations in oceanographic variables are shown in Fig. 2. Temperature and salinity linearly decreased with latitude (Fig. 2a,b), σ_T significantly increased with latitude (Fig. 2c), and mean chl *a* showed 2 marked peaks, the main one at 36° 20′ S (mean ± SE: 3.62 ± 0.96 mg m^{-3}) and a smaller one at the southern border of the surveyed area (36° 50′ S; 2.8 ± 1.48 mg m^{-3}). As a result of the above patterns, the northern border of the species distribution at 35° 50′ S had the highest temperature and salinity and the lowest σ_T and mean chl *a* values (Fig. 2). With the exception of mean chl *a*, which was not significantly related

to other oceanographic variables, bivariate correlations between temperature, salinity and σ_T were all linear and statistically significant (p < 0.01), with the strongest ones found between temperature and: (1) salinity (r = 0.90); and (2) σ_T (r = 0.93) (Fig. 2).

Bathymetric variations in temperature, salinity and σ_T also followed clear patterns (Fig. 3): (1) temperature was minimum at depths close to 104 m, increasing towards shallower and greater depths; (2) salinity increased with depth; and (3) σ_T was maximum at depths close to 120 m, decreasing towards shallower and greater depths. For temperature and salinity, 2 water masses can be clearly distinguished (Fig. 3): from 60 to ca. 120 m depth, the decreasing pattern in temperature and the low salinity values correspond to the SAW, whereas the highest temperature and salinity values at depths >120 m correspond to the STW.

Scallop population patterns

The biomass of *Psychrochlamys patagonica* showed 2 clear peaks (Fig. 2): the main one at 36° 20′ S (mean ± SE: 0.0279 ± 0.0110 kg m^{-2}) and a smaller one at 36° 50′ S (0.0204 ± 0.0041 kg m^{-2}), at the southern border of the surveyed area. At the northern edge of the range of the species distribution (35° 50′ S), abundance was 16 times lower (0.0013 ± 0.0002 kg m^{-2}) than at 36° 50′ S. As a result of this spatial pattern, scallop abundance was related to mean chl *a* through an exponential model of the form $B = 0.0039\,e^{(0.61\,Chlo)}$ (r = 0.79; p < 0.05), where *B* is scallop abundance and *Chlo* is mean chl *a* (Fig. 2).

Individual scallop sizes decreased linearly with temperature and salinity, and increased asymptotically with mean chl *a* (Fig. 4, Table 1). The smallest scallops (mean *H* = 34 mm) were found at the northern distribution edge of the species; these scallops were, on average, 12.7 mm (37%) and 11.5 mm (34%) shorter than those found at 36° 30′ S and 36° 50′ S, respectively (Fig. 4, Table 1). Variations in muscle weight for a standard scallop of 60 mm height (W_{60}) decreased with temperature, mean chl *a* and salinity, meaning significantly lower weights at the northern edge of the study area (Fig. 4, Table 1). Indeed, scallops at latitudes 36° 30′ S, 36° 40′ S and 36° 50′ S were, on average, 11% heavier than those situated at 36° 00′ S, 36° 10′ S and 36° 20′ S.

GAM and GLM relationships

GAM results showed that spatial and oceanographic variables significantly (p < 0.001) explained *Psychrochlamys patagonica* abundance in Uruguayan
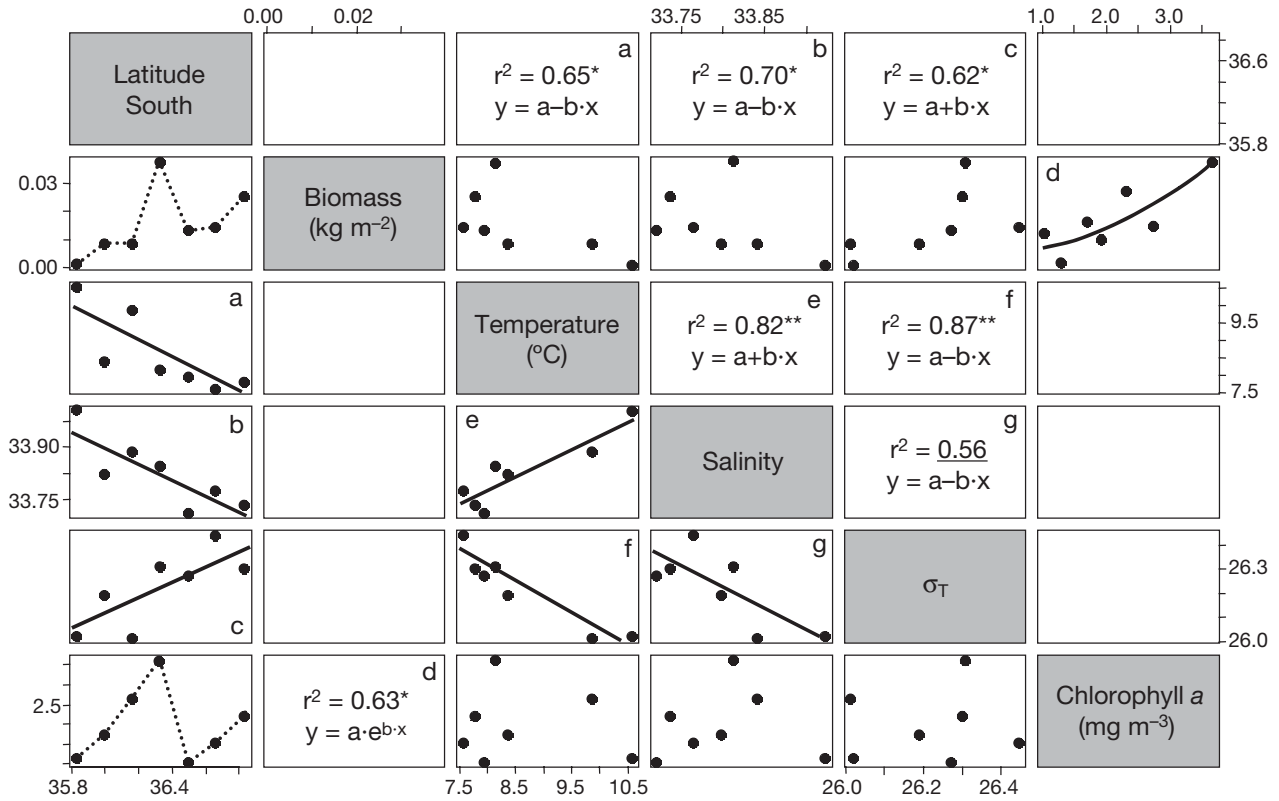
Fig. 2. *Psychrochlamys patagonica*. Relationships among environmental variables and scallop biomass, averaged by latitude. *p < 0.05; **p < 0.01. The underlined value indicates trends that approached significance (0.10 < p < 0.05). Latitude is expressed in centesimal units. Note similar latitudinal patterns in mean chl *a* and scallop biomass. Empty boxes: no relationship found
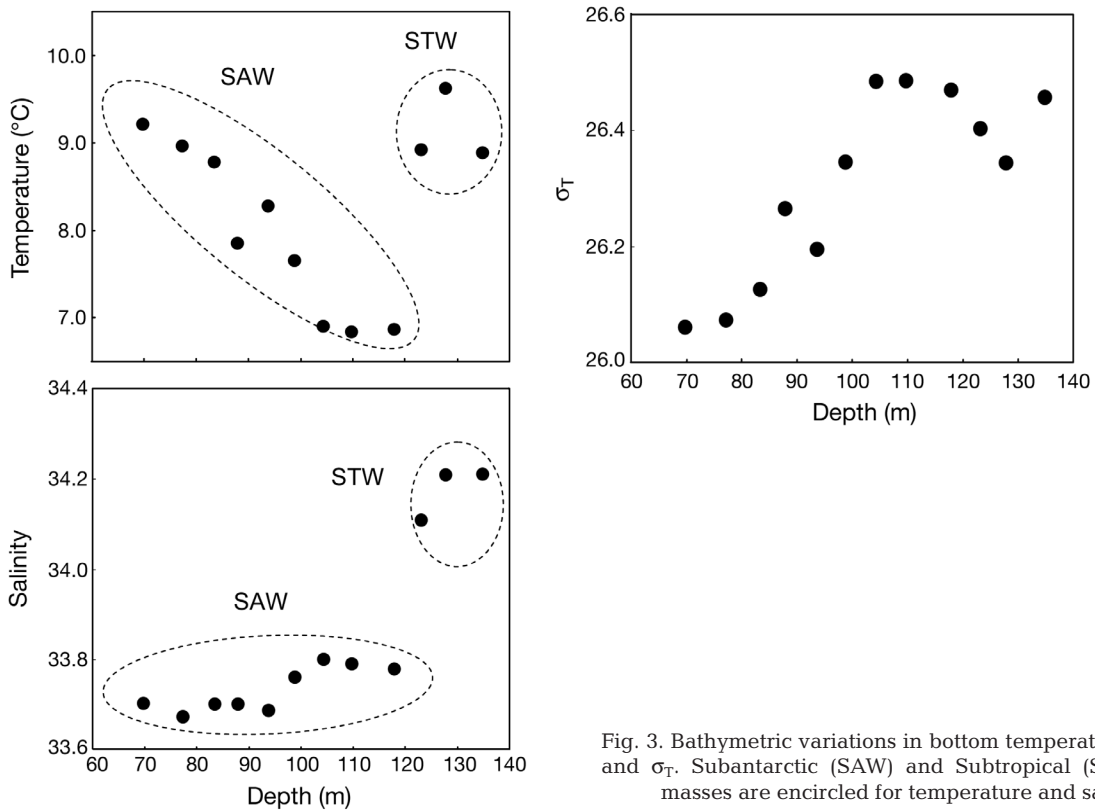

Fig. 3. Bathymetric variations in bottom temperature, salinity and σ_T. Subantarctic (SAW) and Subtropical (STW) water masses are encircled for temperature and salinity
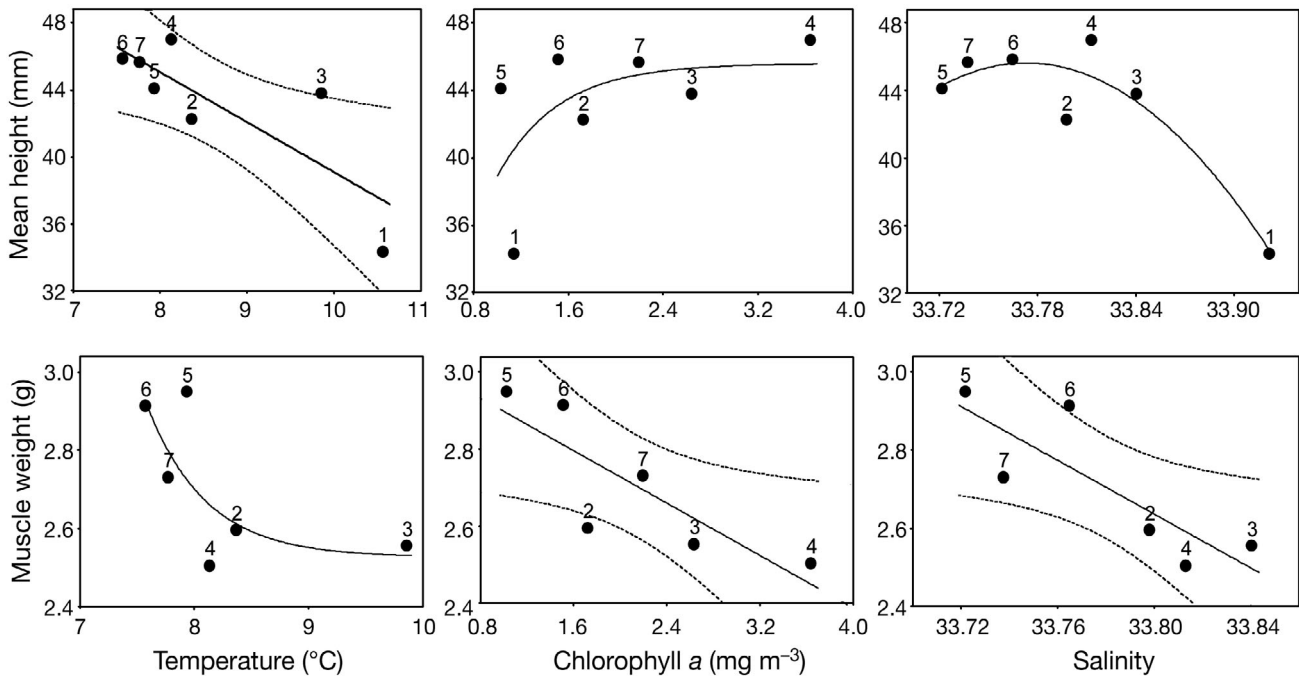
Fig. 4. *Psychrochlamys patagonica.* Bivariate correlation (±95% CI, dashed lines) between both individual mean height and muscle weight and oceanographic variables (temperature, chl *a* and salinity). Model with best goodness of fit shown in each case. Numbers by each point refer to sequentially numbered latitudes in north–south direction from 1 (35° 50' S: northern edge of the species distribution) to 7 (36° 50' S)

waters, with a good overall fit in terms of their deviance and no abnormalities revealed by the analysis of residuals. The best model included temperature, mean chl *a* and depth, together with the 'latitude–longitude interaction' (as a proxy for geographic term) (Table 2). This was clearly indicated by the consistent increase in r^2 and deviance explained, concurrently with a decrease in the GCV score and AIC between the GAMs fitted with and without the latitude–longitude interaction term (Table 2). Salinity and σ_T were

not included in the model (p > 0.05). Abundance showed a non-linear relationship with latitude–longitude, increasing southwards and with water depth, peaking between 90 and 110 m, and declining towards shallower and greater depths (Fig. 5). Scallop abundance was negatively related to temperature, and positively with mean chl *a*, with a peak between 5.5 and 6.5 mg m^{-3}. Among the 4 environmental properties considered, the strongest GAM relationships occurred between scallop abundance and temperature, which explained 68% of the model deviance (Table 2). The GAM clearly achieved lower AIC (Table 2) and an analysis of deviance showed a decrease in the residual deviance of 48.1% (p $[\chi^2]$ < 0.001) and 30.5% (p $[\chi^2]$ = 0.004), respectively, when compared to the linear and quadratic GLMs. Thus, the flexibility offered by GAMs significantly improved the quality of the fits. GAM predictions show that scallops mainly occurred above the 100 m isobath, with major concentrations at the center (36° 20' S to 36° 30' S) and south (36° 50' S) of Uruguayan waters (Fig. 6). This pattern agrees with the 2 peaks in scallop

Table 1. Results of bivariate models between some scallop mean height (mm) and muscle weight (g), and oceanographic variables (temperature in °C, chl *a* in mg m^{-3} and salinity). All correlations were significant. *H*: scallop height; *T*: bottom temperature; W_{60}: adductor muscle weight of 60 mm height scallops; *Chlo*: mean chl *a*; *S*: bottom salinity

Population feature	Model	r	p
Temperature			
Height	$H = 68.91 - 2.98T$	0.81	0.0285
Muscle weight	$W_{60} = 2.52 + 94086e^{(-1.937T)}$	0.74	0.0002
Chl *a*			
Height	$H = 45.59 (1 - e^{(-1.93\,Chlo)})$	0.54	<0.0001
Muscle weight	$W_{60} = 3.06 - 0.17\,Chlo^{(-1.937T)}$	–0.83	0.0391
Salinity			
Height	$H = -5.73E5 + 33982S - 503S^2$	–0.76	0.0473
Muscle weight	$W_{60} = 118.90 - 3.44S$	0.84	0.0384

Table 2. Model selection (GLM and GAM) for scallop biomass (kg m^{-2}). Terms that were not significant (p > 0.05) were dropped from the model. Percent of deviance explained, adjusted r^2, generalized cross-validation score (GCV) and Akaike information criterion (AIC) are given. EDF: estimated degrees of freedom. Note: As each term is added for GAMs, explained deviance, r^2, GCV score and AIC are examined to determine whether the term will be included in the final model (values in bold and italics). Linear and quadratic GLMs were also fitted for comparison purposes, using the variables selected by the best GAM fit. Only most relevant GAM fits were included

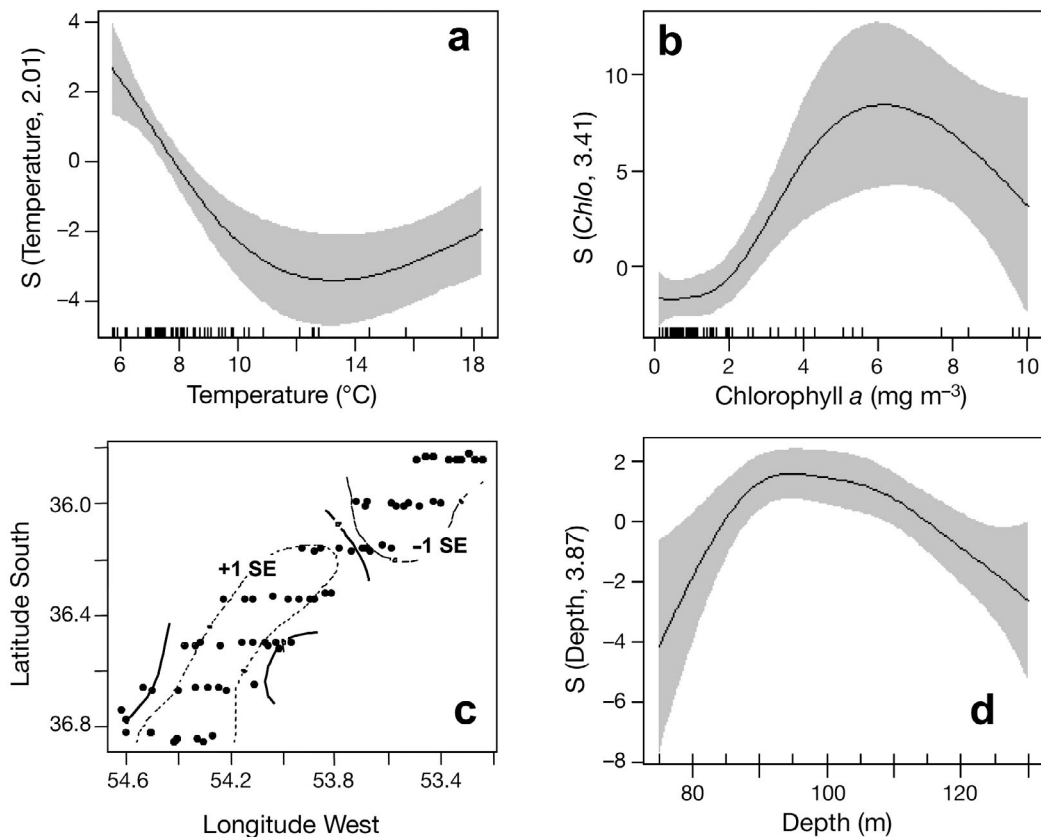| Model	Terms	EDF	Deviance explained (%)	r^2	GCV	AIC
GLM linear	Biomass ~ Temperature + Chl *a* + Depth + Longitude × Latitude + offset (log.Area)	7.00	42.7	0.067	1.11	621
GLM quadratic	Biomass ~ Temperature + (Temperature)^2 + Chl *a* + (Chl *a*)^2 + Depth + (Depth)^2 + Longitude × Latitude + offset (log.Area)	9.00	59.0	0.299	1.16	598
GAM	Biomass ~ s(Temperature) + offset (log.Area)	3.04	65.3	0.133	1.05	615
GAM	Biomass ~ s(Temperature) + s(Chl *a*) + s(Depth) + offset (log.Area)	13.93	68.7	0.245	1.23	595
GAM	Biomass ~ s(Temperature) + s(Longitude, Latitude) + offset (log.Area)	21.52	73.1	0.209	1.47	586
GAM	Biomass ~ s(Temperature) + s(Chl *a*) + s(Longitude, Latitude) + s(Depth) + offset (log.Area)	*21.99*	*78.7*	*0.303*	*1.19*	*576*

Fig. 5. *Psychrochlamys patagonica.* Results of GAM showing relationship (solid line) between abundance and each meaningful environmental predictor: (a) temperature, (b) mean chl *a* (*Chlo*), (c) latitude–longitude and (d) depth. Shaded areas indicate 2 SE above and below estimate of the smooth curve. 'Rug plots' on the *x*-axis indicate range of variables over which measurements were taken. S on the *y*-axis represents the smooth function (spline) for scallop abundance and numbers next to variable name are the estimated degrees of freedom (EDF). For latitude/longitude, bivariate smooth shown as a contour plot with surfaces at +1 and −1 SE over the survey area and sampled locations marked by dots
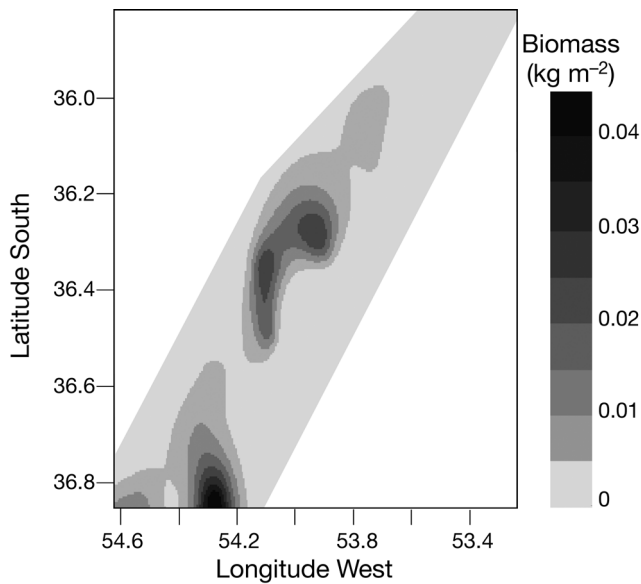
Fig. 6. *Psychrochlamys patagonica.* GAM predictions of abundance through image plots. Latitude and longitude are expressed in centesimal units

biomass shown in Fig. 2. The correlation between observed and predicted abundance was significant ($p < 0.001$; $r^2 = 0.98$) and the null hypotheses $\alpha = 0$ and $\beta = 1$ were not rejected ($O = 3.12 + 0.96P$; $p > 0.50$).

DISCUSSION

Some of the mechanisms limiting species ranges include environmental gradients (temperature: Heilmayer 2003), dispersal barriers (ocean flows: Gaylord & Gaines 2000), and biological interactions (competition: Case et al. 2005). In the present study, the strong relationships between scallop abundance and environmental variables, mainly temperature, imply the existence of an environmental margin (sensu Bridle & Vines 2007) at the northern limit of *Psychrochlamys patagonica* distribution. The species showed strong spatial patterns in abundance, individual size and muscle weight in Uruguayan waters. All these population descriptors significantly decreased towards the northern edge of the population distribution, where sea temperature and salinity were highest, and chl *a* was lowest. The species distribution was also strongly restricted to a depth range between 75 and 135 m, associated with the thermohaline properties of the SAW.

A distinctive pattern of oceanographic conditions was noticeable in this study, related with the confluence of the Brazil and Malvinas/Falkland currents (see also Ortega & Martinez 2007). Both latitudinal and bathymetric patterns shown in this study revealed the presence of 2 distinct water masses, the SAW and the STW, associated with these currents. Considering these water masses with contrasting thermohaline characteristics, the species' northern border of distribution could be primarily explained by the strong gradient occurring at this oceanographic discontinuity. Several macroinvertebrates, such as the gastropods *Odontocymbiola magellanica* and *Adelomelon ancilla* (common predators of *Psychrochlamys patagonica*: Botto et al. 2006), also have the same northern border of distribution in the SAO (Olivier & Scarabino 1972). Thermohaline gradients have been associated with biogeographic boundaries worldwide, constraining species' geographical ranges (Wilson et al. 1996, Gaylord & Gaines 2000).

The GAM built here was useful to model scallop/ habitat relationships and to predict spatial variations in abundance at the northern limit of the scallop's distribution range. Better fits obtained with GAM when compared to those obtained with linear and quadratic GLMs are based on the rationale that the response of scallop abundance along environmental predictors is neither linear nor monotonic. Hence, this more flexible framework resulted in more realistic and informative models. Many of the relationships between environmental features and scallop distribution were nonlinear (Table 2). Although depth, temperature and chl *a* significantly influenced scallop distribution and abundance, the most parsimonious GAM fitted included a latitude–longitude interaction (as a proxy for location). This interaction reflects localized biological processes (e.g. attraction by conspecifics) or the result of a process in which much of the pattern is driven by spatial correlation (Swartzman et al. 1992, Wood & Augustin 2002). Including location in our GAM also improved the spatial predictive ability of the model, highlighting the 2 main high scallop biomass patches. The effects derived by the latitude–longitude interaction, which cannot be quantified separately, are of the utmost importance in shaping macroscale patterns in the scallop population.

Spatial distribution patterns of *Psychrochlamys patagonica* in the northern limit of its range could be related to the presence of the shelf break front created by the SAW–STW confluence (Ortega & Martínez 2007). This front is characterized by a steep gradient in oceanographic variables and high chl *a* concentrations (Martínez & Ortega 2007). These concentrations are important for *P. patagonica* as a suspension-feeder, particularly when it is feeding on phytoplankton (Schejter et al. 2002). However, the decrease in scallop abundance at chl *a* values > 6.0 mg m^{-3} (Fig. 5b) could be explained by the high temperatures occurring in the SAW–STW confluence; these higher temperatures may decrease the effect of food availability on scallop abundance.

GAM relationships predicted a sharp decrease in abundance at temperatures above 9°C, reaffirming this value as the upper limit of temperature tolerance of this species (Heilmayer et al. 2001). The results agree with recent findings showing that temperature is one of the major determinants of habitat suitability for scallop resources (Heilmayer 2003 and references therein) and that species distribution patterns commonly reflect gradients or discontinuities in temperature adaptation (Guisan et al. 2006). A strong empirical relationship between growth efficiency and temperature found in scallops reinforces the idea of a temperature-optimum growth efficiency in these organisms (Heilmayer 2003). Gutiérrez & Defeo (2005) also found that growth rates of *Psychrochlamys patagonica* drastically decreased at the northern edge of its distributional range. Moreover, the decrease in mean individual height and muscle weight with increasing temperature shown in this study could be ascribed to phenotypic plasticity in response to extreme oceanographic conditions, strengthening the hypothesis of environmental limitation at the northern edge of the geographical range of the species. High adult scallop mortalities found at the northern border of the species distribution (Gutiérrez & Defeo 2005) also suggest that thermohaline properties affect the scallop's population dynamics. This is in agreement with the hypothesis that higher mortality caused by adverse environmental conditions in fringe populations is the main mechanism setting the range limits (Zacherl et al. 2003).

In order to understand species range limits, 3 broad questions have to be addressed (Gaston 2003): (1) What biotic and abiotic factors prevent further spread? (2) How do these aspects affect a species' population dynamics? (3) What are the genetics behind species' response to factors determining these range limits? Previous work by Defeo & Gutiérrez (2003) and Gutiérrez & Defeo (2005) and the present study answered the first 2 questions. The northernmost limit of *Psychrochlamys patagonica* could be ascribed mainly to abrupt changes in temperature associated with the Brazil–Malvinas/Falklands Confluence, where water reaches temperatures beyond the species' tolerance limit. These prevailing stressful environmental conditions at the northern edge of distribution cause poor and irregular recruitment, low growth rates and high natural mortality (Gutiérrez & Defeo 2005). Thus, the environmental constraints defined in this study play an important role in determining the population dynamics of this marginal population and therefore its northern distributional range. Whereas temperature seems to be the main variable determining scallop occurrence, mean chl *a* has a strong effect on abundance, with peaks in chl *a* exactly matching high-biomass scallop patches.

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