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Incorporating giant kelp connectivity into management strategies in the southeast Pacific

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ABSTRACT

Intensive harvesting and climate change affect the delivery of multiple ecosystem services provided by giant kelp, *Macrocystis pyrifera,* in the Southeast Pacific region. Amid these threats, dispersal and connectivity are crucial processes that support the replenishment and recovery of giant kelp, yet they remain poorly understood. Here, we assess the connectivity of giant kelp in the Southeast Pacific to inform its conservation and management. To achieve this, we use the outputs of a biophysical model and network analysis to identify critical source and sink areas and key connectivity corridors at multiple spatial and temporal scales. We also assess the influence of seasonal and El Niño Southern Oscillation (ENSO) variability on connectivity in the region. We found that the southern population (36–43°S) is the highest priority for management (e.g. no-take zone) as it serves as a crucial source-sink area, playing a fundamental role in propagule dissemination, local retention and non-local retention. We also identified changes in the connectivity within the central population (28-35°S), influenced by both ENSO events and seasonal variability. Adaptive management strategies, including temporal harvest closures, are recommended to address both inter and intra-annual fluctuations in connectivity. Additionally, through the delineation of management units based on population connectivity, we identify key source areas within each unit that warrant protection. The outputs of our study underscore the importance of integrating connectivity and regional environmental dynamics into conservation frameworks to enhance the resilience of kelp forests in the Southeast Pacific and elsewhere.

1. Introduction

Connectivity is a fundamental process in terrestrial and marine systems that promotes the persistence and recovery of populations through dispersal (Balbar and Metaxas, 2019). It influences the resilience of individual populations to environmental disturbances and the dynamics of entire ecosystems. In the marine realm, oceanic and wind driven currents are the main agents of dispersal, especially during the early life stages of many organisms. The early pelagic stage can be the only opportunity for dispersal for some species, including marine plants. Consequently, understanding connectivity patterns of organisms is essential for effective management (Van der Stocken et al., 2019; Steneck et al., 2009; Elliott et al., 2023) and enhancement of their population viability (Beger et al., 2010).

Assessing connectivity in early life stages often involves tracking the movement and age of drifting individuals (Macaya et al., 2005; Shanks, 2009; Ospina-Álvarez et al., 2012; Catalán et al., 2013) studying larval behaviour (Paris et al., 2008; Castorani et al., 2015; Ospina-Alvarez et al., 2012, 2018) and analysing genetic markers (Hedgecock, 2017; Castorani et al., 2015; Palumbi, 2003; Weersing and Toonen, 2009). However, these methods have limitations in capturing the full species distribution and are typically short-term (Abesamis et al., 2016). To address this, indirect approaches like biophysical models have emerged, combining Individual Based Models (IBMs) with hydrodynamic models. IBMs typically advect particles, forced by flow fields from hydrodynamic models, while incorporating biological parameters of the organism (e.g.

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size, buoyancy, vertical movement, orientation, reproductive time and mortality) (Ospina-Alvarez et al., 2015; Miller, 2007; Miller et al., 2006). The hydrodynamic model typically resolves the circulation including currents, tides and winds information. These coupled biophysical models generate dispersal pathways used to compute connectivity matrices and network analysis, revealing key insights into the dynamics of habitat patches (discrete areas of suitable habitat for a species within a larger landscape), dispersal routes and overall population connectivity (Werner et al., 2007; Treml et al., 2008; Rayfield et al., 2011; Ospina-Alvarez et al., 2020; Pastor et al., 2023). While connectivity analyses using biophysical model have been performed in several species (Ospina-Alvarez et al., 2020; Abecasis et al., 2023; Treml et al., 2008; Blanco et al., 2019), there is a noticeable bias towards animals, with limited research on plants or algae (Bryan-Brown et al. (2017), but see Pastor et al. (2022, 2023), Thompson-Saud et al. (2024), Grech et al. (2018)).

Macrocystis pyrifera, commonly known as giant kelp (or "huiro negro" in Chile or "sargazo gigante" In Peru), has a keystone role along the Southeast Pacific coastline, spanning from 6°S (northern Peru) to 55°S (Patagonia, Chile), covering approximately 6600 km (Hoffmann and Santelices, 1997) (Fig. 1b). *M. pyrifera* reproduces through spores, which typically disperse over short distances using their flagella, travelling a few tens of kilometers within hours to days (Kinlan et al., 2003). However, detached kelp fragments containing viable spores can be transported over much greater distances, sometimes exceeding 100 or even 1000 km, particularly under severe weather conditions, connecting distant populations (Bernardes-Batista et al., 2018; Gaines et al., 2007). Understanding the dynamics of giant kelp ecosystems is particularly relevant in the Southeast Pacific region, where these underwater forests hold both ecological and economic significance. *M. pyrifera* serves as an ecosystem engineer, forming dense kelp forests that serve as essential habitats and shelter for many species (Graham et al., 2007; Pérez-Matus et al., 2017). Furthermore, the species holds substantial economic value, being harvested for alginate extraction and serving as a food source for the abalone industry, primarily targeting *Haliotis rufescens* (Villegas et al., 2019).

Over the past two decades, there has been a notable surge in the extraction of kelp in the Southeast Pacific, driven by the rising global demand for raw seaweed (Villegas et al., 2019; Bularz et al., 2022). Most of this seaweed collection is conducted by small-scale fisheries, collected from natural kelp forests (Porras, 2019). Most of the harvesting occurs in the northern part of the region (around 10 to 32°S), where the kelp forest is perennial (available year-round), unlike the southern population that is annual (Vásquez, 2009). The over-exploitation of the northern population has led to fragmentation and a significant decline in abundance (Buschmann et al., 2006). This increased exploitation has occurred in the absence of regulations, raising concerns about the sustainability of these ecosystems (Porras and Vásquez, 2020). Compounding these pressures, climate change poses an additional threat to kelp forests, potentially altering ocean temperatures and currents, which are crucial for kelp growth and dispersal (Smale, 2020; Beas-Luna et al., 2020). The early life stages of *M. pyrifera* are particularly vulnerable to rising ocean temperatures, with spore settlement and germling development significantly declining beyond 21.7 °C–23.8 °C (Le et al., 2022). The combined effects of over-exploitation and climate-driven changes could further degrade these ecosystems, reducing their resilience and capacity to recover. In addition to direct temperature-driven stress, climate change can also shift herbivore populations, leading to increased grazing pressure on kelp forests (Norderhaug and Christie, 2009). In areas where kelp is not harvested, widespread declines have been observed due to the combined effects of ocean warming and intensified herbivory, particularly from sea urchins and other grazers (Norderhaug and Christie, 2009; Filbee-Dexter et al., 2016). The loss of kelp in these regions highlights the broader vulnerability of these ecosystems, as over-exploitation and climate-driven changes together could further degrade their resilience and capacity to recover.

In response to these growing threats, Chile introduced legislation in 2013 governing kelp extraction along its coast. Kelp forest harvesting is now regulated through TURFs (Territorial Use Rights in Fisheries), which aim to sustainably extract and protect common resources in Chile through a co-management strategy (Albornoz and Glückler, 2020). Similarly, in Peru, giant kelp has been regulated since 2009, prohibiting the removal of kelp without the necessary permits (Avila-Peltroche and Padilla-Vallejos, 2020). This shift towards sustainable extraction represents a significant step towards curbing the indiscriminate exploitation of *M. pyrifera*. Nevertheless, a more thorough understanding of ecosystem processes is required to enhance conservation strategies across various scales. Understanding the connectivity patterns of giant kelp is crucial for spatial prioritisation in conservation and management efforts. Specifically, this knowledge enables the identification of key dispersal pathways and source populations, which are essential for designing effective TURFs. By focusing conservation and sustainable harvesting efforts on these critical areas, it is possible to maintain the ecological integrity and resilience of kelp forests to extraction and environmental changes, ensuring that these habitats continue to support biodiversity and provide economic benefits. This strategic approach aims to optimize conservation outcomes while balancing the needs of local fisheries, promoting a sustainable coexistence between resource use and ecosystem preservation.

The goal of this study is to evaluate the dispersal and connectivity of giant kelp forests in the Southeast Pacific to inform effective management strategies. We approach this by integrating the outputs of a biophysical model with network analysis and graph theory, identifying critical areas that significantly contribute to the connectivity of *M. pyrifera*. Furthermore, we examine how connectivity patterns shift under varying ENSO conditions and across different seasons, aiming to determine the key areas that sustain connectivity within giant kelp forests over time. We discuss how the insights gained from this study can be used to guide future management strategies, including the conservation and sustainable harvesting of these marine ecosystems.

2. Methods

Macrocystis pyrifera, a prominent species of brown algae, has an antitropical distribution, predominantly occurring in temperate regions. This species thrives in subtidal environments and is known for its significant growth, reaching up to 40-m height, thus categorizing it as the largest known algae and benthic organism (Almanza and Buschmann, 2013). Giant kelp forms extensive submarine kelp forests on rocky or thick sandy substrata (Graham et al., 2007). The giant kelp can be found along a significant portion of the Chilean coast and part of the Peruvian coast. Specifically, it ranges from approximately 6 to 55°S (Fig. 1). Within this range, two distinct ecomorphs can be observed: *intergrifolia*, representing the northern population (6–32°S), and *pyrifera*, representing the southern population (37–55°S) (Buschmann et al., 2004).

To study the connectivity dynamics of kelp populations in the Southeast Pacific region, connectivity matrices were computed using biophysical model outputs developed in Thompson-Saud et al. (2024), which applied a biophysical model to the region between 6 and 43°S. South of 43°S, the area around the fjords exhibits highly complex dynamics due to its intricate topography. Adequately representing these dynamics would have required the inclusion of nested models with finer resolution and technical specifications for this ecosystem, which represents a challenge for future research. Thompson-Saud et al. (2024) constructed a kelp density map based on hexagonal cells that were used to discretise the kelp distribution along coastal areas, with cell value corresponding to giant kelp density within each cell. The kelp density data, representing the average kelp coverage from 2015 to 2019, was sourced from a dataset developed by Mora-Soto et al. (2020) using satellite imagery from Google Earth Engine (Fig. 1a) (Gorelick et al., 2017). Ocean circulation was simulated using a Regional Ocean Modelling System (ROMS)-based hydrodynamic model with a 10 km

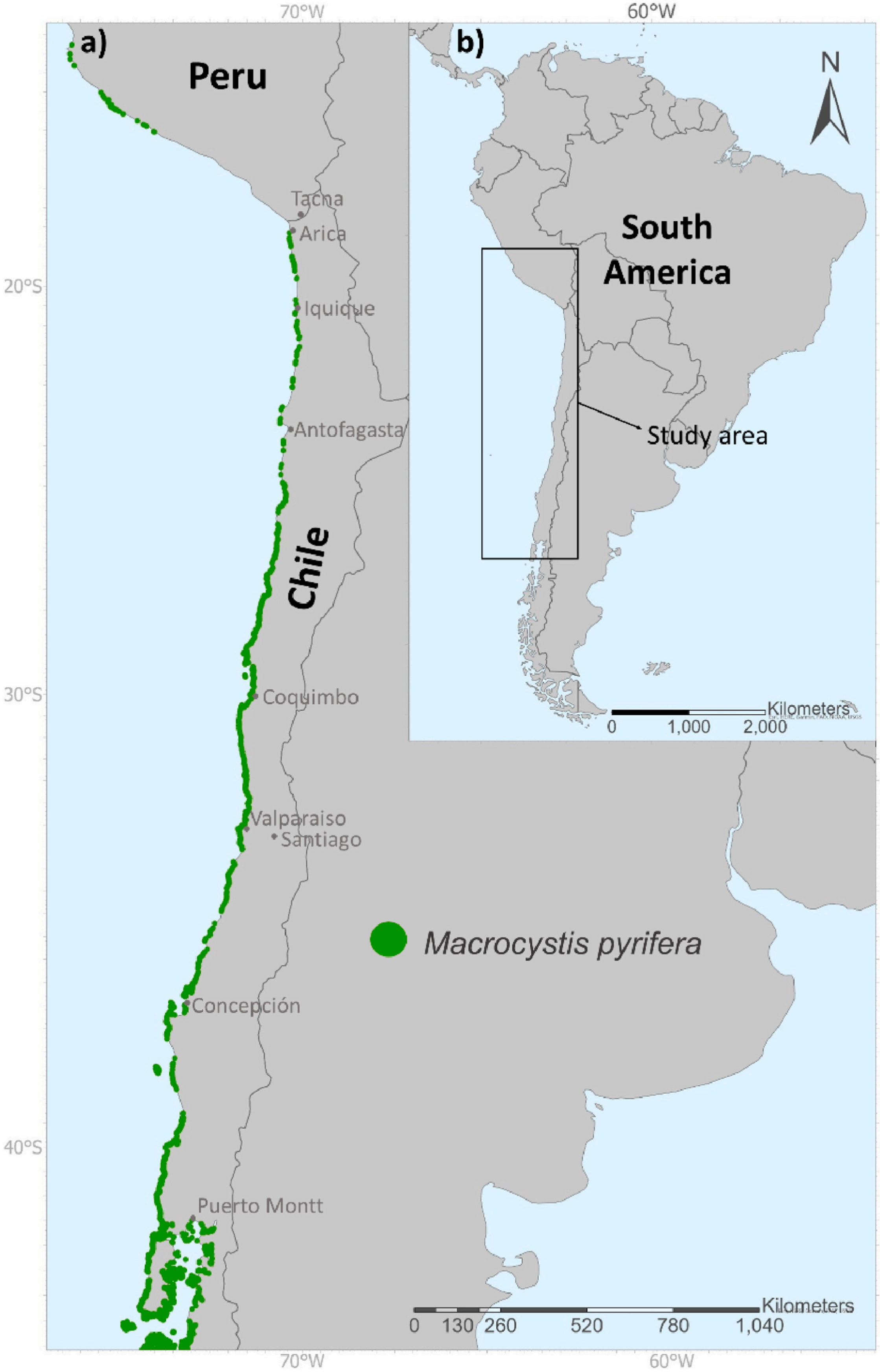

Fig. 1. Distribution of *Macrocystis pyrifera* in the Southeast Pacific. a) Kelp distribution along the Chilean and Peruvian coast. The kelp distribution was obtained from Mora-Soto et al. (2020) b) South America with the Southeast Pacific region on the left side. The maps are in Transverse Cylindrical Equal Area projection.

horizontal resolution and 10 m^2s^{-1} horizontal dispersion. A customized version of Ichthyop, an IBM modified to be used in the Southeast Pacific region, was incorporated to simulate kelp dispersal (Lett et al., 2008). Ichthyop considered parameters like maximum length of individual simulations, reproductive timing and decay rate capturing fertility reduction over time (Table A.1). Each particle represents a floating fertile kelp fragment initially carrying 11,200 spores. The number of spores decreases over time as governed by a decay rate, with further details provided in Thompson-Saud et al. (2024). 5000 particles were released weekly from 1997 to 2008, guided by the density map reflecting kelp distribution. Consequently, areas of high kelp density released more particles compared to areas of lower density. A total of 8, 158,121 spore arrived to kelp forests patches between 1997 and 2008. Particle positions were recorded at specific days (1, 5, 10, 15, 20, 30, 45, 60, 90 and 125) and distances they travelled were measured. In our study, outputs of the biophysical model of Thompson-Saud et al. (2024) were used to compute connectivity matrices, where nodes represent habitat patches of kelp and links between nodes representing the cumulative number of particles (fragments and spores) that moved between nodes. Connectivity matrices were constructed by calculating the number of particles moving between different areas, facilitating subsequent network analyses.

Our study encompassed a comprehensive temporal analysis from 1997 to 2008, allowing us to evaluate the influence of seasonal and inter-annual variability on the connectivity patterns, including assessments during various El Niño Southern Oscillation (ENSO) phases (El Niño, La Niña and neutral) as well as seasonal variations (summer, autumn, winter and spring). ENSO's influence was assessed by months (NOAA, 2024) and seasonal periods were categorized as follows: summer from January to March, autumn from April to June, winter from July to September and spring from October to December. The ROMS hydrodynamic model incorporates variations in oceanographic conditions driven by ENSO phases. This is because both atmospheric forcings (NCEP2 reanalysis; Kanamitsu et al., 2002) and lateral boundary oceanic forcings (ECCO; Stammer et al., 1999) are realistic and capture a wide range of temporal scales, from daily to interannual, including ENSO variability. Consequently, the circulation dynamics simulated by ROMS are intrinsically influenced by ENSO conditions. Since the model successfully captured these dynamics during the study period, it enabled an assessment of kelp dispersal under El Niño, La Niña and neutral conditions. Given the significant influence of ENSO events and seasonal changes on the Southeast Pacific's dynamics, this approach provided a thorough representation of kelp dispersal patterns under varying climatic conditions.

Network analysis and graph theory, which model systems as a collection of interconnected units called graphs, were employed to measure connectivity patterns and to identify subpopulations/units within the giant kelp forest system. In graph theory, a graph consisted of nodes, which in our case, represent habitat patches of kelp in the form of hexagons, that are connected by edges, which represent the potential dispersal routes between these patches. Weights were assigned to the nodes and links to provide information about the strength of the connections. This was achieved by normalizing the connectivity matrices using the maximum and minimum values to ensure that the weights accurately reflect the relative strength of the connections. The network analysis was conducted using the "tidyverse" and "igraph" packages (Wickham et al., 2019; Csardi and Nepusz, 2006) within the R language. Network visualizations were generated using the following R packages: "ggplot2" v.3.2.1, "ggmap" v.3.0.0 and "ggraph" v.2.0.0 (Kahle and Wickham, 2013; Pedersen, 2021; Hadley, 2016).

To assess the overarching population patterns, we calculated a range of network measures (Table 1), enabling the quantification of diverse structural aspects of the population. We performed network measures for the entire period, different ENSO conditions and seasons, using key metrics, including total edges, network density, network diameter, connected components and modularity. The calculations were made for

Table 1
Network measures of the habitat graph and node level that were used to assess connectivity of the giant kelp.

Measure	Function	Ecological and management relevance
Total edges	Indicates the number of pairs of immediately connected nodes	Shows how many connections are formed in the population
Network density[a]	Measures how close the network is to be completed. A complete graph has all possible edges and is equal to 1	Describes the extent to which a population is connected through interactions. It is a ratio of the number of realized interactions to the total number of possible interactions
Network diameter[a]	The maximum number of steps required to traverse the network. Indicates compactness of the graph and overall traversability of the network	Provides insights into the overall efficiency of propagules flow within the population. A small network diameter indicates that the graph is compact, meaning nodes are relatively close to each other in terms of the number of edges that need to be traversed to move from one node to another
Connected components[a]	Number of connected subgraphs (or components). Components are sets of nodes connected to each other by paths (edges)	Provides insights into the structure of the ecosystem. Helps to identify areas that have direct or indirect paths between every pair of nodes within that component
Number of clusters (modularity)[b]	The number of clusters measures the count of distinct groups (or subgraphs) identified within a network. Modularity quantifies the strength of division of the network into these groups by comparing the density of connections within groups to that expected in a random network	Identifies possible metapopulation boundaries
Out-degree[c]	Represents the number of connections or edges going out from a particular node to other nodes in the graph (regardless of their weight)	Indicates how many different nodes a given node can directly influence or interact with. If applied over time, it can be used to infer how the connectivity and dispersal patterns of the population change over time
Out-strength[d]	Is the sum of the weights of all outgoing edges from a node	Indicates the total influence or output a node exerts on its neighbours. It highlights nodes or patches that act as sources, providing significant individuals
In-strength[d]	Is the sum of the weights of all incoming edges to a node.	Indicates the total influence or input a node receives from its neighbours. It highlights nodes or patches that act as sinks (possible settlement areas), receiving significant individuals
Closeness centrality[e]	Measures how central a node is in terms of its average distance to all other nodes in the network. It is the reciprocal of the sum of the shortest path distances from the node to all other nodes.	Measures how quickly information or any influence (e.g. disease or resources) can spread from a particular node to all other nodes in the network
Betweenness centrality[f]	Calculates a node's influence over the flow of information in a graph. A higher value indicates nodes that have greater control of the	Indicates patches that serve as steppingstones and highlights important dispersal routes

(continued on next page)

Table 1 (*continued*)

Measure	Function	Ecological and management relevance
	information flow in the network	
Eigenvector centrality[g]	Evaluates the importance of a node within a network by considering both the number of outgoing and incoming connections it has and the importance of those connections. It assigns higher centrality scores to nodes that are connected to other highly central nodes	Highlights key nodes or patches that are not only well-connected but are also connected to other important patches. Serves to determine highly resilient areas.
Local retention	Shows the ratio of locally produced settlement to local production	Reflects the proportion of propagules that recruit in the same area that they were released
Non-local retention	Shows the ratio of non-locally produced settlement to local production	Reflects the proportion of propagules that recruit in different areas that they were released

[a] Newman (2018).
[b] Rosvall et al. (2009).
[c] Cantwell and Forman (1993).
[d] Barrat et al. (2008).
[e] Freeman (2002).
[f] Freeman (1977) and.
[g] Bonacich (1987).

different times using the graph for each ENSO and season, but we did not account for variability within ENSO phases or seasonal periods in these metrics. By conducting network measures, our primary aim was not to focus on individual metrics but rather to evaluate how the graph changes across different seasons and ENSO phases, thereby providing a broader understanding of temporal connectivity patterns. Additionally, various node level and centrality measures (Table 1) were utilized to gain insights into the distinct roles of individual kelp patches relative to others and infer the attributes of the connectivity of the ecosystem. For instance, out-strength and in-strength were evaluated to determine the directionality (source or sink, respectively) and strength of connections between patches, providing a weighted degree to quantify the contribution of different patches to the overall population structure. The mathematical formulation can be found in Appendix B.

The modularity measure was employed to evaluate the interconnectivity among nodes and potential boundaries in metapopulation for the giant kelp, aiding in the identification of areas exhibiting stronger connectivity among themselves compared to the broader population. This analysis enables the delineation of management units, highlighting regions that are more closely connected and thus essential for effective conservation and resource management (Pastor et al., 2023). We utilized cluster infomap algorithm that works by using random walks to identify groups or communities in a network by maximizing the flow of information within communities and minimizing the flow between communities (Rosvall and Bergstrom, 2008). The Infomap algorithm produces communities that optimize the information-theoretic map equation and detect hierarchical community structures (Rosvall et al., 2009). Utilizing these units, the out-strength measure was applied to delineate key areas serving as sources of kelp fragments per unit. This was done by analysing the connectivity matrices for the entire study area and then normalizing the out-strength values within each unit to obtain relative measures. This normalization allows for a comparative assessment of the importance of each unit in terms of its contribution to kelp fragment dispersal.

Generalized additive models (GAMs) were employed to assess the influence of season and ENSO variability on nodes using various node level measures. The dataset consisted of node differences across seasons and ENSO conditions, aiming to discern whether these changes were statistically significant. The analysis utilized the "mgcv" package (Wood, 2017) in the R language and environment for statistical computing (R Core Team, 2019). Several model families and configurations were tested to identify the best fit for the data. The "performance" package (Lüdecke et al., 2021) was applied to assess overdispersion, aiding in the selection of the family that effectively addressed this issue. Model performance was evaluated by assessing the deviance explained, ensuring convergence, and utilizing the Akaike Information Criteria (AIC) from the "MuMIn" package (Barton and Barton, 2015).

To assess changes in connectivity across various temporal scales, encompassing the entire study duration (1997–2008) and considering distinct seasons and ENSO conditions, we utilized out-degree distribution and node degree measures. Out-degree distribution was employed to visually evaluate habitat connectivity and identify hotspots of outgoing connection of nodes, regardless of kelp density. This approach allowed us to detect structural changes in connectivity patterns over time and identify influential kelp habitats during specific seasons and ENSO phases. By analysing out-degree distributions, we aimed to understand how environmental variability influences connectivity dynamics in the studied ecosystem. On the other hand, node degree distribution was employed for quantitative assessment, enabling us to quantify the connectivity of individual nodes within the graph. This measure involved counting the edges incident to a specific node, offering insights into the extent of its connections with other nodes.

3. Results

From 1997 to 2008, the cumulative habitat graph, which represents the network of habitat patches and their connections over the entire period, comprised 104 nodes and 4461 edges, capturing the connectivity of the population under study. While the number of nodes remained consistent across various habitat graphs during ENSO events and seasonal changes, the number of edges varied, indicating dynamic connectivity. Specifically, the edge count ranged from 3238 during La Niña to 4644 during El Niño and from 3123 in spring to 4330 in autumn (Table 2). Overall, the connectivity observed in the habitat graphs follows a south to north pathway which is consistent with oceanic currents in the region. However, from 36°S and beyond particles are also travelling southward.

3.1. *Network measure of the habitat graph and temporal variability*

The network's connectivity and structure were influenced by seasonal dynamics and ENSO phases (Table 2). During El Niño, the network showed increased connectivity, evidenced by a higher number of edges, resulting in greater network density and a reduced network diameter, suggesting shorter average paths between nodes. In contrast, La Niña phases were marked by decreased connectivity, with fewer edges, lower network density and an expanded network diameter, indicating a more disconnected network structure. El Niño phases were also characterized by a lower number of clusters, indicating fewer distinct network modules and higher inter-node connections, as the population was divided into fewer clusters. Conversely, neutral conditions followed by La Niña exhibited a higher number of clusters, suggesting a greater degree of node segregation into distinct communities and reduced interconnections within the entire population. The clusters formed do not appear to be random, as all the community structures exhibit relatively high modularity (around 0.5), indicating well-defined communities.

Seasonal variations also had an impact on the network. Autumn was identified as the season with the highest connectivity, characterized by the most edges, greatest network density and smallest network diameter, indicating robust connectivity and dependency among kelp patches. In contrast, spring showed the opposite pattern with the lowest number of edges and smallest network density. Notably, spring also showed the highest number of clusters, further underscoring it as the least connected network. Winter and summer exhibited similar patterns, with summer

Table 2
Network measures of the habitat graphs of the giant kelp in the southeast Pacific region, encompassing the entire study period (1997–2008), ENSO conditions (El Niño, La Niña and neutral) and seasons (summer, winter, autumn and spring).

Measure	All	El Niño	La Niña	Neutral	Summer	Autumn	Winter	Spring
Total edges	4841	4644	3238	3994	3680	4330	3675	3123
Network density	0.45	0.43	0.3	0.37	0.34	0.4	0.34	0.29
Network diameter	3	3	4	4	4	3	4	4
Connected components	3	3	3	3	3	3	3	3
Number of clusters (modularity)	9 (0.54)	7 (0.58)	8 (0.55)	9 (0.54)	8 (0.58)	8 (0.54)	8 (0.54)	9 (0.54)

having a slightly higher edge count. Remarkably, throughout all seasons and ENSO conditions, the network maintained three connected components, highlighting the structural resilience of the kelp population network despite environmental fluctuations.

3.2. Node level network measures

The region spanning 36 to 43°S demonstrated significant movement of kelp fragments, both incoming and outgoing. Notably, the nodes around 41°S showed the highest out-strength and in-strength values (Fig. 2a and b). This suggests that the area around 41°S is a key hub in the network, with the most extensive outgoing and incoming connections to other nodes. Not surprisingly, the nodes with the highest non-local retention (76 %) and highest local retention (67 %) were both located in the region around 41°S (Fig. 2f). This insight highlights its potential as a critical focal point for exporting propagules and serving as a settlement area in kelp population dynamics and management strategies.

The geographical region spanning latitudes 36 to 43°S also exhibits the highest closeness centrality, indicating that the propagules in this area are spreading faster to the rest of the population (Fig. 2c). Specifically, habitat patches around 37°S are where propagules are spreading the fastest to the rest of the population. Consequently, any factor affecting this area will have a greater impact on the rest of the population compared to other areas. The area around 41°S also exhibited the highest eigenvector centrality, indicating that this area is well-connected and linked to other important areas of the population (Fig. 2e). As a result, the southern region showed a notable degree of connectivity and resilience to disturbances. Conversely, the central part of the population displayed higher betweenness centrality compared to those located at the extremes (Fig. 2d). This indicates that a significant number of areas within this central part acted as crucial steppingstones for connectivity. Particularly noteworthy is the region around 29°S, the population's midpoint, which demonstrates the highest betweenness centrality.

In analysing temporal changes in node measurements, we selected the most parsimonious statistical model based on criteria including the lowest Akaike Information Criterion (AIC), highest explained deviance and optimal model fit. The chosen model incorporated a wide range of explanatory variables, as specified in Eq. (1).

$$Nodes\_changes = gam(Netwok\_measure \sim Time\ (ENSO\ or\ season) + s(Node, bs='re') \qquad \text{Equation 1}$$

In Eq. (1), *gam* refers to the Generalized Additive Model. *Network_measure* refers to the various network metrics analyzed, excluding betweenness centrality due to its incompatibility with any model family. The *Time* variable represents either *ENSO* phases (El Niño, La Niña and neutral) or *season* (summer, autumn, winter and spring), treated as factorial. The *s(Node, bs = 're')* component represents a random effect smoothing term to account for unexplained variance among individual nodes. The model family for each network measure is specified in supplementary information (Table C.2 and 3).

Analysis during different ENSO phases uncovered notable shifts in network measure patterns across nodes (Table C.2). Seasonal effects demonstrate diverse impacts on network metrics (Table C.3). For instance, degree and closeness centrality exhibit considerable variability across seasons, contrasting with out-strength and local retention, which show minimal seasonal variation. In-strength (i.e., settlement) and non-local retention exhibit similar patterns during spring and summer, as well as autumn and winter. Additionally, eigenvector centrality notably differs primarily during the spring season.

The out-degree, indicative of the number of outgoing connections each node has, was used to visualize variations across distinct ENSO phases and seasons (Fig. 3). We found that nodes are connected to between 4 and 90 other nodes out of a total of 125 nodes. Overall, the connectivity and structure of the population appear to be consistent in the north, somewhat less so in the south, but with notable variability observed in the region between 28 and 35°S across different seasons and ENSO conditions. During El Niño, this area shows high connectivity with around 50–75 connections per node, which decreases during neutral conditions and further decreases during La Niña to between 24 and 40 connections. Autumn appears to have the highest connectivity in this area with around 50 to 75 connections per node, followed by summer, winter and spring with around 5 to 25 connections per node.

All habitat graphs except spring showed properties of a random graph, with degree distribution similar to a Gaussian bell-shaped curve (Fig. D.1). This bell-shaped distribution suggests most nodes have a similar number of connections, with fewer nodes at the extreme high or low end of connections. A normal distribution of node degrees suggests a certain level of regularity and uniformity in the connectivity patterns of nodes. In contrast, spring's node degree distribution appeared more homogeneous, indicating a more even spread of node degrees across the range, excluding highly connected nodes. This pattern implies a structurally different connectivity pattern during spring, lacking the regularity observed in other seasons.

3.3. Identifying communities for management

A comprehensive cluster analysis of the habitat graph was conducted using the previously mentioned cluster Infomap algorithm, covering the period from 1997 to 2008. This analysis identified nine distinct clusters (Fig. 4a), which are important not as biological communities, but as potential metapopulation boundaries that inform strategic management decisions. These clusters are arranged in a south-to-north gradient according to their ecological significance. Notably, Unit 6 emerges as the most extensive management unit, spanning nearly 1000 km, whereas Unit 9 is the most compact, encompassing approximately 260 km. On average, the dimensions of these management units are approximately 400 km in length north to south. The considerably higher population density in the southern extremity has unmasked critical areas in other parts of the population where density is lower. Therefore, the identified management units were used to determine key source areas within each unit. This approach identified key supply areas within each unit, prioritised for management to ensure the preservation of connectivity both within and across the broader region (Fig. 4b).

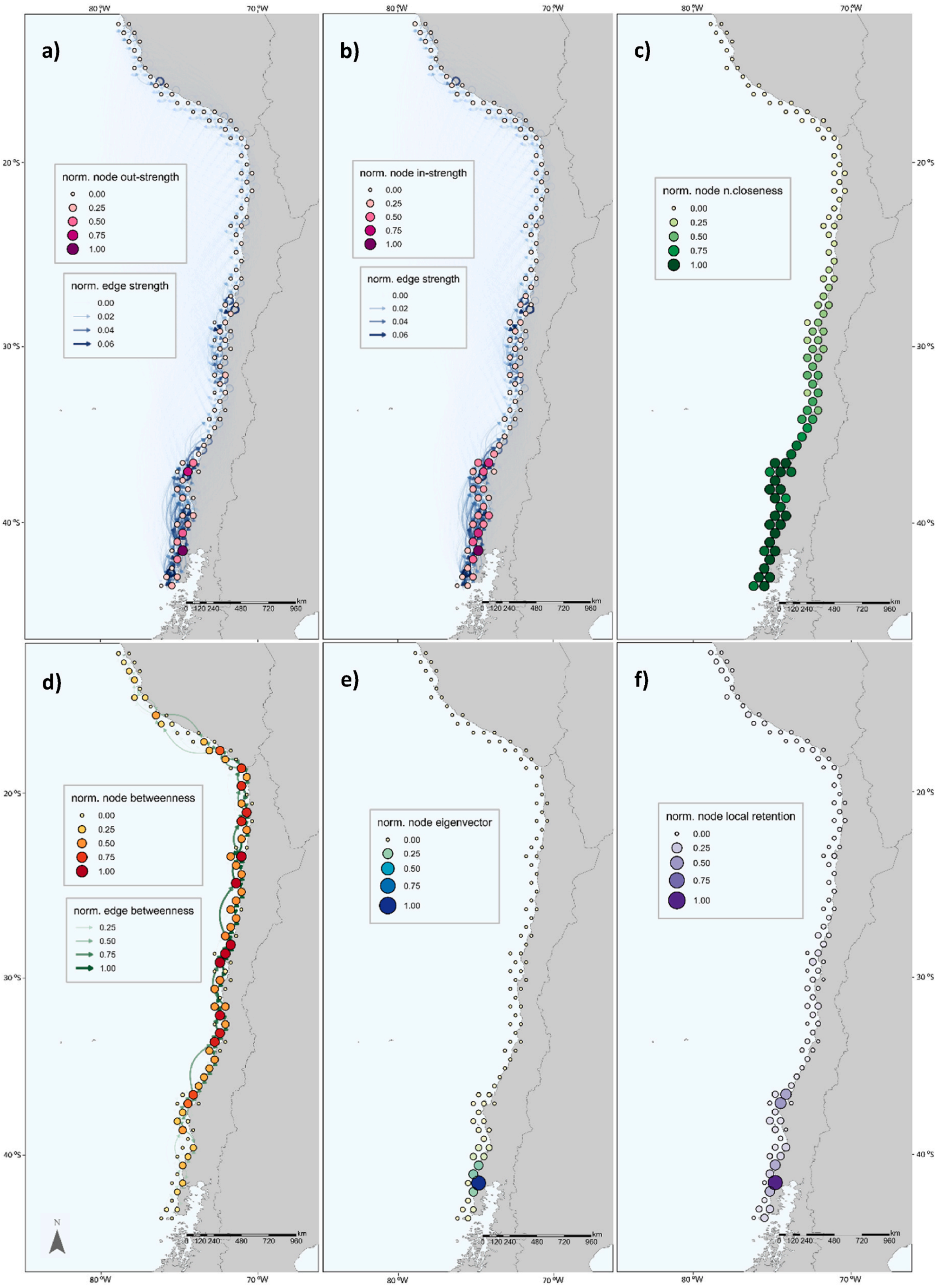

Fig. 2. Maps of kelp fragment displaying node-level connectivity metrics. a) out-strength (source areas), b) In-strength (sink areas), c) closeness (fragments spread velocity), d) betweenness (bridge areas), e) eigenvector (influential areas) and f) local retention (fragment retention) in the southeast Pacific. Circles indicate settlement density of kelp fragments across the region, with the size and colour gradient representing the normalized concentration from low (small, light pink (a and b), light green (c), yellow (d), light blue (e) and light purple (f)) to high (large, dark purple (a and b), green (c), red (d), blue (e) and purple (f)). 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

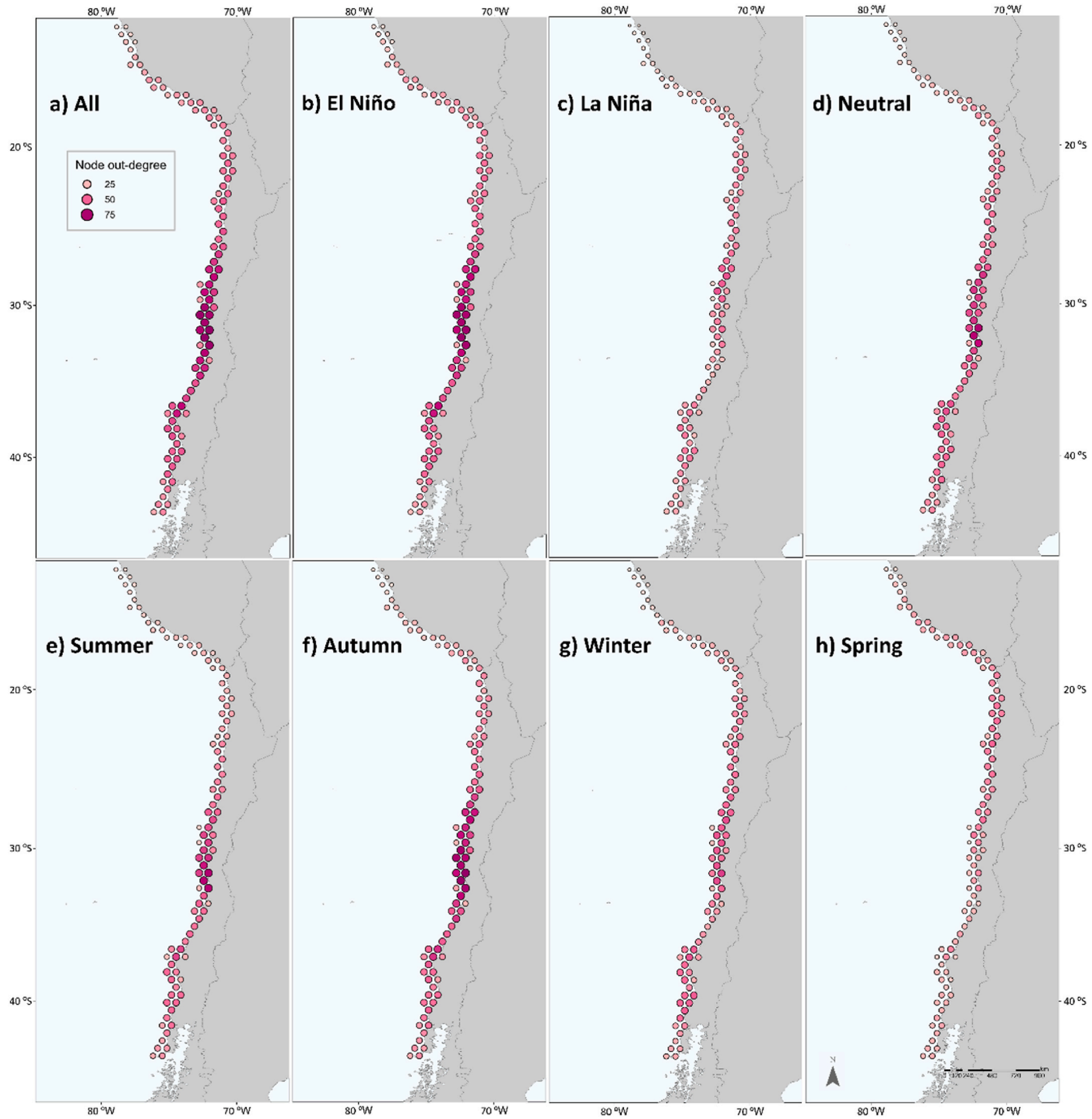

Fig. 3. Maps of kelp fragments showing out-degree (number of connected nodes) centrality in the southeast Pacific during the entire period, different ENSO conditions and seasons. Circles indicate settlement density of kelp fragments across the region, with the size and colour gradient representing the normalized concentration from low (small, light pink) to high (large, dark purple). Map showing out-degree during a) the entire study period, b) El Niño, c) La Niña, d) neutral condition, e) summer, f) autumn, g) winter and h) spring. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

4.1. Network connectivity: regional and temporal variability

Our study on the connectivity dynamics of *Macrocystis pyrifera*, giant kelp, along the southeast Pacific coast underscores the critical significance of the southern population (36–43°S) as a fundamental source-sink area. This region, particularly the nodes situated around 41°S where alongshore wind stress is considerably lower throughout the year, emerges as a key hub for connectivity, propagule dissemination, local retention and non-local retention, indicating a heightened propensity for self-persistence and an important area for the persistence of the entire population as it is significantly contributing to the overall population structure. In contrast, the remaining populations manifest low resilience and connectivity, as the stochastic loss of nodes could induce significant disruptions in the network. However, our findings also reveal

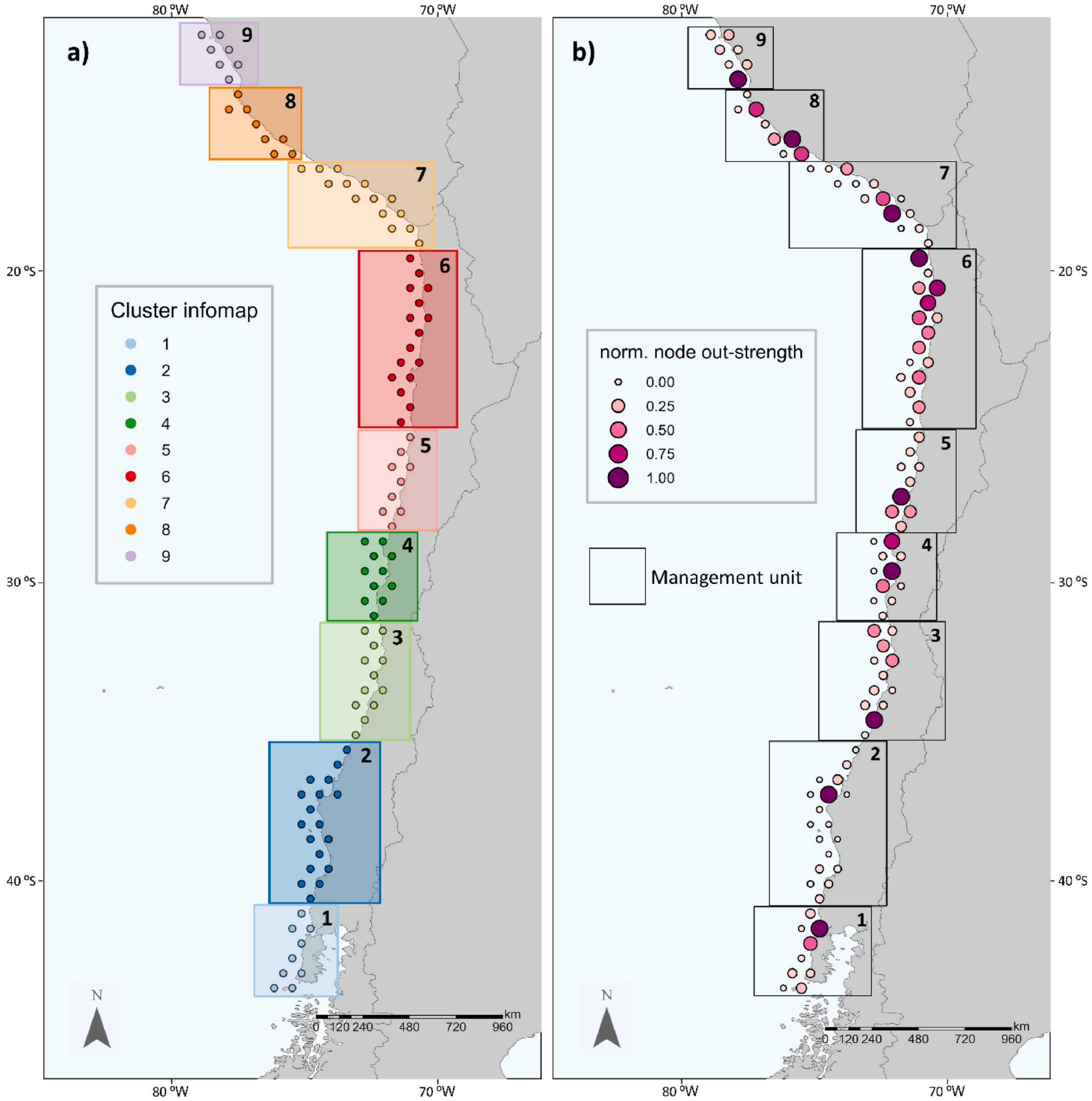

Fig. 4. Maps of kelp fragment showing units (areas that are more connected) and out-strength (source areas) per unit in the southeast Pacific during 1997–2008. a) Map showing the management units determined by the cluster Infomap algorithm. Different colours represent different units and their numbers represent their importance. b) Map showing out-strength applied to each management unit. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the central population's key role as a bridge, fostering connectivity across the entire population and facilitating linkages between the southern and northern extremes. Consequently, the potential disconnection of a central node poses a substantial risk, as it could lead to the isolation of the entire population.

The region between 28 and 35°S, regardless of kelp abundance, exhibits high connectivity, serving as a key hub influenced by seasonal upwelling patterns associated with fluctuations in the Southeast Pacific Subtropical Anticyclone (SPSA; Fig. E.2, 4 and 5) (Sobarzo et al., 2001; Letelier et al., 2009). During autumn, increased connectivity is observed in this central area, attributed to the northward displacement of the SPSA, which halts upwelling activity and reduces offshore dispersion associated with Ekman transport (Muñoz et al., 2023; Rahn et al., 2015). These changes result in the retention of particles in coastal areas, enhancing interaction and connectivity but potentially reducing nutrient availability due to decreased upwelling, which could impact kelp settlement (Hollarsmith et al., 2020). Connectivity decreases during winter due to the resurgence of upwelling in early August, which intensifies in spring and peaks in early January (the beginning of summer) (Muñoz et al., 2023). This enhanced upwelling activity drives westward particle movement, facilitated by increased Ekman transport, ultimately reducing connectivity in the central area. Despite the reduction in connectivity, increased upwelling enriches the environment, promoting favourable conditions for settlement and growth (Vásquez et al., 2007). Similar phenomena could explain the differences associated with ENSO dynamics, with weaker southerly winds during El Niño (Fig. E.3, 4 and 5) leading to a shorter and weaker upwelling season, thereby increasing connectivity between nodes. Conversely, La Niña intensifies southerly winds, strengthening upwelling and reducing connectivity associated with greater east-west activity.

Remarkably, the southern population, characterized by high connectivity and population density, remains more stable over time. The southern region experiences a more stable and weaker upwelling pattern due to the SPSA is just above this area (Montecino et al., 2006). This stability, along with nutrient inputs from coastal runoff, creates an environment conducive to kelp reproduction, settlement and growth. However, the potential southward shift of the Pacific Anticyclone induced by climate change poses a threat to the stability and reduction in size of this productive area (Weidberg et al., 2020). Understanding these intricate seasonal variations and stability dynamics is crucial for anticipating the potential impacts of climate-induced shifts on *M. pyrifera* populations in the southeast Pacific.

4.2. Management of Macrocystis pyrifera in the southeast Pacific

Our study delineates effective management units for the extensive *M. pyrifera* population, with a pronounced focus on the southern region, particularly around 41°S, recognised for its essential role in overall population connectivity. While kelp in this region thrives due to high connectivity and favourable conditions, its protection is crucial as it serves as a source population, supporting the recovery of degraded or overexploited areas in the north. This connectivity is vital, as rapid natural colonization from source populations can significantly enhance recruitment success in areas affected by extraction pressures (Reed et al., 2024). Conservation initiatives such as the establishment of no-take zones in the kelp harvesting, specifically within the identified units 1 and 2, are a key strategy to fortify resilience and protect the integrity of the entire population. No-take zones have demonstrated effectiveness in supporting the resilience and biodiversity of marine ecosystems, including kelp forests, by promoting habitat protection and species recovery (Castilla and Bustamante, 1989).

The system of Territorial Use Rights in Fisheries (TURFs), which has been successfully implemented in Chile, offers a robust foundation for these conservation efforts (Moreno and Revenga, 2014; Gelcich et al., 2012). Leveraging existing TURFs, managers can strategically restrict harvesting in critical source areas such as those around 41°S, ensuring their protection while fostering community involvement in resource management. Studies have shown that kelp density is higher within TURFs compared to open-access areas, reinforcing their role in sustainable resource management (González-Roca et al., 2021). To strengthen this approach, we recommend policy integration at the local and national levels, ensuring that these areas are formally recognised in national conservation strategies and supported by enforcement mechanisms. Implementing this approach involves prohibiting extraction activities within the different TURFs situated in these critical areas. The historical data showcasing lower harvesting in this area provides a compelling rationale for its designation as a no-take zone (Porras and Vásquez, 2020). Meanwhile, it is noteworthy that the concentration of extraction activities for *M. pyrifera* spans from 12 to 32°S along the Peruvian and Chilean continental coast, with the arid climatic conditions contributing to cost efficiencies in raw material drying and processing (Vásquez, 2009; ARCE, 2021). Balancing conservation in high-connectivity areas in the south with sustainable harvesting practices in the north mitigates overexploitation risks while maintaining economic viability (Vásquez, 2009). Adaptive harvesting practices informed by connectivity patterns and co-management frameworks, which emphasize local participation, accommodate multiple stakeholder value judgments and equitable benefit-sharing (Gelcich et al., 2010; De Juan et al., 2017), ensure ecological and economic goals are met simultaneously.

Furthermore, our analysis identified key source areas within each management unit, revealing critical patches that may be overlooked due to the high population density in southern Chile. Recognising and safeguarding these areas within existing management frameworks is essential for effective conservation. In Chile, marine conservation practices emphasize the importance of aligning conservation goals with governance structures (Fernández and Castilla, 2005). Embedding these management units in national conservation plans would enhance their long-term protection and integration into broader restoration strategies. In particular, incorporating these key source areas into existing TURFs would help enforce targeted restrictions in disproportionately important regions within each unit. Additionally, the centrality of certain nodes is key for maintaining connectivity across the population. Prioritising the protection of the area around 29°S mitigates the risk of disconnection and strengthens overall resilience. Moreover, by incorporating ecological connectivity into the spatial prioritisation of kelp, management strategies can influence areas beyond their immediate location through biological and physical mechanisms, such as hydrodynamic connectivity. Actions taken in one part of the marine ecosystem can impact the health and services provided by other areas. By maintaining this interconnectedness, coastal regions can continue to provide essential ecosystem services that help both ecological and human community well-being (Ospina-Alvarez et al., 2020).

The dynamic nature of kelp ecosystems also means that seasonal variations play a role in connectivity. The areas around 28 and 35°S stand out as critical hubs with consistently high connectivity. However, their connectivity patterns are influenced by seasonal upwelling, dictated by the intensity of Southerly winds during different seasons and ENSO conditions. With the expected intensification of ENSO events due to climate change (Cai et al., 2014, 2015; Timmermann et al., 1999), management strategies must consider seasonal variations in connectivity. To ensure resilience against climate change, adaptive management policies should be flexible, enabling dynamic response to ENSO forecasts. To this end, management strategies should not only recognise but also actively address these seasonal variations in connectivity. For instance, during periods of strong upwelling (spring and La Niña), targeted conservation measures or seasonal adjustments to activities impacting the kelp habitat, such as temporarily forbidding kelp extraction, could mitigate potential negative impacts and promote self-recruitment.

The resilience of *M. pyrifera* populations to extreme warming events is a critical aspect of connectivity and conservation in the context of climate change. While kelp-dominated ecosystems are often perceived as highly vulnerable to marine heatwaves, some studies have shown that certain populations can persist despite extreme warming events, possibly due to local oceanographic buffering (Reed et al., 2016; Arafeh-Dalmau et al., 2019). However, this resilience is not uniform, as other populations have experienced significant declines under similar conditions (Arafeh-Dalmau et al., 2019). A comparable effect may be occurring in the Humboldt Current System, where limited warming in recent decades could have provided some protection. However, with ongoing climate change, warming trends are expected to intensify posing new challenges for kelp forest resilience (Smale, 2020). To better understand and mitigate these impacts, incorporating climate variables into connectivity analyses can offer insights into population persistence under future scenarios (Frazão Santos et al., 2020). Additionally, transboundary conservation efforts (Mason et al., 2020; Mazor et al., 2013) could play a crucial role in protecting *M. pyrifera* populations across Chile and Peru, ensuring regional ecological connectivity and enhance the resilience of kelp forests, ensuring their long-term sustainability. Integrating these perspectives into marine spatial planning (Buenafe et al., 2023) and conservation prioritisation (Dabalà et al.,

2023) can help identify key areas for protection, optimize resource allocation and develop adaptive strategies that enhance the resilience of kelp forests amid changing climatic conditions.

Moreover, in the Southeast Pacific, trophic cascades significantly shape *M. pyrifera* ecosystems. Herbivory by sea urchins (*Loxechinus albus*) threatens kelp forests, particularly where predator populations like lobsters (*Jasus frontalis*) and fish species have declined due to overfishing (Vásquez and Buschmann, 1997; Graham et al., 2007). Management strategies that integrate predator conservation into marine spatial planning, such as establishing Marine Protected Areas (MPAs), are critical for maintaining trophic interactions and preventing ecological degradation (Almanza and Buschmann, 2013; Katsanevakis et al., 2011). These strategies should include incentives for fisheries adopting sustainable practices and prioritise multi-species conservation to maintain kelp forest resilience. Protecting these trophic interactions is crucial to maintaining kelp forest resilience, especially as climate change and human pressures exacerbate ecological vulnerabilities in the region. Socioeconomic trade-offs of predator protection must also be addressed, balancing conservation goals with local livelihoods. Involving communities in designing and implementing management strategies fosters long-term ecological and economic sustainability (Gelcich et al., 2010).

5. Conclusion

Our findings provide a nuanced foundation for adaptive and targeted management strategies, emphasizing the importance of the southern population, key source areas, central nodes and seasonal management practices in sustaining the overall connectivity and resilience of the *M. pyrifera* population along the southeast Pacific coast. Furthermore, our study encourages an integrated approach that acknowledges the concentration of extraction activities in the northern region and suggests collaboration between conservation efforts in the south and sustainable harvesting practices in the north. While our study offers valuable insights, there are several limitations that could be addressed in future research. Although the model captures the effects of oceanographic conditions, further research on the interplay of other ecological factors—such as trophic interactions and the influence of fisheries— would provide a more nuanced understanding on the resilience and connectivity of giant kelp. Moreover, expanding the bioavailability data for giant kelp across the entire study region could improve the model's accuracy, particularly in under-sampled or ecologically unique areas. To further refine connectivity assessment, future research could involve running nested models with higher resolution. This approach would offer a more granular exploration of the connectivity and will help to test the efficacy of current TURFs configurations to protect the giant kelp. Lastly, it would be valuable to investigate the long-term effects of climate change on *M. pyrifera* populations, especially in the context of more frequent and intense ENSO events and shifting oceanographic conditions. Overall, our findings and recommendations provide a comprehensive foundation for informed decision-making, emphasizing the urgency of proactive and adaptive management strategies in the conservation of this marine ecosystem.

CRediT authorship contribution statement

G. Thompson-Saud: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **A. Grech:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **S. Choukroun:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis. **S.I. Vásquez:** Writing – review & editing, Investigation, Formal analysis. **A. Ospina-Alvarez:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2025.107661.

Data availability

The data supporting the findings of this study are available for access through the following link: https://doi.org/10.25903/hybj-4d19.

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