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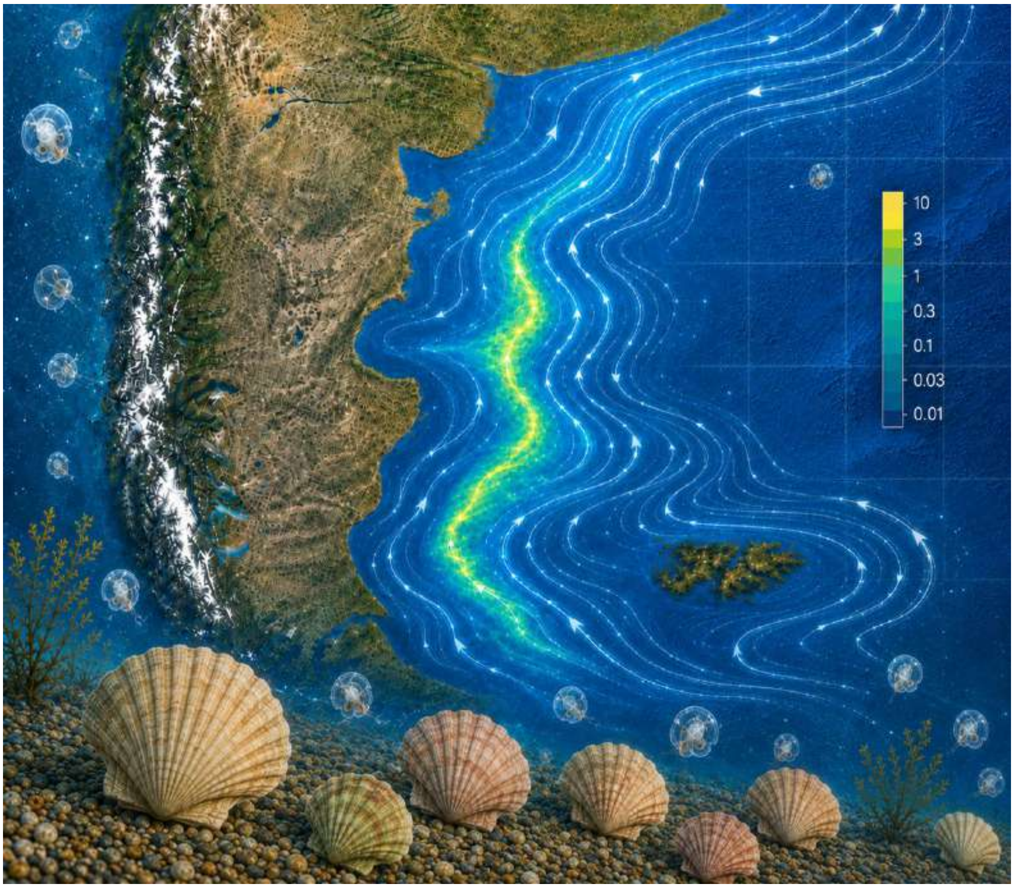

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Informe

What drives Patagonian scallop recruitment? An assessment of the role of oceanographic forcing using gridded oceanographic fields

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ABSTRACT. Recruitment variability in the Patagonian scallop, *Zygochlamys patagonica*, is expected to depend on oceanographic processes acting during the planktotrophic larval phase. This report evaluates whether one-year-lagged gridded oceanographic fields from Copernicus Marine describe spatial and temporal variation in recruitment occurrence and recruit density. Predictors included vertically stratified temperature, salinity, chlorophyll-a, the zonal and meridional components of sea-water velocity, the current speed derived from those components, bathymetry, geographic position, and year, matched to survey observations using the oceanographic year preceding the recruitment surveys. Generalized additive models and Random Forest models were fitted to compare smooth additive responses with flexible non-linear relationships. Random Forests provided the strongest descriptive performance, but leave-one-year-out validation showed weak prospective prediction, indicating that the models mainly describe associations within the observed spatial-temporal domain. Recruitment was strongly structured geographically and showed non-linear responses to salinity, bathymetry, year, and currents. Chlorophyll-a was not dominant, suggesting delayed and spatially displaced trophic pathways. The analysis provides an exploratory basis for future connectivity and particle-tracking models.

RESUMEN. ¿Qué moldea el reclutamiento de la vieira patagónica? Una evaluación del papel del forzamiento oceanográfico mediante capas oceanográficas grilladas. El reclutamiento de la vieira patagónica, *Zygochlamys patagonica*, puede depender de procesos oceanográficos que actúan durante la fase larval planctónica. En este informe se evaluó si las condiciones oceanográficas del año previo a las prospecciones que cuantifican el reclutamiento explican la ocurrencia y densidad de reclutas, usando campos grillados y estratificados verticalmente de Copernicus Marine, incluyendo temperatura, salinidad, clorofila-*a*, los componentes zonal y meridional de la velocidad del agua de mar y la velocidad de corriente derivada de esos componentes, junto con modelos aditivos generalizados y Random Forest. Los Random Forest tuvieron mayor capacidad descriptiva, aunque la validación temporal dejando un año fuera mostró baja capacidad predictiva prospectiva. Los resultados indicaron fuerte estructura espacial y efectos no lineales de salinidad, profundidad, año y corrientes. La clorofila-*a* fue secundaria, posiblemente porque sus efectos sobre el reclutamiento pueden estar mediados por procesos tróficos, rezagos temporales y desplazamientos espaciales. La evaluación constituye un primer paso para integrar forzantes ambientales, conectividad genética y trayectorias de partículas virtuales.

Key words: Patagonian scallop, recruitment, oceanographic forcing, gridded fields, Copernicus Marine, Random Forest, generalized additive models, larval transport.

Palabras clave: Vieira patagónica, reclutamiento, forzantes oceanográficos, campos grillados, Copernicus Marine, Random Forest, modelos aditivos generalizados, transporte larval.

INTRODUCTION

The Patagonian scallop *Zygochlamys patagonica* is one of the most important benthic resources of the Southwestern Atlantic, where dense aggregations occur mainly along the outer continental shelf and shelf-break region. Previous studies have shown that the spatial distribution of Patagonian scallop beds is closely associated with frontal systems, particularly the Patagonian Shelf-Break Front, where enhanced productivity and hydrographic retention may promote the persistence of adult aggregations and the settlement of early life stages (Acha et al. 2004; Bogazzi et al. 2005; Mauna et al. 2008). Because adult scallops are essentially sedentary, spatial and temporal variability in recruitment is expected to depend strongly on processes acting during the planktotrophic larval phase, including larval transport, retention, food availability, temperature-dependent development, and the probability of successful settlement (Cowen and Sponaugle 2009; Franco et al. 2017; Chen et al. 2021).

These species-specific antecedents reinforce the rationale for analysing recruitment through oceanographic forcing rather than only through local adult abundance or static habitat descriptors. Previous descriptions of recently settled spat indicate planktotrophic development in *Z. patagonica*, whereas laboratory observations of early development show that embryonic and trochophore stages unfold over several days at cold-water temperatures, even though the complete larval cycle remains unresolved under controlled conditions (Schejter et al. 2010; Schwartz and Campodónico 2019). A preliminary synthesis of larval biology also framed *Z. patagonica* recruitment as the outcome of an extended reproductive season, potentially asynchronous spawning, food availability near the bottom, and a hypothetical larval duration long enough for transport by shelf-break circulation (Pascual and Zampatti 2009). In addition, field evidence on primary settlement indicates that larval arrival must be followed by encounter with suitable benthic substrates, especially filamentous hydroids, before recruitment becomes visible in surveys (Bremec et al. 2008). This background supports the assumption that recruitment integrates conditions experienced during spawning, larval dispersal, settlement, and early post-settlement survival, making circulation, retention, temperature, food-related processes, and benthic habitat relevant components of the recruitment pathway.

A recent analysis by Torres Alberto et al. (2025) provided evidence that interannual fluctuations in Patagonian scallop recruitment may be associated with the position of the Subantarctic Front (SAF), bottom temperature, and the dynamics of the Brazil-Malvinas Confluence region. In that study, recruitment was higher when the SAF was displaced northwards, a situation interpreted as increasing the time available for larvae to develop before potential export to the open ocean. Conversely, a southward displacement of the SAF was associated with weaker recruitment, presumably because larvae would reach the shelf-water export region before becoming competent to settle. This interpretation is consistent with the broader view that shelf-break and confluence dynamics regulate larval retention versus offshore loss in the Patagonian shelf ecosystem (Franco et al. 2017; Berden et al. 2022; Torres Alberto et al. 2025). The study also highlighted that the relevant environmental window corresponds mainly to September-December of the year preceding recruitment, when larvae are expected to be present in the plankton and phytoplankton production is high (Campodónico et al. 2008; Romero et al. 2006; Torres Alberto et al. 2025).

The approach proposed here extends this framework by increasing both the spatial and temporal resolution at which oceanographic forcing is represented. Rather than using the SAF as a single frontal position or categorical descriptor, we treat the front as a dynamic oceanographic expression emerging from continuous gradients in temperature, salinity, chlorophyll-*a*, and current velocity. This distinction is important because fronts are not ecological drivers by themselves; instead, their biological effects are mediated through the physical and biogeochemical conditions they generate, such as enhanced primary production, horizontal convergence, cross-shelf exchange, thermal structure, and advective pathways (Acha et al. 2004; Bogazzi et al. 2005; Franco et al. 2017). In this sense, the SAF is treated not as a discrete entity, but as a space-time-varying forcing whose local manifestation can be quantified through gridded oceanographic variables. This allows recruitment variability to be evaluated along environmental gradients rather than only in relation to the latitude of a frontal contour.

This higher-resolution perspective is particularly relevant for benthic recruitment because the early life history of scallops integrates processes operating over multiple spatial and temporal scales. Temperature can influence larval development rate and planktotrophic larval duration, currents can determine whether larvae are retained near suitable settlement habitat or exported offshore, and salinity may help characterize water-mass structure associated with frontal variability. Chlorophyll-*a*, in turn, was treated as a depth-resolved modelled proxy for phytoplankton biomass and potential primary production in the selected water-column layer rather than as a direct measure of the food actually available to larvae, post-larvae, or recently settled scallops. Its ecological relevance may arise after trophic transfer, sinking, mixing, or advection, when phytoplankton production is transformed into zooplankton biomass, suspended particles, or detrital material that can become available as food in intermediate waters or near the bottom (Cragg 2006; Cowen and Sponaugle 2009; Franco et al. 2017; Chen et al. 2021).

In this study, gridded Copernicus Marine products describing chlorophyll-*a* concentration (`chl`), sea-water temperature (`thetao`), sea-water salinity (`so`), and the eastward and northward current velocity components (`uo`, `vo`) were processed to characterize the environmental conditions experienced by scallop recruits during the year preceding the survey that quantified recruitment. Chlorophyll-*a* was obtained from the global multiyear biogeochemical product `GLOBAL_MULTIYEAR_BGC_001_029`, whereas temperature, salinity, and current velocity were obtained from the global multiyear physical reanalysis product `GLOBAL_MULTIYEAR_PHY_001_030`; these variables are stored in the NetCDF files with a vertical `depth` dimension and were therefore handled as depth-resolved fields (E.U. Copernicus Marine Service Information 2025a,b). For each survey location, the vertical layer used for each Copernicus variable was selected according to the local ocean-floor depth estimated from GEBCO bathymetry, so that extracted conditions represented the deepest available model layer compatible with the benthic environment of each scallop bed. The use of depth-specific layers from approximately 0.5 to 350 m within the sampled bathymetric range allows the environmental characterization to better represent the benthic and near-bottom context of scallop beds, rather than relying on a single surface layer. Oceanographic variables were extracted at the scale of individual survey observations and then evaluated as predictors of the spatial and temporal variation in recruit density. This approach follows the recommendation that integrated physical-biological analyses are needed to understand larval connectivity, settlement, and recruitment variability in this system.

Finally, we use complementary modelling approaches to evaluate whether one-year-lagged oceanographic conditions can explain the spatial and temporal variation in both the occurrence and the intensity of recruitment. Recruitment occurrence was analysed using Random Forest classification and binomial generalized additive models, whereas recruitment intensity, represented by recruit density, was analysed using Random Forest regression and continuous-response generalized additive models. These approaches are well suited for this exploratory objective because they combine interpretable smooth effects with flexible models capable of representing nonlinear responses, high-order interactions, and predictor effects that may vary across environmental gradients (Breiman 2001; Ishwaran et al. 2008). In contrast to correlation-based analyses using a small number of regional indices, this framework allows the simultaneous evaluation of multiple physical and biogeochemical predictors measured at the location and depth of each observation. The main objective is therefore to determine whether high-resolution oceanographic information from the year preceding the recruitment survey improves our ability to explain recruitment variability, and to identify which manifestations of frontal and shelf-break dynamics are most strongly associated with the occurrence and magnitude of successful recruitment of *Z. patagonica*.

MATERIALS AND METHODS

Study objective

The objective of this analysis was to evaluate whether spatial and temporal variation in Patagonian scallop recruitment, *Zygochlamys patagonica*, could be explained by oceanographic conditions during the year preceding the survey observations that quantified recruitment. Two complementary recruitment responses were analysed. First, recruitment was represented as a binary record indicating whether recruits were observed or not in each survey observation. Second, recruitment was represented as recruit density, expressed in tons per square kilometre, for scallops smaller than 16 mm. These individuals were interpreted as approximately one-year-old recruits. Oceanographic predictors were obtained from Copernicus Marine gridded NetCDF products and were matched directly to the geographic position, sampling year, and local bathymetric depth of each survey observation. The final objective was to construct a one-year-lagged biological–oceanographic data set suitable for exploratory modelling of both recruitment occurrence and recruit density using generalized additive models and Random Forests.

Scallop survey data and recruitment records

Spatial and temporal information on Patagonian scallop recruitment was compiled from stock assessment surveys conducted by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina) and reported in scientific, technical, and cruise reports. These surveys constitute the main source of fishery-independent information for the assessment and management of the Patagonian scallop resource in Argentina (Campodónico et al. 2019). The survey design is based on spatially explicit fishing hauls conducted across scallop beds located along the outer shelf and shelf-break region, where the main commercial aggregations of *Zygochlamys patagonica* occur (Bogazzi et al. 2005; Campodónico et al. 2019). According to the standardized survey descriptions summarized by Campodónico et al. (2019), hauls were arranged on regular spatial grids, commonly separated by approximately 5 nautical miles, and conducted with a non-selective dredge of 2.5 m width and 10 mm internal mesh, towed for 10 min at an average speed of 5.5 km h^{-1}, with haul positions recorded by GPS and shell-height measurements obtained from subsamples of the catch.

For the present analysis, the information reported in INIDEP documents was digitized, standardized, and incorporated into a relational database. Each survey haul was associated with its sampling date, geographic position, fishing gear, management unit, tow geometry, swept area, and size-frequency composition. The database was then exported to a spreadsheet containing, for each observation, the survey year, longitude, latitude, recruit density, fishing gear, weighted size-frequency information, and management unit. Individuals smaller than 16 mm in total shell height were used to define the recruit class, following the interpretation that these individuals are recently settled or approximately one-year-old scallops that would have been in the plankton during the preceding year (Lomovasky et al. 2008; Torres Alberto et al. 2025). From these records, two response variables were derived: a binary variable describing the presence or absence of recorded recruitment in each survey observation, and a continuous variable describing recruit density in tons per square kilometre.

Oceanographic data

Oceanographic predictors were obtained from Copernicus Marine gridded products distributed as NetCDF files. The current implementation used chlorophyll-*a* concentration from Global Ocean Biogeochemistry Hindcast, stored as `chl`; and physical variables from Global Ocean Physics Reanalysis, including sea-water temperature stored as `thetao`, sea-water salinity stored as `so`, and the eastward and northward components of sea-water velocity stored as `uo` and `vo`. In the final data set, these variables were represented as `chla`, `sst`, `sss`, `uo`, and `vo`, respectively. Product metadata indicate that `chl`, `thetao`, `so`, `uo`, and `vo` are provided with the dimensions `time`, `depth`, `latitude`, and `longitude`; consequently, all Copernicus predictors used in the extraction workflow were treated as vertically stratified fields (E.U. Copernicus Marine Service Information 2025a,b). Current speed was computed as a derived variable from the two horizontal velocity components. The variables used in the extraction workflow were therefore:

- `uo`: eastward sea-water velocity component;
- `vo`: northward sea-water velocity component;
- `speed`: current speed, calculated as $U = \sqrt{u^2 + v^2}$ from `uo` and `vo`;
- `sst`: sea-water temperature, extracted from the Copernicus variable `thetao`;
- `sss`: sea-water salinity, extracted from the Copernicus variable `so`;
- `chla`: chlorophyll-*a* concentration, extracted from the Copernicus variable `chl`.

The oceanographic information downloaded as NetCDF files from the Copernicus Marine Data Store catalogue (https://data.marine.copernicus.eu/viewer/expert?view=catalogue) was processed to extract seasonal mean fields for the austral spring, defined here as September–December. These processed layers provided the environmental information used to match Copernicus fields with survey observations; the specific selection, averaging, and extraction procedures are described in the following subsections.

Seasonal averaging of Copernicus fields

The downloaded NetCDF layers contained monthly oceanographic information for the period 1995–2025. These layers were first separated and organized by variable, month, and depth. For each variable and depth level, the monthly layers corresponding to September, October, November, and December were then selected and averaged to obtain an austral-spring mean layer for each year, variable, and depth.

Because the Copernicus variables used here were depth-resolved, this seasonal averaging was performed separately for each available model depth. The resulting annual spring layers were subsequently used to match each survey observation with the oceanographic conditions from the year preceding the recruitment survey.

Table 1

Environmental layers used to construct the predictors for the recruitment analysis. Copernicus Marine NetCDF time series were processed as annual September–December means for each year and model depth. The chlorophyll-*a* predictor was obtained from the vertically stratified biogeochemical product `GLOBAL_MULTIYEAR_BGC_001_029`, whereas temperature, salinity, and current velocity were obtained from the vertically stratified physical reanalysis product `GLOBAL_MULTIYEAR_PHY_001_030`. A GEBCO gridded bathymetric layer was used to estimate local seabed depth at each survey location and to select the deepest valid Copernicus layer above the bottom. The resulting oceanographic and bathymetric predictors were spatially matched to scallop recruitment observations and used in the statistical models.

Predictor group	Variable	Environmental layer used	Processing applied
Zonal current velocity	`uo`	Eastward sea-water velocity from the physical reanalysis product at available model depths	Monthly layers were restricted to September–December, averaged by year and depth, and converted to near-bottom fields using local bathymetry
Meridional current velocity	`vo`	Northward sea-water velocity from the physical reanalysis product at available model depths	Processed with the same annual, seasonal, and bathymetry-adjusted workflow as `uo`
Sea-water temperature	`sst` (from `thetao`)	Sea-water potential temperature from the physical reanalysis product at available model depths	Annual September–December means were calculated by depth and assigned to the deepest valid layer above the seabed
Sea-water salinity	`sss` (from `so`)	Sea-water salinity from the physical reanalysis product at available model depths	Processed by year and depth and assigned to the deepest valid layer above the seabed
Chlorophyll-*a* concentration	`chla` (from `chl`)	Biogeochemical chlorophyll-*a* from the biogeochemical product at available model depths	Monthly values were aggregated by year and depth, then assigned to the deepest valid layer above the seabed
Bathymetric depth	`prof_bathy_m`	GEBCO_2025 gridded bathymetric layer for the study region	Used to estimate local seabed depth at each survey location, expressed in metres, and to guide the selection of the deepest valid Copernicus oceanographic layer shallower than the bottom

Bathymetry-based selection of vertical layers

Because Patagonian scallop observations correspond to benthic survey locations, oceanographic values were extracted from depth layers compatible with the local seabed rather than from a fixed surface layer. Local bottom depth was obtained from GEBCO Gridded Bathymetry Data, specifically the GEBCO_2025 Grid, a global terrain model for oceans and land that provides elevation values in metres at 15 arc-second intervals (GEBCO Compilation Group 2025). Survey coordinates were converted to spatial points in geographic coordinates and projected to the coordinate reference system of the bathymetric raster before extracting bottom depth. Depth values were converted to positive metres using the absolute value of the bathymetric extraction. Bathymetry was the only static two-dimensional environmental layer used in the workflow; its role was to describe local seabed depth and to guide the selection of vertically stratified Copernicus layers.

For each survey location, the script compared the local bathymetric depth with the set of Copernicus depth levels available for the selected variable and year. Candidate layers were defined as those whose depth was less than or equal to the local bottom depth. Among these candidates, the deepest valid layer was selected. This rule ensured that no oceanographic value was extracted from a layer deeper than the seabed. If the deepest compatible layer had a missing value at that grid cell, the extraction proceeded progressively upward through shallower layers until a non-missing value was found. If the local bathymetric depth was shallower than the shallowest available Copernicus layer, the shallowest layer was used.

Formally, for an observation i with bathymetric depth B_i and a set of available Copernicus depths $\{d_1, d_2, \ldots, d_K\}$, the first candidate layer was:

$$d_i^* = \max\{d_k : d_k \leq B_i\}.$$

If the value at d_i^* was missing, the algorithm searched the ordered set of shallower depths until a valid raster value was obtained. This bathymetry-based rule was applied independently to each variable and survey year.

Spatial and temporal matching with recruit observations

For each recruit-density observation, the corresponding oceanographic year was defined as $y - 1$, where y is the survey year. The script therefore created a single set of oceanographic predictors describing September–December conditions during the year preceding the survey that quantified recruitment. The extracted variables were stored using suffixes that identify the one-year temporal lag, for example `uo_lag1`, `vo_lag1`, `sst_lag1`, `sss_lag1`, and `chla_lag1`.

Current speed was calculated after extraction as:

$$U_i = \sqrt{\mathrm{uo}_i^2 + \mathrm{vo}_i^2},$$

where U_i is current speed for survey observation i during the year preceding the survey. The final table therefore included the original biological and survey fields, the extracted bathymetric depth, one-year-lagged oceanographic predictors, and the derived current-speed variable. The resulting data set was exported as an Excel workbook and used as the input table for the Random Forest and GAM analyses described below, together with a summary of missing values for each extracted predictor. An example output for the 2022 spring mean layers is shown in Figure 1.

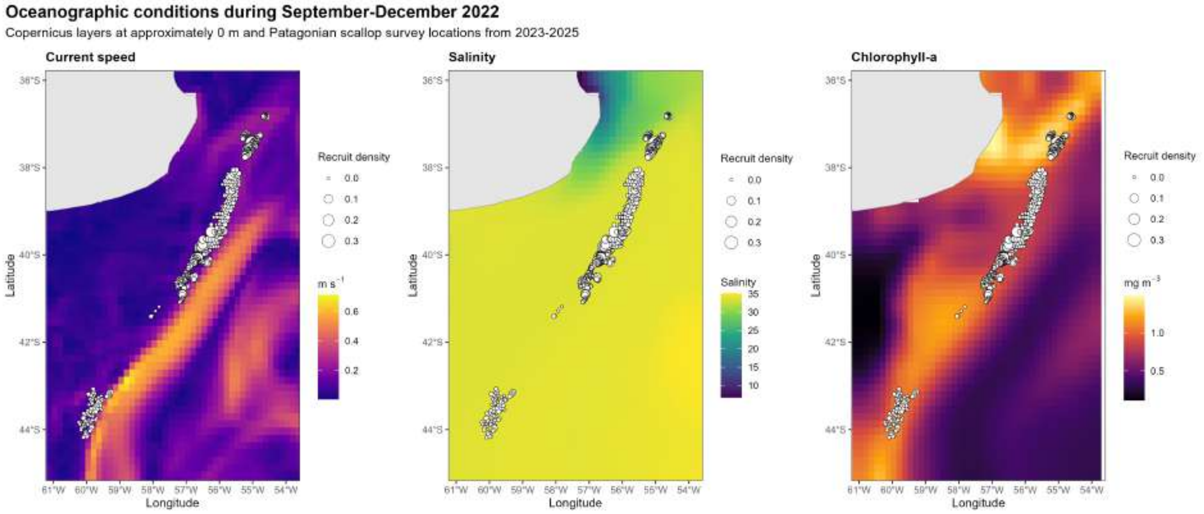

Figure 1: Example of three depth-selected gridded oceanographic layers used to explore their association with the spatial variation in recruit density. The figure illustrates the type of Copernicus Marine information used to compare environmental conditions with spatial patterns of recruitment after seasonal averaging and bathymetry-based vertical-layer selection. For each sampling point and coordinate, the oceanographic value was extracted from the model layer corresponding to the local seabed depth, selecting the closest valid layer above the bottom when necessary.

Generalized additive modelling

Generalized additive models (GAMs) were fitted to evaluate potentially non-linear relationships between recruitment and spatial, bathymetric, and oceanographic covariates. Models were implemented in R using the `mgcv` package (Wood 2017), which estimates smooth functions of predictors through penalized regression splines. The analyses considered two complementary response variables: the binary record of recruitment occurrence in each survey observation and the density of recruits expressed in tons per square kilometre.

For the binary response, a binomial GAM with a logit link was used to estimate the probability that recruitment was recorded at a given survey location. For the density response, a Gamma GAM with a log link was used to model variation in recruit density. In both cases, the same set of predictors was considered: latitude, longitude, sampling year, local bathymetric depth, zonal and meridional current velocity, sea-water salinity, chlorophyll-*a* concentration, and derived current speed. The oceanographic predictors used in these models corresponded to the September–December environmental window of the year preceding the survey observation, which represents the period most directly associated with the larval phase preceding recruitment.

Each predictor was included as a smooth term, allowing flexible responses without imposing a predefined linear form. Model smoothness was selected by restricted maximum likelihood, reducing the risk of overfitting while allowing non-linear patterns to be captured when supported by the data. Model fit was evaluated by comparing observed and fitted values: for the binomial model, predicted recruitment probabilities were compared with the observed presence or absence of recruitment; for the density model, fitted values were compared with observed recruit densities.

The relative contribution and shape of each predictor effect were evaluated using partial-effect plots, in which the fitted smooth for each covariate was visualized while holding the remaining variables constant. To compare the magnitude of the effects of spatial, bathymetric, and oceanographic predictors, an effect-size index was calculated for each smooth term as the range of the estimated partial effect, defined as the difference between the maximum and minimum fitted values of the corresponding smooth function. Partial-effect panels were ordered according to decreasing effect magnitude to facilitate comparison among predictors. This index was used as a descriptive measure of the amplitude of each fitted effect and should not be interpreted as an independent test of statistical significance, because it may be influenced by the observed range of each covariate, the distribution of sampling points, and uncertainty in poorly sampled regions of the predictor space.

Random Forest modelling

The two recruitment responses were also analysed using Random Forest models implemented with the `randomForestSRC` R package (Ishwaran and Kogalur 2024, 2007). A classification Random Forest was fitted to the binary recruitment record to estimate the probability of recruitment occurrence, whereas a regression Random Forest was fitted to recruit density to estimate variation in tons per square kilometre. Using both model types allowed the analysis to distinguish between factors associated with the occurrence of recruitment and factors associated with the magnitude of recruitment where density was evaluated.

Both Random Forest analyses used the same predictor set considered in the GAMs: latitude, longitude, sampling year, local bathymetric depth, zonal and meridional current velocity, sea-water salinity, chlorophyll-*a* concentration, and current speed for the one-year lag. Missing predictor values were handled internally by imputation during model fitting. For each Random Forest, the number of candidate variables evaluated at each split and the minimum terminal-node size were optimized using the tuning procedure available for the algorithm before fitting the final model.

Model performance was evaluated using out-of-bag predictions, which provide an internal validation because each prediction is obtained from trees that were not fitted using the corresponding observation. For the classification model, performance was summarized by comparing observed recruitment occurrence with the predicted classes and associated probabilities. For the regression model, performance was evaluated by comparing observed and predicted recruit densities. Variable importance was estimated from each fitted Random Forest and used to rank the relative contribution of the predictors. Partial dependence curves were then calculated for the most relevant predictors to describe their marginal association with either the predicted probability of recruitment or the predicted recruit density while averaging over the remaining variables.

Model interpretation

The GAM and Random Forest analyses were used as exploratory and predictive tools. GAMs provide interpretable smooth effects for individual predictors, whereas Random Forests can represent nonlinear relationships and interactions among predictors. Together, these approaches are useful for detecting environmental associations that may not be well captured by simple linear models. However, smooth terms, variable importance, and partial dependence plots were interpreted as descriptive evidence of association rather than direct evidence of causality. The one-year-lagged design provides a biologically meaningful temporal ordering, but causal interpretation would require additional assumptions about larval supply, larval transport, settlement, post-settlement mortality, survey catchability, and the spatial sampling design.

Reproducibility

All analyses were conducted in R (R Core Team 2025). NetCDF processing and raster extraction used the package `terra` (Hijmans 2025); survey and spatial operations used `sf` (Pebesma 2018), `dplyr` (Wickham et al. 2023), and `openxlsx` (Schauberger and Walker 2025); visualization used `ggplot2` (Wickham 2016), `rnaturalearth` (South and Massicotte 2025), `viridis` (Garnier et al. 2024), and `patchwork` (Pedersen 2024); generalized additive models were fitted using `mgcv` (Wood 2017); and Random Forest models were fitted using `randomForestSRC` (Ishwaran and Kogalur 2024, 2007). The workflow was organized into scripts for: (i) reading and checking Copernicus NetCDF products; (ii) calculating September–December seasonal means by year and depth; (iii) extracting one-year-lagged oceanographic predictors at recruitment survey locations using a bathymetry-based depth rule; (iv) deriving current speed from `uo` and `vo`; (v) producing illustrative oceanographic maps; and (vi) fitting and interpreting generalized additive and Random Forest models for both recruitment occurrence and recruit density.

RESULTS

The models provided complementary descriptions of Patagonian scallop recruitment depending on whether recruitment was analysed as a continuous density response or as a binary occurrence response. In general, Random Forest models showed a stronger ability to reproduce the observed patterns than the generalized additive models (GAMs), whereas the GAMs provided smoother and more interpretable marginal effects. Across model types, spatial predictors (Longitude and Latitude of survey tows) were consistently important, but their relative contribution differed depending on whether the response variable represented the occurrence of recruitment or the magnitude of recruit density.

For recruit density, the Random Forest regression showed a very close agreement between observed and predicted values (Fig. 2A). Predicted densities followed the one-to-one relationship across the full observed range, including the highest recruit-density values. The coefficient of determination was very high for both the apparent fit ($R^2 = 0.996$) and the out-of-bag predictions ($R^2_{\text{OOB}} = 0.992$), indicating that the model retained high predictive performance under the internal validation used by the Random Forest. This contrasted strongly with the continuous-response GAM, which showed a much weaker fit (Fig. 3A). In that model, predicted values were compressed into a relatively narrow range, high observed recruit densities were strongly underestimated, and the overall coefficient of determination was low ($R^2 = 0.086$). Thus, the continuous GAM captured only broad average tendencies, whereas the Random Forest regression reproduced much more of the observed heterogeneity in recruit density.

The ranking of predictors in the Random Forest regression indicated that salinity was the most important variable for explaining recruit density, followed by longitude, latitude, year, chlorophyll-*a*, current speed, zonal current velocity, meridional current velocity, and bathymetric depth (Fig. 2B). The corresponding partial responses showed marked non-linearities (Fig. 2C). Predicted recruit density remained relatively low and stable across most of the salinity range but increased sharply at the highest salinities, above approximately 34 PSU. Spatial effects were also evident: predicted density increased toward the northern part of the study region and showed a strong longitudinal gradient, with a minimum at intermediate longitudes and higher predicted values toward the western sector. The year effect suggested temporal variability, with higher predicted densities in the early 2000s and again around 2020, and lower predicted values around the late 2000s and at the end of the series. Chlorophyll-*a* showed a weak positive tendency after low concentrations, whereas the current-related variables and bathymetry displayed threshold-like responses rather than simple monotonic effects.

The continuous-response GAM also identified spatial structure as a dominant component, but the ordering and shape of the effects differed from the Random Forest regression (Fig. 3B). Latitude and longitude showed the largest smooth effects, followed by current speed and meridional current velocity. The latitude effect increased strongly across the sampled domain, whereas the longitude effect decreased toward the eastern part of the region. Current speed showed a generally negative effect, while meridional current velocity showed a positive tendency. Salinity, zonal current velocity, bathymetric depth, chlorophyll-*a*, and year had weaker or more uncertain effects. This indicates that, when constrained to additive smooth terms, the GAM emphasized broad spatial and current-related gradients but did not capture the strong threshold-like salinity response and high-density observations represented by the Random Forest regression.

For the binary recruitment response, the Random Forest classification model showed an almost perfect out-of-bag classification of recruitment occurrence (Fig. 4A). Most observations with recorded recruitment were classified as recruitment, and most observations without recorded recruitment were classified as no

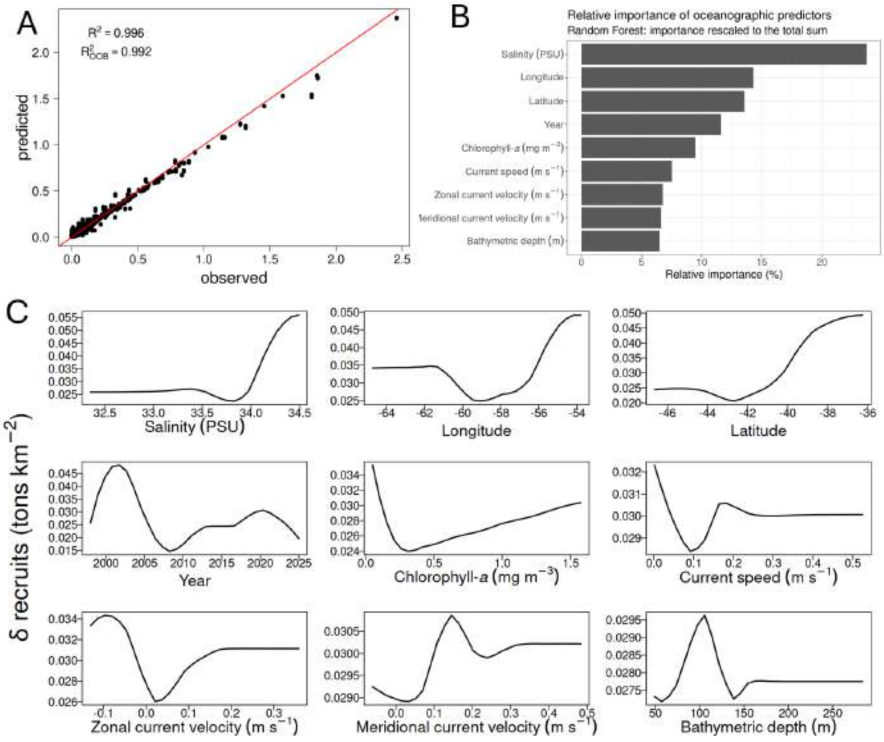

Figure 2: Random Forest regression model for recruit density and the contribution of oceanographic predictors. (A) Relationship between observed recruitment data and recruit density estimated by the Random Forest model. (B) Relative importance of the oceanographic variables included as predictors in the model. (C) Partial responses of the oceanographic variables, shown in order of importance, illustrating the marginal effect of each predictor on predicted recruit density while averaging over the remaining variables.

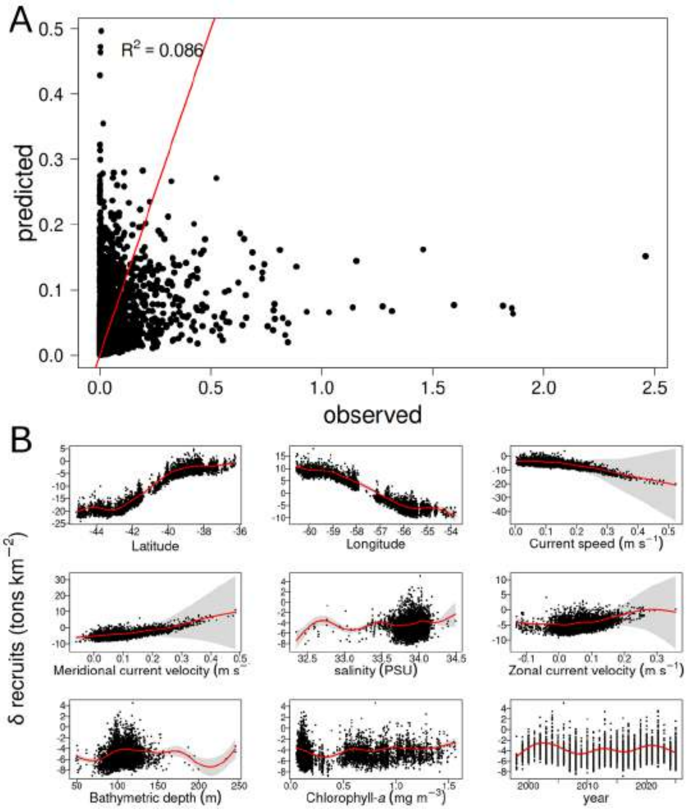

Figure 3: Generalized additive model for recruit density. (A) Relationship between observed recruitment data and values fitted by the additive model. (B) Partial effects of the covariates included in the model, shown in order of importance according to the magnitude of their estimated effects. The curves summarize the marginal response of recruit density to each predictor while holding the remaining covariates constant.

recruitment. The confusion matrix showed only 5 recruitment observations classified as no recruitment and 12 no-recruitment observations classified as recruitment, whereas 22 122 recruitment observations and 6 822 no-recruitment observations were correctly classified. This indicates that the classification Random Forest separated the two observed recruitment states much more clearly than the binomial GAM.

The variable-importance ranking for the classification Random Forest differed from the ranking obtained for recruit density (Fig. 4B). Year was the most important predictor of recruitment occurrence, followed by latitude, bathymetric depth, longitude, and salinity. Chlorophyll-*a* and the current variables contributed less to classification performance. This contrasts with the Random Forest regression, where salinity was the dominant predictor and bathymetric depth was the least important variable. The difference suggests that the environmental and spatial conditions associated with the occurrence of recruitment were not identical to those associated with variation in recruit density once recruits were present.

Partial responses from the classification Random Forest showed that recruitment probability varied non-linearly along temporal, spatial, bathymetric, and oceanographic gradients (Fig. 4C). Recruitment probability was highest in particular years and declined in the most recent part of the series. Spatially, the model indicated strong variation with both latitude and longitude, including a reduction in predicted recruitment probability in part of the central-to-eastern domain. Bathymetry showed a pronounced effect, with lower predicted probabilities around intermediate depths and higher probabilities at shallower and deeper portions of the sampled range. Salinity, chlorophyll-*a*, and current variables showed more moderate but still non-linear responses, including local minima or plateaus rather than simple linear trends.

The binomial GAM showed a weaker classification performance than the Random Forest classification model (Fig. 5A). Among observations with recorded recruitment, 13 945 were classified as recruitment and 8 146 were classified as no recruitment. Among observations without recorded recruitment, 5 372 were classified as no recruitment and 1 462 were classified as recruitment. Thus, the binomial GAM retained useful discriminatory capacity, particularly for identifying observations without recruitment, but it misclassified a substantial fraction of recruitment observations. Compared with the Random Forest classification model, the binomial GAM provided a smoother and more conservative separation between recruitment states.

Despite its lower classification performance, the binomial GAM highlighted several strong marginal effects on recruitment probability (Fig. 5B). Latitude produced a sharp transition from low to high probability of recruitment, indicating a strong spatial threshold. Longitude also showed a strong effect, with high probabilities over part of the western-to-central range and a marked decline toward the eastern end of the sampled domain. Salinity was associated with high recruitment probability over much of the observed range, but the probability decreased strongly at the highest salinities. Zonal current velocity, bathymetric depth, year, meridional current velocity, current speed, and chlorophyll-*a* showed additional non-linear effects of smaller or more localized magnitude. The colours of the points indicate that observed recruitment and no-recruitment records overlapped across much of the predictor space, which helps explain the lower classification performance of the binomial GAM relative to the Random Forest.

When the Random Forest was evaluated with leave-one-year-out cross-validation, predictive performance decreased sharply relative to the model fitted with all observations (Fig. 6); the same was observed for the gam regression model (data not shown here). The R^2 values obtained after excluding complete survey years were consistently far below the full-data R^2, and remained low across the whole time series, with only moderate increases in a few years. The annual pattern in cross-validated R^2 did not match the temporal variation in recruit density: years with higher recruitment intensity were not associated with systematically higher or lower predictive performance. Thus, the ability of the Random Forest to reproduce recruit density within the full data set did not translate into reliable prediction of entire years left out from model fitting.

DISCUSSION

This assessment should be interpreted as a first step toward evaluating the potential environmental forcings of Patagonian scallop recruitment. By linking recruitment records with gridded oceanographic fields, the analysis provides an initial description of the spatial and environmental conditions associated with recruitment occurrence and recruit density. However, the relationships identified here should not be viewed as direct evidence of causality. Instead, they define a set of candidate variables, regions, and temporal windows that can guide future analyses based on more detailed environmental information and more explicit representations of larval transport.

Future work incorporating finer-resolution oceanographic products, improved descriptions of spawning and larval development, and the modelling of virtual-particle trajectories could provide a closer approximation to the mechanisms that connect environmental forcing with observed recruitment. Such approaches would be particularly valuable because the environmental conditions that affect recruitment in one scallop bed may originate in, or be mediated by, processes occurring in another region. For example, hydrographic conditions, currents, retention zones, or frontal dynamics upstream of a sampled bed may influence larval survival, transport, and settlement elsewhere. Therefore, the spatial associations detected in this study should be considered hypotheses about regional connectivity and cross-regional forcing, rather than only local relationships between recruitment and the environmental conditions measured at the sampling position.

This interpretation is consistent with the broader scallop-recruitment literature, which emphasizes that recruitment is produced by the combined outcome of larval development, planktonic transport, settlement, early post-settlement survival, and the spatial structure of adult aggregations. In scallops, larval development rate and the duration of the planktotrophic phase are strongly conditioned by temperature, while larval performance and settlement success also depend on salinity, food availability, and the physical pathways that determine dispersal or retention (Cragg 2016). At the population scale, scallop beds tend to be spatially aggregated, and their local persistence is shaped by depth, substrate, currents, food supply, salinity, turbidity, and the degree to which different grounds are self-sustaining or connected through larval exchange (Brand 2016). Therefore, the strong effects of latitude, longitude, salinity, and currents observed here are consistent with the view that scallop recruitment is not governed by a single local variable, but by the interaction between larval ecology and spatially structured hydrographic connectivity (Orensanz et al. 2016).

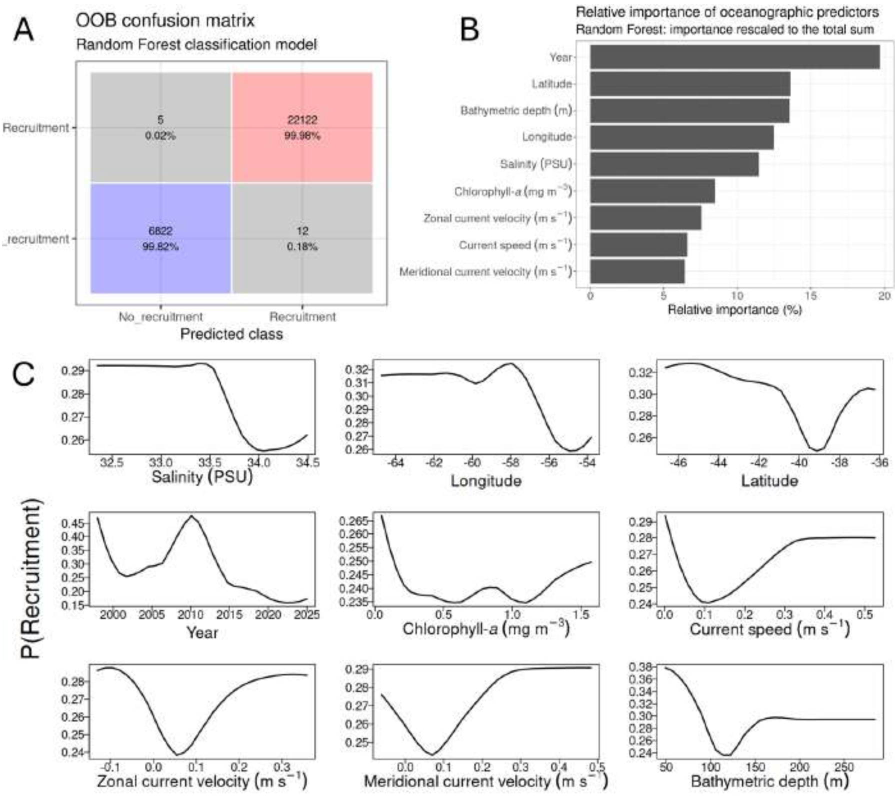

Figure 4: Random Forest classification model for estimating the probability of recruitment in the Patagonian scallop. (A) Confusion matrix of the Random Forest model used to classify recruitment occurrence. (B) Relative importance of the oceanographic variables included as predictors in the Random Forest model. (C) Partial responses of the oceanographic variables, shown in order of importance, illustrating the marginal effect of each predictor on the predicted probability of recruitment while averaging over the remaining variables.

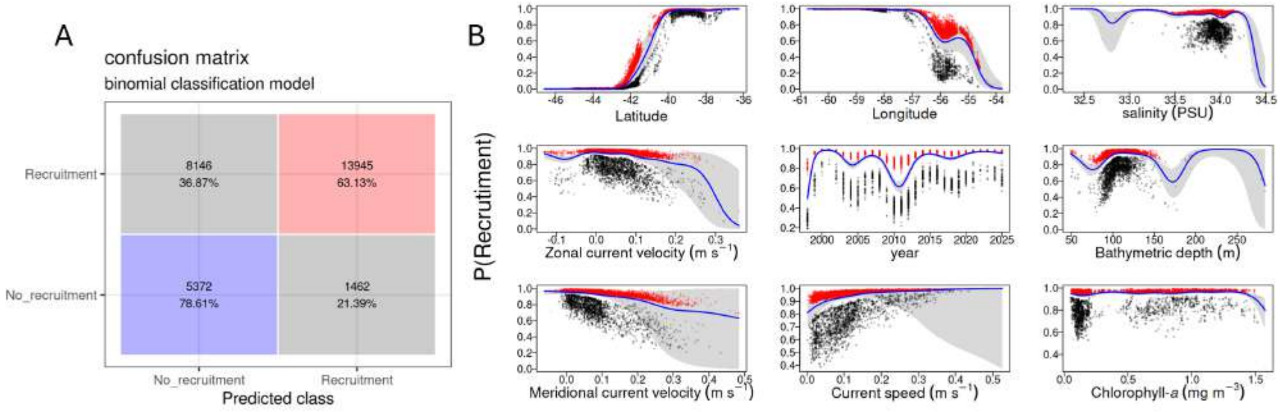

Figure 5: Binomial generalized additive model for the occurrence of Patagonian scallop recruitment. (A) Confusion matrix for the classification of observed recruitment records. (B) Partial responses of the predictors on the estimated probability of recruitment, shown in order of importance according to the magnitude of their effects. The curves summarize the marginal response of recruitment probability to each predictor while holding the remaining covariates constant. Points indicate the observed recruitment state at each sampling instance: red points correspond to observations where recruitment was recorded, whereas black points correspond to observations where recruitment was not recorded.

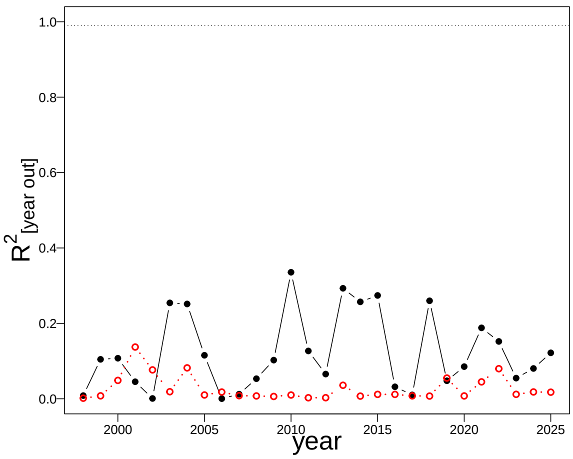

Figure 6: Variation in the cross-validated predictive performance of the Random Forest regression model for recruit density, estimated by leaving out each year and predicting it with the model. The upper dashed line represents the R^2 obtained using all data, whereas the red line and open symbols indicate recruit density in tons per km^2. No correlation is observed between the R^2 values and recruitment intensity.

Taken together, the four model–response combinations indicate that recruitment occurrence and recruit density were structured by related but not identical predictor sets. Spatial position was important in all approaches, confirming a strong geographic component to recruitment variability. Salinity was particularly important for explaining the magnitude of recruit density in the Random Forest regression and also influenced recruitment probability in the binomial GAM, but it was less dominant in the Random Forest classification model. Bathymetric depth contributed more strongly to the binary occurrence models than to the density regression, suggesting that depth may help discriminate whether recruitment occurs but may be less informative about the magnitude of recruitment. Year was especially important in the Random Forest classification model, indicating that temporal variation was more relevant for classifying recruitment occurrence than for explaining continuous density in the GAM. Chlorophyll-*a* and current-related variables contributed to all models, but their effects were generally secondary and strongly non-linear.

The strong salinity effect, together with the temperature-related interpretation developed in previous work, can be viewed as an indirect expression of shifts in the Subantarctic Front rather than as the effect of salinity alone. In the shelf-break region, changes in the position of the SAF should be reflected in the local water-mass structure, including salinity, temperature, and current fields. Thus, the increase in predicted recruit density at the highest salinities is consistent with the idea that favourable recruitment years may correspond to frontal configurations that increase larval retention or delay offshore export. This interpretation agrees with Torres Alberto et al. (2025), who found higher Patagonian scallop recruitment when the SAF was displaced northwards and linked this pattern to bottom temperature and the Brazil–Malvinas Confluence dynamics. The present results therefore support the same general mechanism, but describe it through local gridded environmental variables rather than through a single frontal-position index.

The partial effects of latitude and longitude add a spatial component to this interpretation. Across the models, recruitment occurrence and recruit density were not distributed uniformly along the shelf-break system; instead, the highest probabilities and predicted densities were associated with scallop beds located toward the northern and western portion of the sampled domain influenced by the SAF. This pattern suggests that geographic position may summarize persistent differences in exposure to frontal waters, retention zones, and advective pathways. In this sense, latitude and longitude should not be interpreted only as spatial coordinates, but also as proxies for the position of each scallop bed relative to the hydrographic structure of the shelf break and to the regional circulation associated with the SAF.

The greater frequency and intensity of recruitment in scallop beds located farther north and west of the SAF is consistent with the mechanism proposed by Torres Alberto et al. (2025). If a northward displacement of the SAF increases the time available for larvae to develop before export from the shelf, then beds situated in sectors where frontal displacement favours retention or delayed offshore transport would be expected to show both more frequent recruitment and higher recruit densities. The spatial partial effects therefore reinforce the interpretation that recruitment variability is linked not only to local salinity, temperature, or current values, but also to the relative position of each scallop bed within a dynamic frontal-connectivity system.

The same spatial signal should also be interpreted in light of previous information on benthic settlement habitat. Studies of primary settlement indicate that recently settled *Z. patagonica* spat are associated mainly with filamentous hydroids, particularly *Symplectoscyphus subdichotomus*, and secondarily with adult scallops or their epibionts (Bremec et al. 2008). As a background interpretation, this implies that favourable oceanographic conditions may increase larval supply or retention, but measurable recruitment should occur only where larvae also encounter suitable settlement surfaces and where post-settlement losses caused by predation, sedimentation, or disturbance remain low. Therefore, the gridded predictors analysed here should be viewed as describing broad environmental and transport-related suitability, whereas part of the unexplained variation may reflect fine-scale benthic structure not represented in the models.

One notable outcome of the analysis was that chlorophyll-*a* did not emerge as a determining variable in the partial effects of most model evaluations. Although chlorophyll-*a* is commonly interpreted as a proxy for phytoplankton biomass and potential food availability, its weak or secondary effect in these models suggests that the relationship between phytoplankton biomass and scallop recruitment is not expressed as a simple local or immediate association. This is especially relevant because chlorophyll-*a* can influence recruitment only after being translated into food availability, larval condition, settlement success, or early post-settlement survival.

Chlorophyll-*a* variability may therefore affect recruitment only after additional biological and physical transformations. Part of the phytoplankton signal may be transferred through zooplankton production, faecal pellets, sinking organic particles, and later detrital pathways before becoming relevant to larvae, post-larvae, or recently settled scallops. These trophic conversions may also introduce temporal lags, so that chlorophyll-*a* anomalies in one season could be reflected in food availability, larval condition, settlement success, or recruit survival during the following year or even later. At the same time, advection and particle sinking may displace this signal horizontally, meaning that the region where chlorophyll-*a* is produced may not coincide with the region where its trophic consequences influence recruitment.

This unknown spatial displacement makes the chlorophyll-*a* pathway difficult to represent with the point-based matching strategy used in this assessment. Nevertheless, it may also be one of the most promising directions for future work. Coupling chlorophyll-*a* fields with zooplankton dynamics, sinking-particle or detritus pathways, and virtual-particle trajectories could help evaluate whether productivity in one region contributes to recruitment variability in another. Although such a framework would be more complex than the present exploratory models, it could provide fruitful insights into delayed and spatially displaced food-web mechanisms underlying interannual variation in Patagonian scallop recruitment.

Overall, Random Forests provided the strongest predictive performance for both response types, especially for recruit density, where the regression Random Forest reproduced the observed values much more accurately than the Gamma GAM. The GAMs, in contrast, emphasized broad additive gradients and made the direction of individual smooth effects easier to interpret, but they were less able to reproduce extreme values or sharp multivariate thresholds. The comparison between binary and continuous analyses therefore suggests that different mechanisms or predictor combinations may control the occurrence of recruitment and the subsequent density of recruits, and that flexible machine-learning models captured these complex associations more effectively than additive smooth models.

However, when predictive performance was evaluated under a stricter temporal cross-validation scheme, the apparent predictive advantage of the models was not retained. In this validation, all observations from a complete survey year were excluded from model fitting, the models were trained with the remaining years, and recruit density was then predicted for the year held out from the analysis. Under this leave-one-year-out approach, predictive performance was very poor for both the Random Forest regression and the Gamma GAM, indicating that neither modelling framework was able to reliably anticipate recruit density for an unsampled year.

This result indicates that the high out-of-bag performance of the Random Forest should not be interpreted as evidence of strong forecasting ability. The good internal fit most likely reflects the incorporation of a strong spatial signal in recruitment, because out-of-bag predictions still draw on trees trained within the same temporal domain and nearby regions of the predictor space. Predicting an entire year left out of model fitting requires temporal extrapolation, and both Random Forest and GAM models showed limited ability to do so. Thus, the models are useful for describing spatial and environmental associations within the observed data set, but their capacity for true prospective prediction of future recruitment remains weak.

These results connect naturally with the complementary genetic-connectivity assessment of the Patagonian scallop (Kittlein and Austrich 2025). Genetic connectivity provides empirical evidence of realized biological exchange among scallop beds, whereas the present analysis identifies the oceanographic and environmental conditions associated with recruitment variability. Future work should integrate both sources of evidence with virtual-particle trajectory models and the gridded predictors evaluated here, testing whether genetically connected regions are also linked by plausible larval transport pathways and whether particular circulation regimes, frontal positions, salinity structures, current fields, or productivity patterns coincide with stronger or weaker recruitment. Such an integrated framework would move the analysis from local predictor–recruitment associations toward a regional connectivity perspective, improving the interpretation of recruitment fluctuations, the identification of source and sink areas, and management strategies that consider not only individual scallop beds but also the oceanographic links among them.

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