



The biophysical dynamics of giant kelp, *Macrocystis pyrifera*: Seasonal patterns and dispersal mechanisms in the southeast Pacific

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Abstract

Aim: Dispersal and connectivity play important roles in shaping the population structure of giant kelp, *Macrocystis pyrifera*, across the western coast of South America. Its high potential dispersal capacity suggests the existence of metapopulations, where discrete habitat patches or groups of patches form subpopulations that interact at some level. However, the dispersal patterns of giant kelp in this region have not been quantified. This study assesses the dispersal and settlement of *Macrocystis pyrifera* in the southeast Pacific, specifically focusing on the impact of environmental variables and ocean currents within the Humboldt Current System.

Location: Southeast Pacific (coast of Chile and Peru).

Time Period: 1997–2008.

Major Taxa Studied: *Macrocystis pyrifera* (giant kelp).

Methods: Using a combination of hydrodynamic and individual-based models, we analysed kelp fragment movements over 12 years, with a particular emphasis on the effects of the El Niño–Southern Oscillation (ENSO) and seasonal changes.

Results: Our results highlight a key settlement area in the southern Chilean region. We found that shorter travel distances of kelp fragments increased the likelihood of reaching a suitable habitat, underscoring the importance of local environmental conditions. We delineated intricate northward dispersal paths for kelp fragments, which appear to be governed by the interplay of wind and ocean current dynamics. Seasonal variations, notably in autumn and winter, favour the likelihood of reaching a settlement area due to favourable winds. Furthermore, ENSO events appear to influence dispersal distances, with fragments travelling the longest distances during El Niño phases.

Main Conclusion: These findings are essential for informing kelp conservation strategies in the context of climate change, emphasizing the necessity of considering local and seasonal environmental factors alongside ENSO impacts.

A. Grech and A. Ospina-Alvarez should be considered joint senior author.

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KEYWORDS

biophysical modelling, dispersal, ENSO (El Niño–Southern Oscillation), Humboldt Current System, individual-based modelling, kelp, *Macrocystis pyrifera*

1 | INTRODUCTION

The effective dispersal and connectivity of coastal and marine organisms are critical for the resilience of marine ecosystems in the face of environmental changes and in sustaining their ecological functions. Dispersal (the movement of organisms or their propagules from their natal place to a new location) and connectivity (the process linking separate populations through dispersal; Balbar & Metaxas, 2019), play essential roles in maintaining genetic diversity and ecological stability (Balbar & Metaxas, 2019; Cowen et al., 2007; Steinberg et al., 2016). Marine currents, including oceanic, coastal and tidal, are vital in driving this dispersal, particularly during the first stage of life (e.g., spores, seeds, fruits, eggs, larvae, etc.) as they enable these entities to travel passively with the prevailing currents. For some sessile species, early-stage drift represents the only mechanism of dispersal. The identification of dispersal pathways is critical when managing marine species with a pelagic phase (Steneck et al., 2009; Van der Stocken et al., 2019) because the protection of key areas of supply and connectivity can enhance population viability (Beger et al., 2010; Pastor et al., 2023). Nevertheless, quantitative information on dispersal and connectivity is often overlooked in management plans (but see Balbar & Metaxas, 2019; Ospina-Alvarez et al., 2020; Pastor et al., 2023) due to the challenges in assessing it and the significant costs (both financial and time consuming) associated with gathering empirical data on the scale of dispersal (Magris et al., 2014).

Focusing on giant kelp, *Macrocystis pyrifera*, understanding its dispersal and connectivity is key to comprehending its population dynamics and distribution along the southeast Pacific coast (Figure 1). This brown alga is widely dispersed in temperate regions, exhibiting an antitropical distribution and can be found in both the west and east of South America, west of North America, South Atlantic, South Africa, central and southern New Zealand and South Australia. The erect plant typically grows in the subtidal zone and can reach up to 40 m in length, making it the largest algae and benthic organism in the world. *M. pyrifera* forms dense submarine kelp forests on rocky or thick sand substratum (Graham et al., 2007). The giant kelp plays a crucial ecological role along the southeast Pacific coast, serving as an ecosystem engineer species by creating extensive kelp forests that offer habitat and shelter to a myriad of marine organisms. Additionally, *M. pyrifera* holds significant economic importance, as it is used for alginate extraction and serves as a primary food source for the abalone industry (*Haliotis rufescens*; Villegas et al., 2019). Most of the seaweed extraction is carried out by small-scale fisheries, which harvest from natural kelp forests, representing a vital resource for numerous coastal communities reliant on fisheries

(Márquez Porras, 2019). For a decade, the indiscriminate extraction of kelp forests, due to the absence of regulations, led to a high level of exploitation. Despite the current implementation of marine conservation measures by Chile and Peru, such as the establishment of five marine protected areas and 799 Territorial Use Rights in Fisheries (TURF) in Chile and six MPAs in Peru aimed at promoting sustainable extraction of marine resources, the giant kelp has continued to be indiscriminately harvested, resulting in significant deterioration.

The reproductive period of the kelp varies significantly depending on environmental conditions and nutrient availability (Buschmann et al., 2006; Carney & Edwards, 2010). It has a complex life cycle with macroscopic sporophyte and microscopic gametes. Spores can move short distances by using their two flagella before settling (Kinlan et al., 2003). This mode of dispersal via flagella is considered the primary mechanism for spore dispersal (Gaylord et al., 2004). Typically, the dispersal ranges of *M. pyrifera* spores, along with those of other marine macroalgae, are confined temporally and spatially, amounting to durations of hours to days and spanning a few tens of kilometres (Gaines et al., 2007; Reed et al., 1992; Wanner et al., 2024). Nevertheless, under severe weather and oceanic conditions, the spatial extent of dispersal can dramatically increase, enabling the transport of kelp fragments that contain spores over distances surpassing 100 and even 1000 km (Gaines et al., 2007). Taking kelp fragments into consideration, *M. pyrifera* emerges as an organism with the capacity for Long Pelagic Dispersion Phases (LPDP)—extended periods of pelagic dispersal lasting beyond 4 months (Ramirez-Romero et al., 2023). With aerocysts providing buoyancy, kelp rafts and the spores contained in the sorus of the sporophytes remain afloat and are carried by currents and winds. The buoyant nature of *M. pyrifera* significantly influences its distribution, rendering it a pivotal factor in shaping the geographic range of this species. Floating fertile fragments of *M. pyrifera* can drift up to 2700 km (Bernardes-Batista et al., 2018). The detached plant survives up to 125 days, during which time the spores can remain reproductive (Hernández-Carmona et al., 2006; Hobday, 2000; Macaya et al., 2005). In the southeast Pacific region, Macaya and Zuccarello (2010) documented a notable low haplotype variability relative to other macroalgal species, suggesting a pronounced genetic connectivity within the population. Additionally, Macaya et al. (2005) recovered fertile kelp rafts, underscoring the potential role of dispersal in fostering genetic interconnectedness among individuals within the species. These findings collectively imply that dispersal mechanisms may play a pivotal role in shaping the genetic structure of the southeast Pacific population of giant kelp.

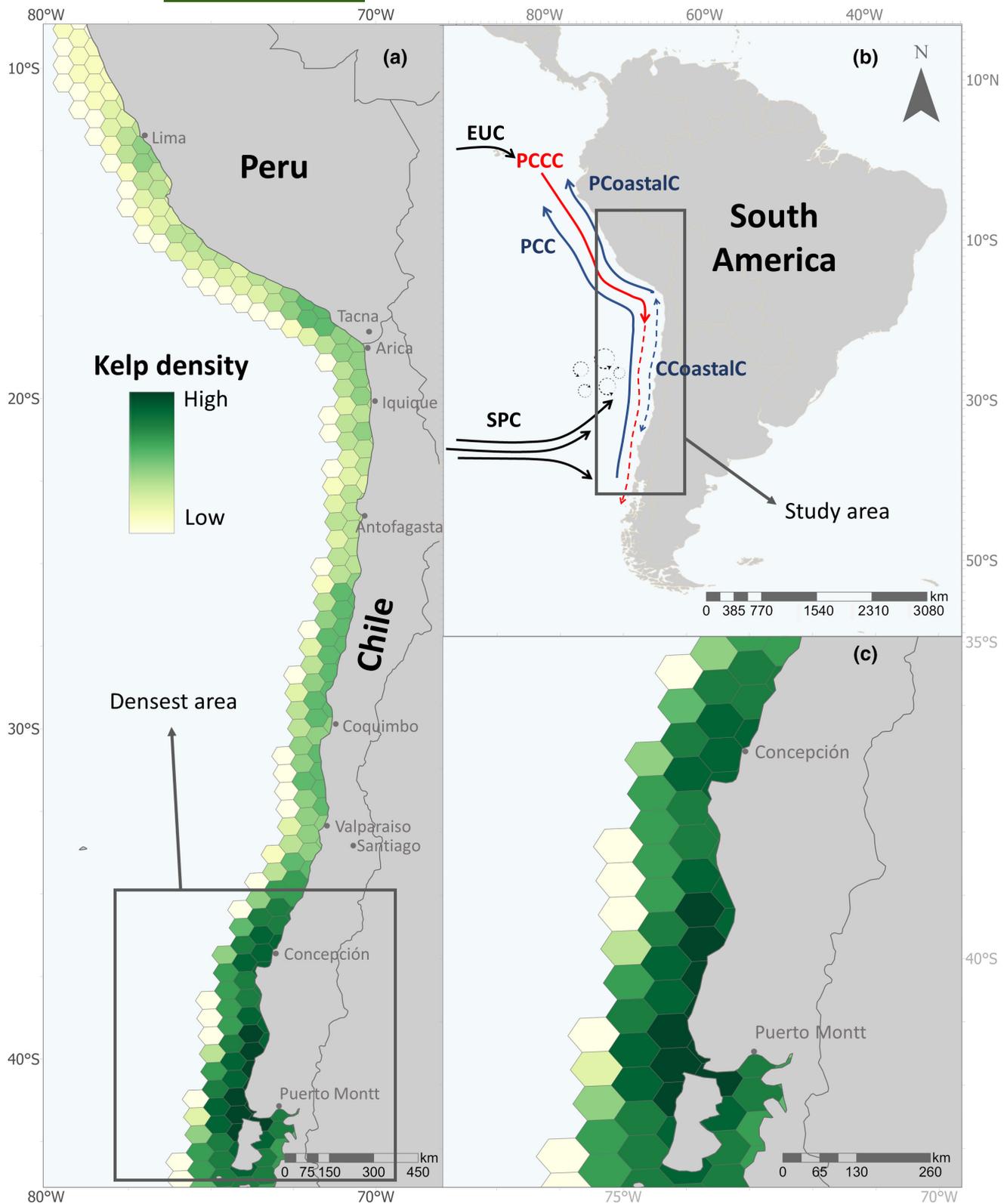


FIGURE 1 Distribution and oceanographic influences on *Macrocystis pyrifera* in the southeast Pacific. (a) Kelp density gradient along the Chilean and Peruvian coast, with darker green indicating higher density kelp forests and lighter green indicating sparser populations. The kelp inhabits primarily in the coastal areas, with lower resolution extending further into the ocean. (b) South America and the prevailing surface currents of the southeast Pacific. Red and blue arrows denote warm and cold currents, respectively, including the Chile Coastal Current (CCoastalC), Peru Coastal Current (PCoastalC), Peru-Chile Counter Current (PCCC) and Peru-Chile Current (PCC), with their origins traced back to the South Pacific Current (SPC) and Equatorial Under Current (EUC). Arrows circled in black signify regions of eddy formation. (c) The southern Chilean coast highlighting the area with the densest kelp forest populations relative to other regions. All the maps are in transverse cylindrical equal area projection.

The long-distance dispersal capacity of *M. pyrifera* suggests the existence of metapopulations, where discrete habitat patches or groups of patches form subpopulations that interact at some level (Castorani et al., 2015; Van der Stocken et al., 2019). Biophysical models have been demonstrated as a useful tool to assess the dispersal and connectivity of *M. pyrifera* in other regions. For instance, Alberto et al. (2011) used biophysical modelling in the Santa Barbara Channel to investigate *M. pyrifera* populations, revealing that ocean currents are a primary factor in explaining connectivity patterns. Similarly, Castorani et al. (2015) observed that well-connected kelp populations exhibited reduced extinction risk, highlighting the role of enhancing demographic connectivity. These studies underscore the potential utility of biophysical models in deepening our understanding of critical ecosystem processes involving giant kelp. Yet, there is a notable absence of biophysical models to elucidate the dynamics of the giant kelp in the South American region.

This study aims to evaluate the potential dispersal of *M. pyrifera* along the southeast Pacific coast using a biophysical model. Our goal is to explain the dispersion of the giant kelp along the Humboldt Current System (HCS) to improve understanding of population dynamics. To achieve this, we implemented a coupled hydrodynamic individual-based model to simulate the movement of giant kelp fragments, which release spores. We assessed factors (e.g., season and ENSO) that influence changes in the dynamics of the coastal ocean and subsequently affect the transport and dispersion of giant kelp fragments in this eastern boundary upwelling system, noted for its exceptionally high primary productivity. The output of the biophysical model was used to assess the key determinants that impact kelp dispersal distance and the likelihood of successfully reaching a suitable habitat.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area, situated in the HCS of the southeast Pacific basin (Figure 1b), spans from approximately 10° to 43°S. It encompasses the extensive coastlines of Chile (6435 km) and Peru (3080 km) which fall within the HCS. *M. pyrifera* distribution stretches along most of the Chilean coast and parts of the Peruvian coast, from 6° to 55°S. In this region, ocean temperatures near the equator (at 6°S) typically range from 19°C to 23.5°C in summer and 15.9°C to 18.2°C in winter, while further south (at 55°S), summer temperatures range from 8.5°C to 10.5°C and in winter, they drop to 5.4°C to 6.6°C. However, the optimal temperature range for *M. pyrifera*, where the majority of plants are found, generally falls between 10°C and 20°C. Two distinct ecomorphs are identified: *intergrifolia*, representing the northern population (6°–32°S), and *pyrifera*, the southern population (37°–55°S; Buschmann et al., 2004), divided by a notable upwelling area around 37°S (Aguirre et al., 2012). The distinction between the two ecomorphs lies in the morphology of

their holdfasts: while *pyrifera* is characterized by tall holdfasts, *intergrifolia* exhibits flattened ones.

2.2 | Coastal conditions

The HCS, originating from the South Pacific Current, is characterized by its cold, low-salinity, nutrient-rich waters, flowing northward along South America's western coast from southern Chile (~42°S) to northern Peru and Ecuador (~4°S). The upper ocean flow, the Peru-Chile current system (PCCS), features the equatorward movement of cooler sub-Antarctic Surface Water (SASW) north of 45°S (Chaigneau & Pizarro, 2005; Montecino & Lange, 2009). The PCCS is significantly influenced by the south-eastern Pacific atmospheric anticyclone, leading to intense upwelling and high productivity. From 1997 to 2008, the study period, El Niño and La Niña events notably affected the region's oceanography (Figure S1), impacting the strength and behaviour of the HCS and upwelling patterns. Seasonal variations, driven by the South Pacific Anticyclone, also influenced the HCS, with varying intensity and upwelling in different seasons. For a comprehensive background on the oceanographic conditions, please refer to Appendix S1.

2.3 | Kelp distribution

The kelp forest distribution map (Figure 1a) was obtained from a dataset derived from Mora-Soto et al. (2020), which used satellite imagery from Google Earth Engine. This methodology facilitated the detection of *M. pyrifera* canopies that extend to the ocean surface, as well as identifying submerged portions within open ocean waters, typically ranging from the intertidal zone down to depths of about 30–40 m. The dataset represents the mean kelp coverage from 2015 to 2019. However, it should be noted that the map also includes green algae due to limitations in their algorithm, which cannot distinguish between giant kelp and green algae (*Ulvophyceae*; Mora-Soto et al., 2020). We extracted the map distribution and further refined it in ArcGIS Pro 2.8.0. For enhanced accuracy, polygons indicating kelp presence in habitats where kelp does not grow, such as rivers or sandy beaches, were meticulously vetted and removed. Conversely, regions known for kelp harvesting yet absent in the initial dataset, particularly along the southern Peruvian coast, were added to the kelp density map to reflect actual conditions. To further evaluate the accuracy of the map, we conducted a comparison with the locations of TURFs where giant kelp harvesting is claimed. This analysis revealed a high level of accuracy in the map's depiction of kelp distribution. Subsequently, a kelp density map was generated using a grid of 321 hexagons. Each hexagon has a side length of 34 km, yielding an area of around 3000 km². This map highlights the kelp distribution along the coastline with varying densities using the kelp distribution

extracted from Mora-Soto et al. (2020). Notably, the southern regions of Chile exhibit denser kelp populations compared to other areas (Figure 1c).

2.4 | Coupled hydrodynamic-individual based model

Ocean circulation along the Peru-Chile system was modelled using a three-dimensional hydrodynamic framework based on the regional ocean modelling system (ROMS) customized for the HCS, being more suitable for this area. The ROMS configuration has a 10km horizontal resolution spanning 10°N to 50°S and 68°W to 132°W. For this study, the domain was delimited at 43°S as areas beyond this latitude require nested models due to complex hydrodynamics, particularly among the fiords. The model incorporates hydrographic forcings, such as temperature, salinity, wind stress, surface heat flux and transport and freshwater flux, along with initial and lateral boundary conditions, including temperature, salinity, currents and sea surface elevation. Bathymetric data with a 4 km resolution informed the seafloor contours of the model. Simulations spanned from 1996 to 2008, providing daily outputs, with 1996 serving as a spin-up year excluded from the analysis.

This hydrodynamic model was coupled with a customized version of Ichthyop (Lett et al., 2008), an individual-based model (IBM) tool that incorporates daily ROMS outputs to simulate the physical and biological influences on *M. pyrifera* floating fragments (Table 1). These fragments were depicted between the model as virtual particles, representing fertile kelp fragments, such as fronds with aerocystis and sporophylls and emulating their dispersal mechanism (Macaya et al., 2005). However, it is important to note that the model does not explicitly represent the physical characteristics of the kelp fragments, such as their size, morphology or arrangement of fronds

and sporophylls. Instead, the focus is on simulating the dispersal of virtual particles representing floating fragments in response to hydrodynamic forces. Each virtual particle embodying an average spore count of 11,200 spores, as this is the average number of spores per gram of sporophyll tissue per hour that kelp fragments have after detachment (Hernández-Carmona et al., 2006). In accordance with the experiments conducted by Hernández-Carmona et al. (2006), a decay rate (Equation 1) was incorporated to model the decrease in spore numbers over time.

$$N_{(t)} = 13,321.2 \times e^{-0.000509 \times t} - 2121.1 \quad (1)$$

where: $N_{(t)}$ is the number of spores at time, t (h), 13321.2 is the initial number of spores (adjusted for the decay curve), 0.000509 is the decay rate, -2121.1 is the constant to fit the curve to the data.

The virtual particles remained afloat for up to 125 days or until beaching, aligning with evidence of their reproductive capacity duration (Hernández-Carmona et al., 2006). Although exposure to water temperatures above 20°C has been linked to reduced reproductive capacity (Macaya et al., 2005; Rothäusler et al., 2009), this was not integrated into the model because most of the particles were in cooler waters. A sensitivity analysis determined that by releasing 5000 particles at 5 m depth per simulation run was effective, with releases concentrated in areas reflective of kelp density distribution (Figure 1a) and avoiding waters deeper than 500 m, given that kelp forests are typically confined to coastal regions. This choice was based on the understanding that, for the resolution of the model, a depth of 500m serves as the limit for the coastal system. The model dynamically adjusts the release of virtual particles based on local density conditions, with higher kelp densities resulting in the release of additional particles to reflect increased particle dispersal in crowded areas. While the model does not directly address the physical characteristics of the fragments, the

Category	Parameters	State/description
Particle-tracking model	Total number of particles released	5000 for each release
	Particle types/classes	Particles representing floating fronds/fragments releasing spores
Initiation of pelagic phase	Release location	Known location of <i>M. pyrifera</i> forests (Figure 1a)
	Release events coverage	From 1997 to 2008
	Frequency of release events	Once a week all year round
Transport and movement	Maximum length of pelagic phase	125 days
	Horizontal dispersion	10 m ² s ⁻¹
	Buoyancy	Positive
	Vertical migration	No
	Direct wind drift	Yes, included as forcing
Settlement	Settlement rate	Decay rate (Equation 1)

TABLE 1 Summary of the main input parameters used for the biophysical model of *M. pyrifera* in the southeast Pacific region.

incorporation of density-dependent particle release allows for a realistic representation of the dispersal dynamics observed in natural kelp populations. From 1997 to 2008, there were 10,685,141 recorded spores released.

The IBM was operational from 1997 to 2008, a period marked by significant El Niño and La Niña events, with weekly particle releases. Due to computational constraints, particle positions were evaluated on specific days post-release (1, 5, 10, 15, 20, 30, 45, 60, 90 and 125) and dispersal distances were calculated using sea distance metrics, a measurement similar to the Euclidean distance but adjusted to account for geographical features along the coastline. To report the distance travelled, we used measurements obtained on day 30, as by then nearly 90% of the spores that reached the settlement area had already done so.

2.5 | Statistical analysis

The generalized additive model (GAM) was used to evaluate the factors affecting the likelihood of a virtual particle, representing a kelp fragment releasing spores, reaching a suitable habitat (defined as within 500m of water depth). We chose the GAM to explore and visualize the complex relationships between environmental variables and particle transport rather than to test specific hypotheses or derive inferential statistics about natural phenomena. Unlike simpler methods such as ANOVA, which are critiqued by White et al. (2014) for their over-reliance on *p*-values in ecological simulation studies, GAMs allow for the modelling of nonlinearities and interactions in a flexible, non-parametric framework. This approach is particularly suited to our data, where the goal is to understand complex patterns and relationships rather than to make inferential claims based on controlled sample sizes. The dataset included all particle trajectories. The analysis was performed using the 'mgcv' package (Wood, 2017) within the R language and environment for statistical computing (R Core Team, 2019).

Different model families and configurations were tested to ascertain the optimal fit for the study's data. The 'DHARMA' package (Hartig, 2020) was used to evaluate overdispersion, selecting the family that most effectively mitigated this issue. A range of model structures was considered, from simpler forms without splines to more complex ones that incorporated multiple splines and interactions among variables. Model performance was evaluated by examining the deviance explained, checking for convergence and employing the Akaike Information Criteria (AIC) from the 'MuMIn' package (Barton & Barton, 2015).

The primary response variable 'settlement success' (the likelihood of arriving to a suitable habitat) was analysed in relation to ENSO phases (El Niño, La Niña and neutral), seasonal periods (summer, autumn, winter and spring), particle travel durations and the geographical coordinates (longitude and latitude) of particle release points. An identification variable (ID) was also included to address the potential autocorrelation in data from repeated measures of the particles' positions.

3 | RESULTS

3.1 | Settlement of kelp spores

A total of 8,158,121 spore release events took place in kelp forests between 1997 and 2008. Our findings suggest that virtual particles with shorter drift periods have a higher likelihood of releasing spores that reach settlement areas. Specifically, 45.7% of particles successfully reached settlement areas within the first 5 days, 35% within the next 20 days and the remaining 19.3% over the subsequent 100 days. Notably, 1.5% of kelp fragments reached settlement areas in the last 35 days of viability and reproductive capability. A significant northward drift was observed in 82% of cases (excluding local settlement), with a noted southward shift from approximately 37°S. The primary settlement zones were identified between 45 and 35°S in southern Chile (Figures 2 and 3), whereas the zones between 26 and 13°S exhibited the lowest kelp fragments arrival rates.

The model to assess the likelihood of reaching a settlement area operates with binary outcomes, classifying them as either 'true' (in the coastal area) or 'false' (outside of the coastal area). The analysis of this binary nature involved logistic regression within a GAM, utilizing a binomial family. This resulting model comprises a comprehensive range of explanatory variables, encompassing both linear and curvilinear relationships, as outlined in Equation 2 (Figure S3.2).

$$\text{Settlement success} = \text{gam}(\text{settle} \sim s(\text{days travelled}) + \text{ENSO} \times \text{season} + s(\text{lon}_{\text{ini}}, \text{lat}_{\text{ini}}) + s(\text{id}, \text{bs} = \text{re})) \quad (2)$$

In Equation 2, ENSO variable accounts for El Niño, La Niña and neutral conditions, while the *season* encompasses the four seasons, both treated as factorial with their interaction included due to their impact on settlement. *Days travelled* represents the time elapsed since the kelp fragment's detachment, with lon_{ini} and lat_{ini} denoting initial coordinates. These, alongside *ID* are numerical factors with non-linear relationships modelled by splines. *ID* also controls for unexplained variance between fragments. This methodological approach facilitates an in-depth evaluation of settlement likelihood factors along the coastline.

All factors, including ENSO phase, season, initial coordinates, days travelled and ID, significantly influenced settlement outcomes ($p < 0.05$). The analysis underscored that winter (79.4% of the spores reached a settlement area, $p < 0.001$) and autumn (78.6%, $p < 0.001$) exhibited the highest number of kelp fragments arriving in settlement areas, displaying significant differences (Tables S2.1 and S2.2). Conversely, the lowest kelp fragment counts in settlement areas were observed during spring (73.5%, $p < 0.001$), followed by summer (71.7%, $p < 0.001$). Regarding ENSO conditions, it was found that El Niño periods resulted in significantly higher numbers of kelp fragments reaching settlement areas (78.1%, $p < 0.001$), followed by neutral periods (76%, $p < 0.001$) and La Niña conditions exhibited the lowest (75.8%, $p < 0.001$; Tables S2.1 and S2.2). Notably, the interaction between ENSO and season demonstrated an influence on kelp fragments dispersion. The highest kelp fragments settling rate

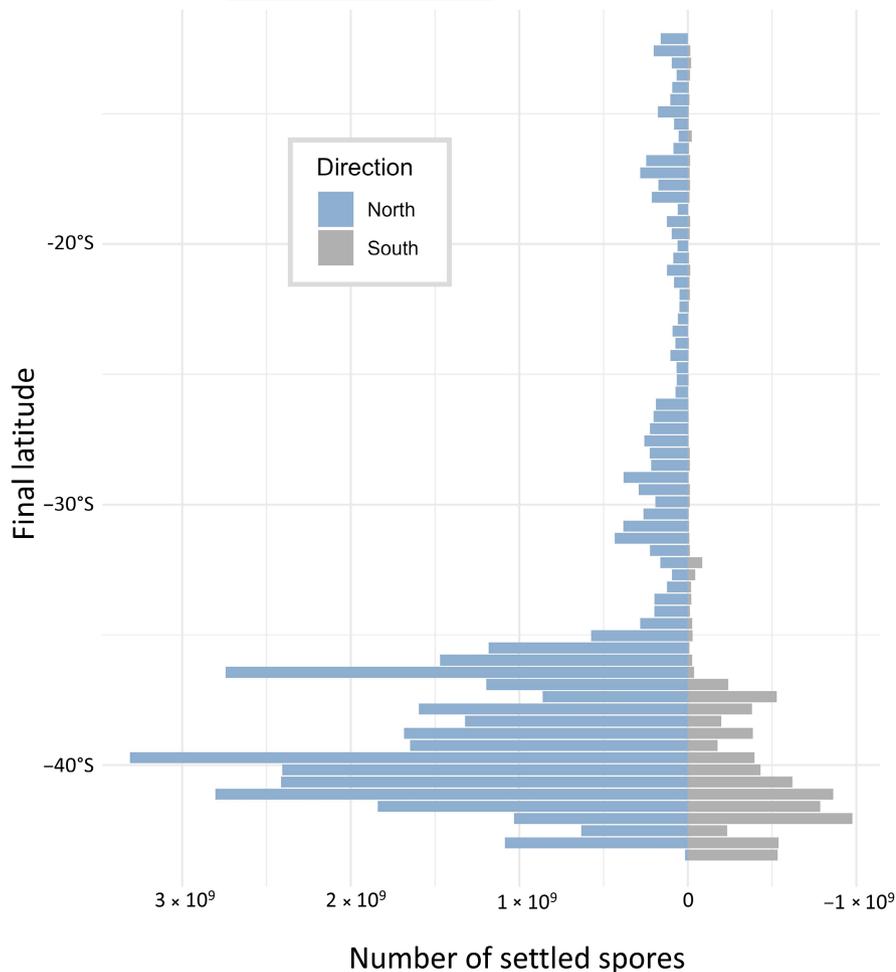


FIGURE 2 Histogram of kelp fragment spore settlement along latitudinal gradients in the Humboldt current system (1997–2008). The x-axis quantifies settled particles, scaled in billions. The y-axis represents the final latitude of kelp fragment settlement, ranging from 45°S to 10°S . Colour coding distinguishes the direction of fragment drift: Northward drift is depicted in blue, while southward drift is shown in grey.

was observed during El Niño in autumn (78.1%, $p < 0.001$) and the lowest was observed during La Niña in summer (74.1%, $p < 0.001$; Table S2.3). Summer, followed by spring was consistently the lowest through all the ENSO conditions. Autumn was higher during El Niño and La Niña, but not during neutral condition, which occurred in the winter.

3.2 | Dispersal distance

Kelp fragments displayed a median dispersal distance of 48.94 km, ranging from a minimum of less than a meter (0.8 m) to a maximum of 2051.33 km. Long-distance dispersal was uncommon, with such events classified as outliers as it can be observed in Figure 4. Furthermore, it is improbable for a kelp fragment to travel such extensive distances, as it is likely to be carried into deep water or break down into detritus before reaching thousands of kilometres. A positive relation was evident between travel duration and dispersal distance, kelp fragments averaged 18.58 km on the first day, extending up to 305.19 km by day 125. A directional bias was also observed: 52.2% of spore-releasing kelp fragments drifted northeast (Figure S4.3), and those travelling over 200 km exclusively followed this trajectory. Additionally, 25.1% moved northwest. It was noted that the further a kelp fragment travelled, the less likely it was to reach a settlement area.

The longest distances travelled by kelp fragments were recorded between 30°S and 20°S from 1997 to 2000 (Figure 5), with a noted decrease in subsequent years. Peak average distances were in 1998, 1999, 2003 and 2007 at 90.3, 90.6, 90.8 and 95.1 km, respectively. In contrast, 2001, 2006 and 2008 show the shortest distances with 45.7, 48.9 and 52.6 km, respectively (Figure S5.4; Table S5.4).

We found that ENSO phases and season at release influenced the dispersal distance of kelp fragments. With kelp fragments covering greater distances during spring (mean = 264.3, median = 256.3, SD = 155.3) followed by summer (mean = 238, median = 218.7, SD = 152.4), winter (mean = 198.3, median = 166.7, SD = 145.1) and the shortest distance during autumn (mean = 149.5, median = 121.2, SD = 119.3). El Niño recorded the longest dispersal distance (mean = 212.7, median = 183.5, SD = 151.8), followed by La Niña (mean = 198.1, median = 166.3, SD = 144.7) and neutral (mean = 182.4, median = 150.7, SD = 139.4). ENSO and season interactions also impact the distance travelled by kelp fragments, with the longest distances during neutral conditions in spring (mean = 284.9, median = 280.4, SD = 151.4). Autumn consistently displayed the shortest travel distances for kelp fragments across all ENSO conditions, while spring was associated with the longest distances during neutral and La Niña (mean = 294.1, median = 301, SD = 174.3) conditions, while during El Niño, the summer led to the longest fragments travels (mean = 294.9, median = 279.4, SD = 168.9).

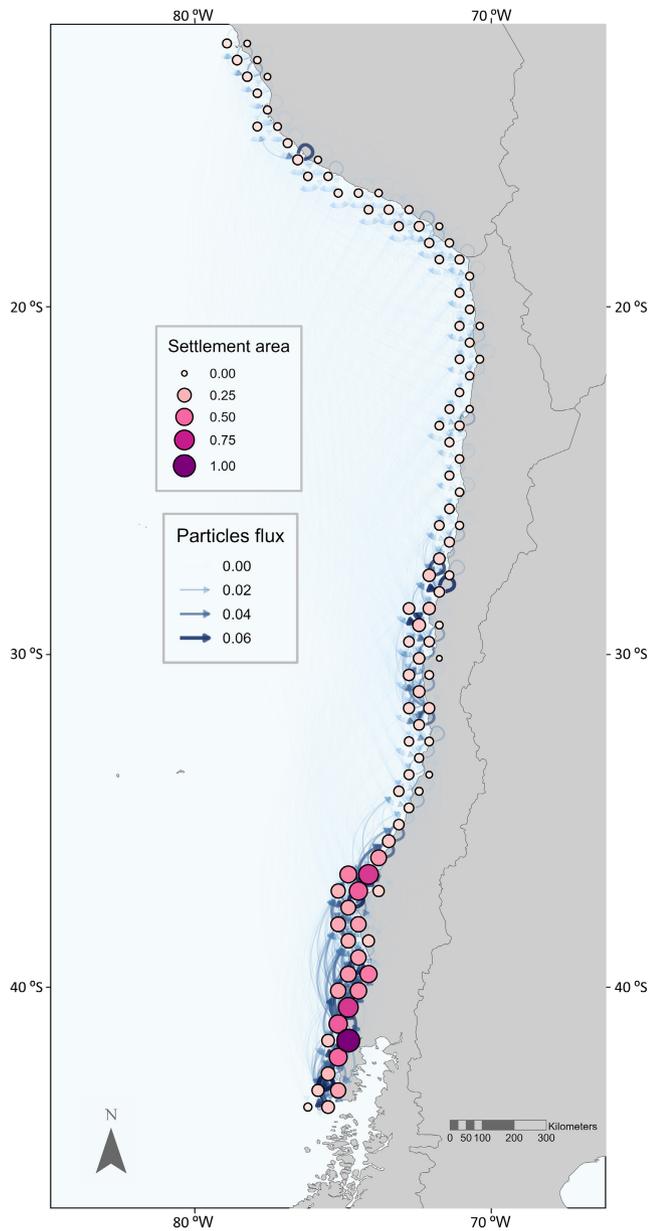


FIGURE 3 Map of kelp fragment settlement and dispersal pathways in the southeast Pacific. Circles indicate the settlement density of kelp fragments spores, which is the normalized number of spores reaching a suitable habitat, across the region, with the size and colour gradient representing the normalized concentration from low (small, light pink) to high (large, dark purple). Arrows illustrate the normalized flux of kelp fragments, with direction and thickness indicating the movement and relative quantity of fragments travelling from their release points to settlement areas. In regions of minimal flux, the arrows are nearly transparent to emphasize areas with significant flux.

4 | DISCUSSION

We assessed the complex dispersal dynamics of the giant kelp, *Macrocystis pyrifera*, along the southeast Pacific coast through a coupling of hydrodynamic and individual-based modelling. Our decadal-scale analysis highlights the influence of travel duration on the

settlement success of kelp spores, with shorter travel times increasing settlement likelihood. Moreover, our research has established a direct relationship between the length of travel and the distances covered, suggesting that while longer dispersal events are less common, they are crucial for maintaining the connectivity among kelp populations along the South American coast. Nonetheless, the rarity of long-distance dispersal underscores the importance of localized processes in the persistence of kelp populations. These insights inform the necessity for conservation and management efforts to focus on local scales, such as implementing a spatial management unit of 50km sections.

4.1 | Trajectory patterns of kelp fragments

Kelp fragments predominantly showed a northward trajectory. This trend suggests an enhanced potential for connections with northern populations, a phenomenon also noted in other marine species in this region (Blanco et al., 2019; Ospina-Alvarez et al., 2018). Prevailing wind patterns and the HCS's northward flow likely drive this dispersion pattern. Nonetheless, southward movement was recorded below approximately 36°S, aligning with the northernmost range of the giant kelp's southern populations (Buschmann et al., 2004). This geographical demarcation also corresponds with a well-documented upwelling zone near 37°S (Aguirre et al., 2012). Here, the seasonal shift of the South Pacific anticyclone disrupts the prevailing southern winds during winter, leading to the emergence of seasonal upwelling (Aguirre et al., 2012). Such conditions increase the likelihood of southward transport during winter. Additionally, ENSO may amplify this effect when the anticyclone weakens (Montecinos & Gomez, 2010). Climate change further complicates these patterns by driving the Pacific Anticyclone southward, shifting the intense upwelling zone to around 34°S in spring (Weidberg et al., 2020). Over time, this could shrink the southern giant kelp population due to reduced southward dispersal.

Our results also highlighted the spatial variability in kelp fragment dispersal. We found that most of the kelp fragments might be originated from the southern region of Chile, where the kelp is more abundant. This pattern suggests a potential source-sink dynamic, where populations in the south might act as sources that supply kelp fragments to populations in the north. However, additional analysis is required to validate and comprehensively assess this pattern. While infrequent, the occurrence of long-distance dispersal events from this southern population to the north suggests a potential role in maintaining genetic diversity and potentially facilitating recovery in the event of local disturbances (Steinberg et al., 2016). Therefore, management strategies need to also consider the protection of these source populations in the southern region. Nevertheless, it is important to note that this pattern is primarily driven by the very high kelp density in the southern area. Hence, a finer scale analysis to clearly understand the role of this area in relation to the rest of the population is needed.

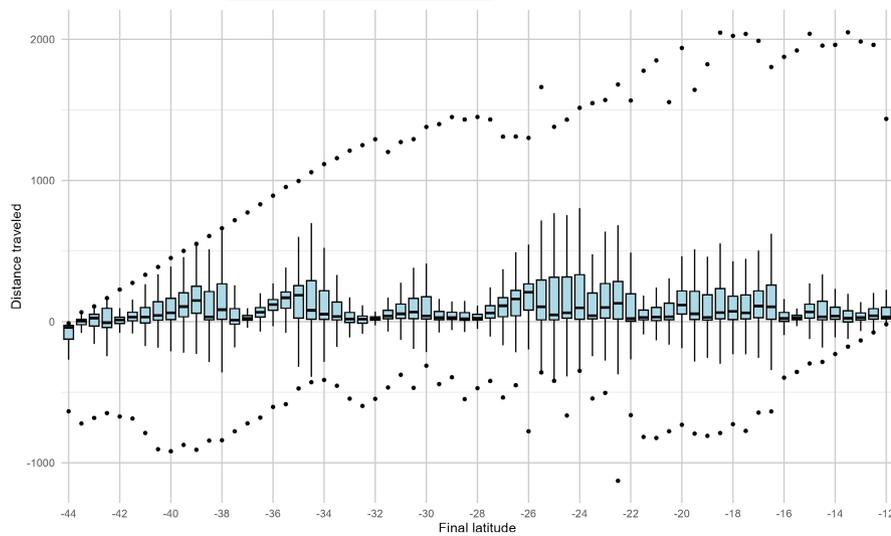


FIGURE 4 Boxplot of dispersal distances for kelp fragments by latitude: Northward versus southward settlement trajectories in the southeast Pacific (1997–2008). Positive values indicate northward travel, while negative values indicate southward travel. The black dots represent the minimum and maximum observed values (outliers).

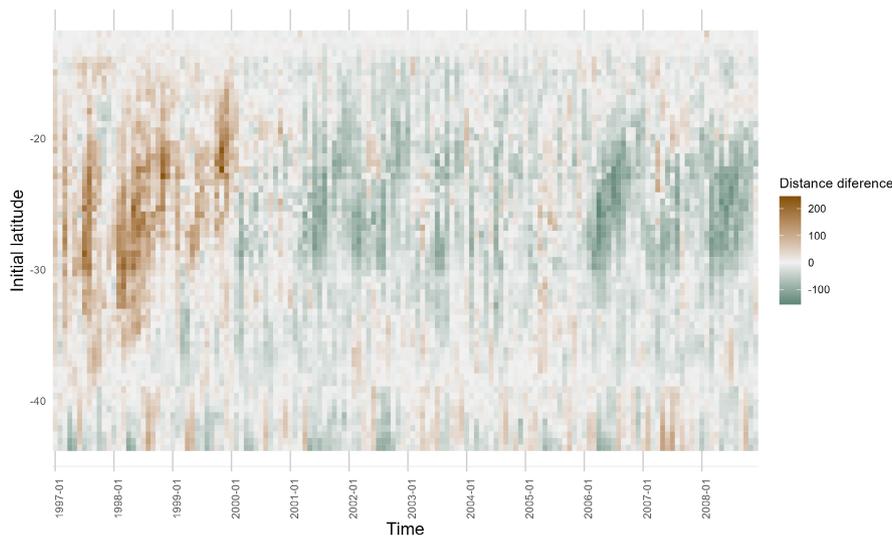


FIGURE 5 Temporal variation matrix of monthly kelp fragment dispersal distances in the southeast Pacific (1997–2008). This matrix illustrates the monthly deviations in average kelp fragment dispersal distance compared to the multi-year monthly average, highlighting increases or decreases in travel distances (km).

4.2 | Influence of seasonal changes on kelp dispersal and settlement

Our research has uncovered a significant link between seasonal changes and the dispersal and settlement patterns of kelp fragments in the southeast Pacific. While our investigation primarily focused on distinct seasonal periods, it is plausible that the transition between seasons may exhibit a more pronounced effect on these patterns. However, it is important to note that our model has not explicitly considered this transition period. We found that autumn and winter see increased settlement, coinciding with the intensification of the Westerlies and the weakening of the Pacific Anticyclone, which shifts north-westward during these seasons (Falvey & Garreaud, 2007; Montecinos et al., 2011). The dominance of westerly winds during this time propels the kelp fragments towards the land, enhancing settlement. Conversely, spring and summer bring

stronger anticyclonic conditions and weaker Westerlies, giving rise to easterly trade winds. This shift, along with stronger southern winds, triggers upwelling and escalates Ekman transport, displacing surface waters—and thus kelp fragments—westward, away from the coast (Pérez-Santos et al., 2019).

The variations in kelp fragment dispersal distances across seasons are closely linked to the intensity of the Pacific Anticyclone. Kelp fragments tend to travel greater distances during spring (256.3 km) and summer (218.7 km), a trend that lessens in autumn (121.2 km) and winter (166.7 km). This seasonal pattern reflects the meteorological changes along the coastline, heavily influenced by the Pacific Anticyclone's varying strength (Falvey & Garreaud, 2007). In the warmer months, atmospheric conditions are marked by decreased wind turbulence and heightened stability, largely due to the anticyclone's fortification. As a high-pressure system, the Pacific Anticyclone suppresses storm formation (Montecinos & Aceituno, 2003) and

strengthens southern winds, enhancing the northward movement of kelp fragments via the coastal jet (Garreaud & Falvey, 2009). This effect is augmented by surface currents responding to wind-induced stress. The interplay of these meteorological and oceanic factors might be contributing to more kelp fragments moving north without encountering significant obstacles and reaching longer distances. However, it is important to note that while kelp fragments may travel greater distances during warmer months, shorter distances still present a higher likelihood of spores reaching settlement areas. In contrast, when the Pacific Anticyclone and the southern winds weaken and the coastal weather conditions become more turbulent and the northward transport decreases, kelp fragments experienced constrained dispersal. This is largely attributable to the emergence of disruptive weather events, such as storms, which impede the fragments' progress and often cause them to accumulate in specific areas, thus limiting their capacity to travel longer distances. This contrast in dispersal dynamics across different seasons underscores the significant impact of meteorological and oceanic factors on the dispersal behaviour of kelp fragments in the southeast Pacific.

4.3 | Influence of ENSO events on kelp dispersal and settlement

We also observed a robust influence of ENSO conditions on both settlement probability and dispersal distance of kelp fragments. Notably, during El Niño conditions, there is a higher likelihood of kelp fragments arriving at settlement areas (78.1%) and longer distance travelled (183.5km), compared to La Niña conditions showing the lowest likelihood of fragments reaching settlement areas (75.8%) and shorter dispersion distance (166.3km). The differential settlement rates and distance dispersal during ENSO phases can be attributed to the intensified oceanic and atmospheric patterns (Wang et al., 2017). Specifically, La Niña conditions result in a notable intensification of the trade winds at the HCS (Alheit & Niquen, 2004; Vargas et al., 2007; Wang et al., 2017), leading to extended and more intense upwelling, especially in central and southern Chile (Montecinos & Gomez, 2010). This could result in kelp fragments being dispersed offshore, away from kelp forest areas, as well as restrict the dispersion and thus the travel distance of buoyant particles, as they are more likely to become entrapped within nearshore water masses. In contrast, El Niño weakens the trade winds, enhancing westerly winds and reducing upwelling (Tsonis et al., 2005), thereby a larger proportion of fragments might be retained in coastal areas and dispersed more extensively. Moreover, the longest dispersal distances were observed in the early years of the study, particularly during the significant El Niño event around 1998. These findings align with prior research that demonstrates that during El Niño phases, reduced coastal winds and altered ocean dynamics, including enhanced poleward undercurrents, increased eddy kinetic energy and disrupted upwelling patterns, contribute to longer-distance travel of particles along the southeast Pacific coast

(Astudillo et al., 2019; Colas et al., 2008; Conejero et al., 2020; Strub et al., 2019).

With climate change potentially intensifying and increasing the frequency of ENSO events (Cai et al., 2014, 2021; Timmermann et al., 1999), adaptive management strategies must consider these variations, such as temporary harvesting closures, which vary depending on the ENSO phenomenon and the season. El Niño conditions, characterized by warmer sea temperatures and weakened upwelling, can disrupt the reproductive patterns of *M. pyrifera*, potentially leading to altered reproductive timing or even kelp mortality (Dayton et al., 1992; Steneck et al., 2013; Tegner et al., 1997). Conversely, La Niña conditions, with cooler waters and stronger upwelling, may support kelp reproduction but also present challenges in ensuring settlement due to localized dispersion (Cai et al., 2015; Tegner et al., 1997). Understanding these effects is vital for predicting how kelp populations might respond to future climate changes along the southeast Pacific coast. Conservation efforts should be informed by these insights, with a focus on preserving genetic diversity and protecting source populations through effective local management (Balbar & Metaxas, 2019; Cowen et al., 2007; Steinberg et al., 2016), emphasizing the implementation of spatial management units spanning 50km sections. Future modelling efforts should also incorporate the interplay between kelp ecosystem conservation and human activities, thereby providing comprehensive guidance for integrative spatial management (Ospina-Alvarez et al., 2020). Additionally, the development of detailed databases that specifically map out locations and features is crucial for generating more accurate assessments of the key processes underpinning social-ecological systems in coastal regions (e.g., kelp harvesting). Such integrated approaches are essential for ensuring the sustainability of these valuable ecosystems and the communities that depend on them.

5 | CONCLUSION

This study provides valuable insights into the potential dispersal and settlement patterns of giant kelp in the southeast Pacific region. It revealed the influence of ENSO conditions and seasonal variations on dispersal distances and the probabilities of reaching a settlement area. Even though kelp fragments dispersal is not the main source of spore dispersal and there are other important factors that influence kelp dispersal, such as successful spore release, spore viability and transportation to the seafloor (Gaylord et al., 2004), these findings provide an important insight in the giant kelp dispersal dynamics and could have implications for the management and conservation of this ecologically important species. To ensure the resilience of giant kelp populations in the face of environmental changes, it is essential to prioritize the protection of nearshore areas where most of the kelp is located, consider the influence of ENSO conditions and seasonal variations and promote connectivity between populations in the southern and northern regions of the ecosystem.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest regarding the publication of this paper.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available for access through the following link: <https://doi.org/10.25903/e8x4-ag45>. Researchers interested in exploring additional details can also contact the corresponding author, Gabriela Thompson-Saud, at gabriela.thompsonsaud@my.jcu.edu.au for further information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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