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EDITED BY
Christophe William Vieira,
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Zi-Min Hu,
Yantai University, China

*CORRESPONDENCE
Filipe Alberto
albertof@uwm.edu

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Range wide genetic differentiation in the bull kelp *Nereocystis luetkeana* with a seascape genetic focus on the Salish Sea

Lily Gierke[1], Nelson C. Coelho[1,2], Tarang Khangaonkar[3], Tom Mumford[4] and Filipe Alberto[1]*

[1]Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, United States, [2]Department of Computational and Systems Biology, Pittsburgh Center for Evolutionary Biology and Medicine, University of Pittsburgh School of Medicine, Pittsburgh, PA, United States, [3]Pacific Northwest National Laboratories, Seattle, WA, United States, [4]Retired, Olympia, WA, United States

Introduction: In temperate regions, one of the most critical determinants of present range-wide genetic diversity was the Pleistocene climate oscillations, the most recent one created by the last glacial maximum (LGM). This study aimed to describe *N. luetkeana* genetic structure across its entire range (Alaska to California) and test different models of population connectivity within the Salish Sea. This region was colonized after the LGM and has been under increased disturbance in recent decades.

Methods: We utilized microsatellite markers to study *N. luetkeana* genetic diversity at 53 sites across its range. Using higher sampling density in the Salish Sea, we employed a seascape genetics approach and tested isolation by hydrodynamic transport and environment models.

Results: At the species distribution scale, we found four main groups of genetic co-ancestry, Alaska; Washington with Vancouver Island's outer coast and Juan de Fuca Strait; Washington's inner Salish Sea; and Oregon with California. The highest allelic richness (AR) levels were found in California, near the trailing range edge, although AR was also high in Alaska. The inner Salish Sea region had the poorest diversity across the species distribution. Nevertheless, a pattern of isolation by hydrodynamic transport and environment was supported in this region.

Discussion: The levels of allelic, private allele richness and genetic differentiation suggest that during the LGM, bull kelp had both northern and southern glacial refugia in the Prince of Wales Island-Haida Gwaii region and Central California, respectively. Genetic diversity in Northern California sites seems resilient to recent disturbances, whereas the low levels of genetic diversity in the inner Salish Sea are concerning.

KEYWORDS

kelp forest, genetic diversity, glacial refugia, mating system, dispersal, microsatellite markers, bull kelp

Introduction

The range-wide distribution of species' genetic diversity results from evolutionary, ecological, and biogeographic processes. In temperate regions, the most important determinant of current range-wide genetic diversity was the Pleistocene glacial-interglacial climate oscillations, the most recent one created by the last glacial maximum (LGM) 20,000 years ago (Clark et al., 2009), which resulted in range contraction and expansions. Under the expansion-contraction model (ECM), when the glaciers retreated, wide-spread recolonization into higher latitudes (the leading-edge) occurred across many taxa of species (Blanchette et al., 2008; Kelly and Palumbi, 2010; Lindstrom et al., 2011). For many marine taxa, where fossil records are rare or absent, the present patterns of genetic structure and diversity are the single indicator of how the LGM shaped the species range (Marko, 2004). The ECM posits that glacial refugia were located in one or several regions at lower latitudes. Depending on the taxa dispersal capacity, these LGM refugia (the trailing-edge) hold currently higher genetic diversity than found in regions colonized after the glaciers retreated. While genetic diversity patterns according to ECM expectations are found across terrestrial and aquatic taxa in many regions of the world (Huntley and Birks, 1983; Hewitt, 1996; Williams et al., 1998; Hewitt, 2003; Provan and Bennett, 2008), there are many exceptions. Several higher latitude coastal regions in the Northeast Pacific coast remained unglaciated, serving as glacial refugia for many species (Hickerson and Ross, 2001; Hickerson and Cunningham, 2005; Marko et al., 2010). These higher-latitude glacial refugia are detectable today by the additional hotspots of genetic diversity observed across the latitudinal range of species distributions.

It is generally accepted that high genetic diversity, often found at the trailing-edge, can confer resilience to rapidly changing environments by providing the necessary variation for an evolutionary response (Reusch et al., 2005; Sgrò et al., 2011; Bernhardt and Leslie, 2013). At the leading-edge, the strength of the founder effect (Excoffier et al., 2009) will dictate how much genetic diversity is lost due to drift and inbreeding (Saccheri et al., 1998) or kept allowing for adaptation to new environments (Hughes et al., 2008). Studying the current partition of range-wide genetic diversity and differentiation informs our predictions on how species will respond to increased Anthropocene pressure (Thuiller et al., 2008). Marine ecosystems face an increased risk of degradation and species loss due to global climate change (Doney et al., 2012; Pörtner et al., 2022). Habitat destruction has already led to declines in the size of populations and increased fragmentation, resulting in reductions and shifts in species range (Poloczanska et al., 2013; Smale and Wernberg, 2013; Pinsky et al., 2020). These impacts can also result in rapid losses of intraspecific genetic diversity (Bálint et al., 2011; Pauls et al., 2013) that are better understood when the biogeographic patterns built over a much longer time-scaler are known. Although both leading and trailing-edge are predicted to shift polewards, the latter contracts the species range outside the current lower latitude distribution limit. Where genetic refugia occurred only at lower latitudes, contractions of the current trailing-edge might disproportionately impact a higher fraction of a species' genetic diversity. With climate change predictions, populations at the trailing-edges that cannot acclimatize or adapt will depend on dispersal to higher latitudes or face extirpation. How much will species be able to naturally shift their trailing-edge and maintain the levels of genetic diversity they hold is a timely but complex question (Pinsky et al., 2020). A non-exhaustive list of determinants will be habitat size, suitability at higher latitudes, and the interplay between dispersal capacity and climate velocity, i.e., how fast changes will occur (Burrows et al., 2011; Pinsky et al., 2013). Understanding the partition of genetic diversity and differentiation will assist in the decision-making related to assisted evolution (van Oppen et al., 2015; Coleman and Goold, 2019) and migration (Schlaepfer et al., 2009; Aitken and Whitlock, 2013), as well as determine ex-situ conservation priorities (Schoen and Brown, 2001; Hoban et al., 2020).

The dispersal potential of a species can be inferred from estimates of population genetic differentiation - a measure of how gene flow across long temporal scales shapes genetic structure (Pritchard et al., 2000; Waples and Gaggiotti, 2006). This genetic structure can result from historical barriers to gene flow, range shifts, or expansions from glacial refugia (Maggs et al., 2008; Assis et al., 2014). The most apparent feature controlling gene flow is the geographic distance between populations; dispersal is typically limited by distance, and thus, geographically closer individuals are often more genetically similar than individuals further away (Wright, 1943). Geographic distance and genetic differentiation share a positive linear relationship under the isolation by distance (IBD) or the stepping stone model of IBD (Wright, 1943; Kimura and Weiss, 1964). In complex systems, however, more than geography alone is needed to predict patterns of genetic structure, and IBD models may have a poor fit for empirical data. In marine species, ocean currents are an essential means of dispersal for many marine species with pelagic dispersal and often brake the linear association of gene flow and geography (Selkoe et al., 2008; Selkoe et al., 2016). The model of isolation by oceanographic distance (IBOD) describes a pattern in which ocean currents influence gene flow more than spatial distance alone (Selkoe et al., 2008; White et al., 2010; Alberto et al., 2011; Riginos and Liggins, 2013). Therefore, modeling the oceanographic transport by ocean currents can result in a better understanding of population structure and connectivity in marine species and is particularly useful in species with limited dispersal life histories.

Although ocean currents may extend the dispersal of gametes, heterogeneity between source and destination environments can affect the establishment of migrants and decrease gene flow between different environments (Sexton et al., 2014). This pattern of isolation by environment (IBE) is characterized by an association between genetic differentiation and environmental distance independent of geographic distance (Wang and Bradburd, 2014). IBE alone does not explain the forces that drive this pattern, but IBE can be used to describe the pattern. Under certain conditions, IBE may lead to, or be caused by, isolation by adaptation, where fitness differences prevent some genotypes from persisting in some non-native environments (Nosil et al., 2008).

In the temperate reefs of the world, kelp forests provide a complex three-dimensional structure characterized by a dynamic

canopy that further influences the physical conditions and ecosystem processes. This engineering role is probably the most important factor explaining the high diversity supported by kelp forests (Miller et al., 2018). Globally, recent marine heatwaves and climate forecasts have sparked concerns about the persistence of kelp forests under climate change (Wernberg et al., 2016; Assis et al., 2018; Smale et al., 2020). In the Northeast Pacific, the bull kelp, *Nereocystis luetkeana*, is one of two large kelp species with a canopy that reaches the surface, providing structure for complex habitat niches (Siddon et al., 2008). Due to its fast growth rate, bull kelp forests have high productivity and play a key role in nutrient cycling in coastal marine ecosystems (Foster and Schiel, 1985; Graham et al., 2008). Recent declines in bed density have caused concern for some populations, specifically in northern California (Rogers-Bennett and Catton, 2019; Arafeh-Dalmau et al., 2023), and the Puget Sound (Berry et al., 2021).

Bull kelp's role as an ecosystem engineer, the geological history of the range it inhabits, and the regional extinction threats it faces all call for an overdue study of its genetic diversity. Our study had two main goals: 1) describe *N. luetkeana* genetic structure across its entire range (Alaska to California) using microsatellite markers, and 2) test different models of population connectivity within the Salish Sea, a region that was colonized after the LGM and faces increased disturbance in recent decades.

Materials and methods

Study species; the bull kelp

Nereocystis luetkeana, or bull kelp, is an annual brown alga in the order Laminariales with distribution limited to the Northeast Pacific Ocean. Like other brown algae, it has a haplodiplontic life cycle in which adult diploid sporophytes release from sori haploid zoospores that produce unisexual, haploid gametophytes. The microscopic gametophyte stage develops from the germinating zoospores after these settle on the benthos. Gametophytes reproduce sexually producing the sporophyte stage. *N. luetkeana* differs from other kelps in that spore-filled tissues, called sori, abscise completely from the blade and fall to the benthos releasing haploid zoospores (Walker, 1980). The blades of bull kelp are held near the surface of the water by a gas-filled, spherical pneumatocyst at the end of a long, slim stipe (~1/3 inch in diameter), attached to the substratum with a hapterous holdfast. Sori are produced near the proximal end of the blade and their abscission happens between June and November, with the species reproducing annually. Spore dispersal from sori begins shortly before abscission and continues up to an hour post-abscission (Amsler and Neushul, 1989). Although zoospores are flagellated, mobility is minimal and thus negligible in dispersal (Norton, 1992). Because sori are located near the water surface, after their abscission, the proportion of zoospores released in the water column before reaching the seafloor, which is presently unknown, may limit their dispersal potential. However, other kelp species demonstrate that long-distance dispersal can be mediated by ocean currents transporting drifting sporophytes released from the substrate during storms. This 'rafting' is due to the pneumatocysts that afford positive buoyancy and facilitate floating. For example, in giant kelp, *Macrocystis pyrifera*, adult sporophytes were observed with viable sori after traveling over long distances (Reed, 1987; Hernández-Carmona et al., 2006), and sporophylls were found to maintain buoyancy for up to 21 days (Macaya et al., 2005). Rafts of *N. luetkeana* have been found far from both the southern and northern edges of the species distribution (Miller and Estes, 1989; Selivanova and Zhigadlova, 1997; Gibson et al., 2010).

Sample collections and DNA extraction

We sampled fifty-three sites across the geographic range of *N. luetkeana*, ranging from Herring Island, Alaska (59.65°N, 151.59°W) to Cambria Bay, California (35.53°N, 121.09°W), from May 2016 to August 2017. We collected a higher sampling site density inside the Salish Sea, the inner water body composed of the Strait of Georgia in British Columbia, Canada, and Puget Sound in Washington, USA (Figure 1, Table 1). Within each site, the average number of specimens collected was 40, ranging from 7 to 51, resulting in 2,188 individuals. We sampled specimens haphazardly, separated by at least 2 meters, by cutting 2-4 cm pieces of blade tissue in a non-destructive manner. We wiped the sampled blade tissue to remove epiphytes before storing the tissue in silica gel desiccant for preservation until DNA extraction. Next, we used a Tissue Lyser II (Qiagen, Valencia, CA) to homogenize the silica-dried tissue to a fine powder before extracting DNA using the DNeasy Nucleospin 96 Plant Kit II (Machery-Nagel, Duren, Germany) following the kit protocol.

Microsatellite loci genotyping

We characterized microsatellite regions for *N. luetkeana* (see supporting material) and used seven of the resulting microsatellite loci (Ner-2, Ner-4, Ner-6, Ner-9, Ner-11, Ner-13, and Ner-14, Table S2). We prepared PCRs in a total reaction volume of 15 µL comprised of 10 µM primer, 10 mM dNTP's per base (Promega, Madison, WI), 25 mM MgCl2, 3.0 µl 5X PCR buffer, and 0.5 U GoTaq Polymerase. Thermocycler conditions consisted of a 5-minute denaturation step at 95°C, followed by 33 cycles of 20 seconds each at 95°C, 20 seconds at an annealing temperature of 57°C - 61°C, 30 seconds at 72°C followed by a final elongation step of 20 minutes at 72°C using an Eppendorf thermocycler (Eppendorf, USA). We sized microsatellite PCR fragments using fragment analysis on a 96-capillary DNA sequencer ABI 3730xl at the Madison Biotechnologies Center. We scored the resulting microsatellite fragments with STRand (https://www.vgl.ucdavis.edu/informatics/strand.php) and binned them into discrete allele sizes with the R (R Core Team, 2021) package "MsatAllele" (Alberto, 2009). The presence of null alleles was evaluated with MICRO-CHECKER v.2.2.3 (Van Oosterhout et al., 2004).

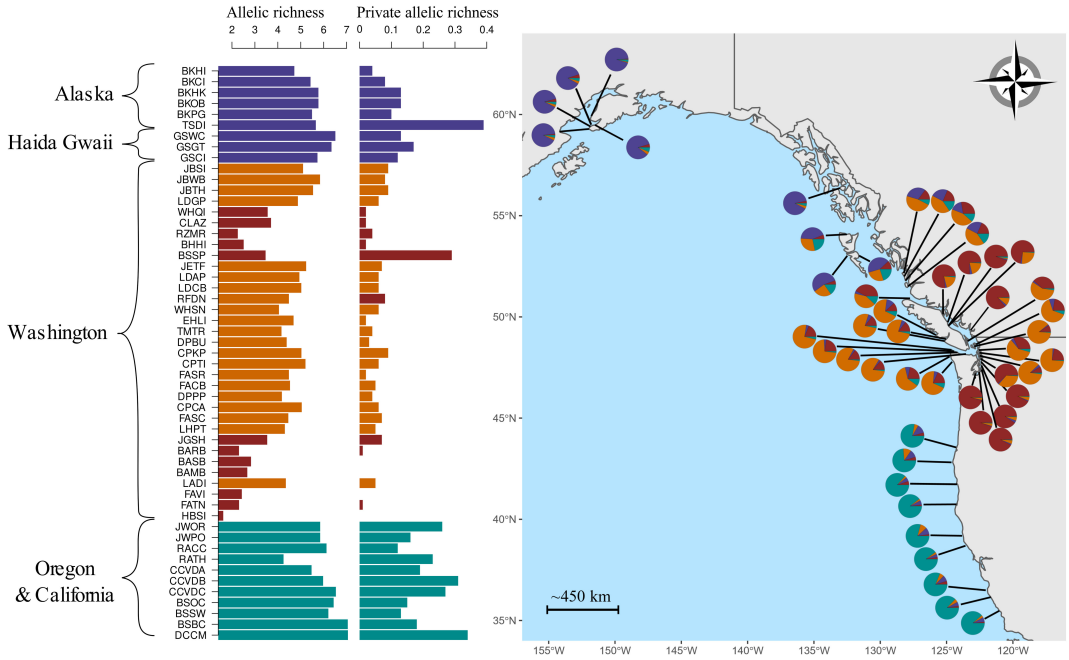

FIGURE 1
Genetic diversity of *Nereocystis luetkeana* across its distribution range in the northeast Pacific. On the right side, the sample locations are indicated on the map. For each site, a pie chart shows the average proportions of individual assignment to the four groups of genetic co-ancestry estimated with STRUCTURE. The barplots on the left side show within-population genetic diversity as measured by microsatellite allelic richness and private allele richness, standardized by a sample size of seven. Sites are ordered by decreasing latitude; the codes for each site are given with additional information provided in Table 1. The color for different bars represents the group of genetic co-ancestry (STRUCTURE) with the maximum proportion of average individual assignment for that site.

TABLE 1 Population genetics summary statistics for sampled sites of *Nereocystis luetkeana*.

Population	Pop	Code	Latitude	Longitude	*n*	*AR*	*pAR*	F_{IS}	HWE test	# Loci (HD/HE)	LD
Herring Island	1	BKHI	59° 39’ 9.72”N	151° 35’ 40.92”W	51	4.62	0.18	0.100	N.S.	(0/0)	1
Cohen Island	2	BKCI	59° 32’ 30.00”N	151° 32’ 30.00”W	50	5.54	0.28	0.228	Sign.	(3/0)	0
Hezketh Island	3	BKHK	59° 30’ 21.60”N	151° 30’ 15.60”W	50	5.85	0.35	0.221	Sign.	(4/0)	0
Outside Beach	4	BKOB	59° 27’ 51.00”N	151° 42’ 33.60”W	50	5.74	0.29	0.157	Sign.	(2/0)	1
Port Graham	5	BKPG	59° 22’ 14.400”N	151° 53’ 23.40”W	51	5.54	0.27	0.086	Sign.	(1/0)	6
Dasani Island	6	TSDI	55° 45’ 39.21”N	133° 16’ 45.96”W	40	5.64	0.56	0.163	Sign.	(2/0)	1
Cape Edenshaw	7	GSWC	54° 6’ 25.16”N	132° 21’ 59.08”W	33	6.47	0.30	0.114	N.S.	(0/0)	0
Tana’s Bay	8	GSGT	53° 11’ 40.27”N	132° 35’ 31.88”W	32	6.20	0.31	0.088	N.S.	(0/0)	0
Cumshewa Island	9	GSCI	53° 1’ 50.41”N	131° 36’ 9.65”W	26	5.84	0.22	0.131	Sign.	(1/0)	0
Starfish Island	10	JBSI	51° 40’ 45.90”N	128° 7’ 33.90”W	50	5.01	0.20	0.181	Sign.	(3/0)	3
West Beach	11	JBWB	51° 38’ 57.48”N	128° 9’ 15.90”W	51	5.78	0.20	0.173	Sign.	(3/0)	4
Calvert Island	12	JBTH	51° 24’ 41.76”N	127° 55’ 6.90”W	50	5.55	0.20	0.197	Sign.	(3/0)	0
God’s Pocket	13	LDGP	50° 52’ 39.79”N	127° 38’ 53.18”W	40	4.87	0.21	0.112	Sign.	(3/0)	5
Campbell River	14	WHQI	50° 2’ 15.12”N	125° 14’ 31.02”W	40	3.59	0.10	0.091	Sign.	(2/0)	5
Cape Lazo Shoal	15	CLAZ	49° 41’ 56.70”N	124° 50’ 39.09”W	33	3.74	0.09	0.053	N.S.	(1/0)	1
Maude Reef	16	RZMR	49° 29’ 57.00”N	124° 40’ 54.60”W	40	2.15	0.10	-0.108	N.S.	(0/1)	1

(Continued)

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TABLE 1 Continued

Population	Pop	Code	Latitude	Longitude	*n*	*AR*	*pAR*	F_{IS}	HWE test	# Loci (HD/HE)	LD
Hornby Island	17	BHHI	49° 29’ 57.00”	124° 40’ 54.60”W	40	2.53	0.05	-0.079	N.S.	(0/0)	3
Stanley Park	18	BSSP	49° 18’ 10.44”N	123° 6’ 45.61”W	42	3.46	0.43	0.012	N.S.	(0/0)	0
Tofino	19	JETF	49° 6’ 7.77”N	125° 56’ 53.95”W	45	5.10	0.17	0.071	N.S.	(0/0)	0
Aguilar Point	20	LDAP	48° 48’ 54.59”N	125° 10’ 32.92”W	20	4.87	0.15	0.104	N.S.	(0/0)	2
Cape Beale	21	LDCB	48° 47’ 30.00”N	125° 12’ 47.99”W	20	4.97	0.17	0.019	N.S.	(0/0)	0
Dodd’s Narrows	22	RFDN	49° 8’ 9.66”N	123° 49’ 6.60”W	45	4.53	0.21	0.201	Sign.	(3/0)	3
Sansum Narrows	23	WHSN	48° 46’ 51.82”N	123° 33’ 25.52”W	40	4.17	0.21	0.240	Sign.	(2/0)	0
Lumni Island	24	EHLI	48° 39’ 0.52”N	122° 37’ 31.60”W	38	4.63	0.09	0.073	N.S.	(0/0)	0
Turn Rock	25	TMTR	48° 32’ 5.97”N	122° 57’ 51.94”W	40	4.25	0.11	0.042	Sign.	(2/0)	0
Ben Uhre Island	26	DPBU	48° 24’ 18.36”N	122° 37’ 39.50”W	40	4.37	0.11	0.157	Sign.	(3/0)	2
Koitlah Point	27	CPKP	48° 23’ 31.56”N	124° 38’ 40.56”W	40	5.06	0.23	-0.051	N.S.	(0/0)	1
Tatoosh Island	28	CPTI	48° 23’ 28.32”N	124° 44’ 15.38”W	40	5.12	0.16	0.107	Sign.	(1/0)	0
Snow Creek	29	FASR	48° 21’ 12.32”N	124° 32’ 41.83”W	39	4.53	0.10	0.077	N.S.	(1/0)	0
Callam Bay	30	FACB	48° 15’ 24.17”N	124° 16’ 31.31”W	40	4.56	0.14	0.029	N.S.	(0/0)	0
Partridge Point	31	DPPP	48° 13’ 55.92”N	122° 46’ 10.49”W	40	4.17	0.10	0.077	N.S.	(0/0)	0
Cape Alava	32	CPCA	48° 10’ 22.22”N	124° 45’ 2.95”W	26	4.94	0.21	0.027	N.S.	(0/0)	0
Salt Creek	33	FASC	48° 9’ 57.29”N	123° 41’ 49.51”W	39	4.47	0.15	0.025	N.S.	(0/0)	0
Port Townsend	34	LHPT	48° 8’ 33.38”N	122° 46’ 57.03”W	31	4.32	0.11	0.099	Sign.	(2/0)	0
Scatchet Head	35	JGSH	47° 54’ 36.04”N	122° 24’ 50.06”W	40	3.56	0.16	0.022	N.S.	(0/0)	0
Richmond Beach	36	BARB	47° 46’ 16.07”N	122° 23’ 39.26”W	40	2.36	0.03	0.166	N.S.	(0/0)	0
Shilshole Bay	37	BASB	47° 40’ 54.66”N	122° 24’ 32.87”W	41	2.82	0.03	0.108	N.S.	(0/0)	0
Magnolia Bluff	38	BAMB	47° 40’ 50.70”N	122° 23’ 55.07”W	40	2.67	0.04	0.138	N.S.	(0/0)	0
Destruction Island	39	LADI	47° 40’ 29.53”N	124° 28’ 51.53”W	44	4.43	0.14	0.113	N.S.	(1/0)	0
Vashon Island	40	FAVI	47° 22’ 49.48”N	122° 31’ 3.54”W	7	2.43	0.04	0.106	N.S.	(0/0)	0
Tacoma Narrows	41	FATN	47° 15’ 30.49”N	122° 32’ 58.50”W	47	2.29	0.06	0.189	N.S.	(1/0)	0
Squaxin Island	42	HBSI	47° 10’ 1.75”N	122° 53’ 41.67”W	40	1.63	0.02	0.434	Sign.	(2/0)	0
Otter Rock	43	JWOR	44° 45’ 51.08”N	124° 4’ 51.72”W	49	5.76	0.48	0.097	Sign.	(1/0)	4
Port Orford	44	JWPO	42° 44’ 17.83”N	124° 29’ 58.03”W	50	5.96	0.37	0.096	Sign.	(1/0)	4
Crescent City	45	RACC	41° 44’ 53.63”N	124° 12’ 33.74”W	50	6.05	0.35	0.075	Sign.	(3/0)	0
Trinidad Harbor	46	RATH	41° 3’ 20.14”N	124° 8’ 48.02”W	50	4.30	0.35	0.070	N.S.	(1/0)	2
Van Damm A	47	CCVA	39° 16’ 21.48”N	123° 47’ 32.04”W	44	5.47	0.39	0.194	Sign.	(4/0)	0
Van Damm B	48	CCVB	39° 16’ 5.76”N	123° 48’ 2.28”W	41	5.97	0.55	0.146	Sign.	(2/0)	3
Van Damm C	49	CCVC	39° 16’ 9.78”N	123° 47’ 36.18”W	48	6.53	0.50	0.072	Sign.	(3/0)	0
Ocean Cove	50	BSOC	38° 33’ 4.27”N	123° 18’ 26.52”W	50	6.49	0.39	0.119	Sign.	(2/0)	8
Stillwater Cove	51	BSSW	36° 33’ 34.83”N	121° 57’ 7.15”W	50	6.23	0.38	0.203	Sign.	(3/0)	4
Big Creek	52	BSBC	36° 33’ 34.83”N	121° 36’ 0.61”W	51	6.95	0.42	0.032	N.S.	(0/0)	0
Cambria	53	DCCM	35° 31’ 56.44”N	121° 5’ 5.93”W	50	7.00	0.60	0.027	Sign.	(2/1)	1

Population name; Pop, order by decreasing latitude; Code, population short code; geographic coordinates in degrees, minutes, seconds; n, sample size; AR, standardized allelic richness, pAR standardized private allele richness, both based on seven specimen per site; Average F_{IS} (Weir and Cockerham, 1984) across loci; HWE test, was the overall test significance after sequential Bonferroni multiple testing correction; #Loci, number of loci with significant heterozygote deficit (HD) or excess (HE) out of seven loci, after sequential Bonferroni correction. LD, number of pairs of loci, out of 21 pairs, that were significantly associated after sequential Bonferroni correction.

Population genetics summary statistics

Genepop version 4.2 (Rousset, 2008) was used to estimate and test linkage disequilibrium between loci (LD), test for Hardy Weinberg Equilibrium (HWE) within all populations, and estimate genetic differentiation between populations (pairwise F_{ST}). HWE and LD tests were interpreted after a sequential Bonferroni correction for multiple testing was applied to α values (Holm, 1979). An additional genetic differentiation metric was estimated, Jost's D_{EST}, using the R package "diversity" (Keenan et al., 2013). Jost's D_{EST} is included because it is not affected by differences in within-population heterozygosity like F_{ST} (Jost, 2008). Finally, we estimated allelic richness and private allele richness standardized for a sample size of seven individuals (the minimum among sampled sites) using HP-RARE (Kalinowski, 2005). Using the same approach, regional allele and private allele diversity were estimated for the genetically differentiated groups estimated below.

Range-wide genetic differentiation

We used the program STRUCTURE to characterize large-scale patterns of genetic differentiation across the entire distribution of *N. luetkeana* (Pritchard et al., 2000). We used the admixture model for all runs with allele frequencies correlated among populations with an initial burn-in of 250 000 steps and 750 000 (Monte Carlo Markov Chain) repetitions. We ran ten runs per k (number of genetic co-ancestry groups) and let k range from 1 to 8. We then used the Puechmaille method in StructureSelector to determine k (Puechmaille, 2016; Li and Liu, 2018). This method accounts for varying sample sizes between populations. Finally, STRUCTURE outputs were submitted to CLUMPAK to align runs for each k value (Kopelman et al., 2015). To visualize the relatedness between different groups of genetic co-ancestry, we produced a network based on Cavalli-Sforza and Edwards chord distances between sites, using R packages "adegenet" (Jombart, 2008) and "igraph" (Csardi and Nepusz, 2006). The network was pruned by sequentially removing edges with decreasing genetic distance up to one step before two separate networks of connected sites formed.

Additionally, to test for isolation-by-environment (Wang and Bradburd, 2014) that could explain the genetic clusters estimated by STRUCTURE analysis, we ran a canonical correspondence analysis (CCA) in R package "CCA" (González et al., 2008). The response variables were the assignment probabilities (Q-values) for each site to belong to each of four genetic co-ancestry groups detected by STRUCTURE (see results). The environmental predictor variables were site-specific values obtained from NASA's MODIS AQUIS satellite for photosynthetically active radiation (PAR), particulate organic carbon (POC), summer sea surface temperature (SST), spring SST, fall SST, winter SST, light attenuation (measured as kd490) and chlorophyll-a (Chl *a*). We obtained monthly environmental data from 2002 to 2016, collected by NASA's MODIS satellite and accessed through ERDDAP (https://coastwatch.pfeg.noaa.gov/erddap). We used long-term average and seasonal variation (for SST) conditions, hypothesized to affect the physiology of bull kelp. In addition, as predictor variables, we included the latitude and longitude of each site to control for spatial autocorrelation. We used a step-wise model-building approach in the R package "vegan" (Oksanen et al., 2022) to select the best model for the data and used variance partitioning to quantify the variation explained by the tested variables (Borcard et al., 1992; Økland and Eilertsen, 1994).

Seascape genetics in the Salish Sea

The seascape genetics analysis detailed below was only performed for the Salish Sea and adjacent North East Pacific coast sites where we had a higher sampling density and an available hydrodynamic transport model (Yang and Khangaonkar, 2010).

Defining an environmental distance between sites

Environmental data were obtained from NASA's MODIS satellite and accessed through ERDDAP. We characterized pairwise environmental distances using the absolute difference between sites for each of eight variables: photosynthetically active radiation (PAR), particulate organic carbon (POC), particulate inorganic carbon (PIC), summer sea surface temperature (SST), spring SST, fall SST, winter SST, light attenuation (kd490) and chlorophyll-a (Chl *a*).

Characterizing an oceanographic distance

We used the Salish Sea Model (Yang and Khangaonkar, 2010) to simulate particle transport times in the General NOAA Operational Modeling Environment, GNOME (Zelenke et al., 2012), with the intent of estimating oceanographic distance. The average distance between sampled sites often exceeds the species dispersal in a single generation. This constitutes a challenge when using hydrodynamic models to estimate single-generation dispersal because most pairwise site connectivity values would be zero, thus not informative on pairwise site genetic differentiation. One way to tackle this limitation is to consider multiple-generation stepping-stone gene flow to estimate connectivity appropriately, i.e., two sites may be connected through intermediate site(s) across an undetermined numbers of generations (Yang et al., 2016). This approach requires simulating transport from additional kelps beds than just those sampled, hereafter referred to as stepping stone connectivity sites (SSC-sites). We selected SSC-sites using historical kelp bed maps provided by the British Columbia Coastal Resource Information Management System (https://forms.gov.bc.ca/databc-data-request/). Using QGIS Geographic Information System (http://www.qgis.org), we overlaid a 25 km grid over the map of historical kelp bed cover and sampling sites. We selected SSC-sites from the center of grid cells that contained kelp but where no

sample had been collected for this study. Therefore, 42 SSC-sites and 33 sample sites were considered (Supplementary Figure S1). Using the GNOME modeling platform, one thousand particles were released from each site and tracked for 14 days, assuming the same spore longevity as *Macrocystis pyrifera* (Macaya et al., 2005). Spore releases were done separately for 13 periods (every 14 days long) from June to November to cover the season when sori are observed in *N. luetkeana* (Maxell and Miller, 1996). We estimated the probability of transport between pairs of sites as the proportion of particles released from the source site *i* that made it to the destination site *j*. From these transport probabilities, we estimated stepping stone connectivity between sampling sites using a directed network created using R package "igraph" (Csardi and Nepusz, 2006). Network nodes were composed of sample and SSC-sites while edges (the links between nodes) had weights representing the log probability of transport between sites. The shortest path along the network between all pairs of sample sites was found using Dijkstra's algorithm (Dijsktra, 1959) in igraph. Finally, the directional stepping-stone connectivity between site *i* and *j* was measured by summing the log-transformed transport probabilities along the shortest path (Hock and Mumby, 2015). Because this is an asymmetric distance (both *i* to *j* and *j* to *i*), we used the mean value to obtain a single pairwise distance value.

Modeling genetic differentiation

We fitted a multiple linear regression model to estimate how pairwise genetic differentiation, as measured by F_{ST}, could be explained by over-the-water Euclidean distance (isolation by distance, IBD), environmental distance (isolation by environment, IBE) and oceanographic distance (isolation by oceanographic distance, IBOD). Multiple linear regression models were run in R and Akaike information criterion (AIC) to select the best model by eliminating all predictors that had a poor fit with genetic differentiation. A hierarchical partition of variance was used to estimate the proportion variance in genetic differentiation explained independently by the significant predictors remaining in the optimized model. Multicollinearity among predictor variables was checked using the variance inflation factor (VIF).

Results

Allele diversity and within-population genetic analysis

On average, the seven microsatellite markers amplified 25 alleles across the 53 populations, with a maximum of 40 for Ner-11 and a minimum of 14 for Ner-19. Mean allelic richness (*AR*), standardized to 7 individuals per site, ranged between 1.6 and 7.0 alleles·locus^{-1}, with the highest values observed in central California at the southern limit of the species distribution (Figure 1). Lower *AR* values were observed in the inner regions of the Salish Sea, with the lowest value of 1.6 found in Squaxin Island (HBSI), the Puget Sound site farthest from the ocean. Generally, a decreasing *AR* pattern was observed with increasing isolation from the ocean into the Salish Sea (Figure 2). We found intermediate *AR* for the oceanic coast of British Columbia and Washington. At lower latitudes in Oregon and California, *AR* increased, reaching maximum levels at the southernmost sites in California (Figure 1). *AR* values also increased north from the Washington state region in Haida Gwaii, where it was near maximum, and in Alaska at the northern extent of the distribution. Genetic differentiation for all populations, as measured by global F_{ST}, was 0.1567.

Given the patterns of genetic differentiation reported below, standardized regional private allele richness, using three populations, was estimated in HP-RARE for Alaska; Haida Gwaii; Pacific coast of Washington including the Strait of Juan de Fuca; Salish Sea; and Oregon combined with California. California and Oregon had the highest average number of private alleles (1.67), followed by Alaska (1.23), Haida Gwaii (1.00), coastal Washington and Juan de Fuca (0.54), and Salish Sea (0.36). Private allele richness (*pAR*) was also estimated at the site level (Figure 1). The only site sampled in southern Alaska, Dasani Island, part of the larger Prince of Wales Island (TSDI), showed high *pAR* that exceeded the values observed in all Haida Gwaii sites (Figure 1). In the Salish Sea, the kelp bed in Stanley Park (Vancouver) also had higher *pAR* than all other Salish Sea sites. Cambria, the site closest to the southern distribution edge in California, had the highest *pAR* across all sites.

About half of the sites (50.9%) had significant heterozygote deficiency, as indicated after Bonferroni correction was applied to the exact test results. Within these sites, the number of markers with significant F_{IS} ranged from one to four out of seven (Table 1). The correlation coefficient (*r*) between the number of makers showing positive F_{IS} and flagged for potentially having null alleles (MICRO-CHECKER) was 0.74, while *r* between the former and the number of loci pairs with significant linkage disequilibrium was only 0.27. After sequential Bonferroni correction, the maximum number of pairs of loci with significant LD within a population was 8 (out of 21), observed in BSOC. Only eight sites had more than three pairs of loci in LD, whereas 31 sites had zero. The pair of loci Ner-11 and Ner 14 had the most significant LD cases in 11 sites (out of 53), whereas Ner-11 and Ner-13 were significant in 13 sites. Only four pairs of loci (out of 21 pairs) had significant LD in more than four sites.

Range-wide genetic differentiation

STRUCTURE analysis estimated four (*k*) groups of genetic co-ancestry distributed geographically coherently along the entire sampling distribution (Figures 1, 3). An exception to the continuous distribution of these groups was a genetic break observed between the group made by the innermost regions of the Strait of Georgia and Puget Sound (Figure 1). This inner Salish Sea genetic group, characterized by low genetic diversity, was interrupted by sites located in the adjacent eastern areas to the Strait of Juan de Fuca (SJF), which were assigned to the SJF and outer coast dominant group (Figure 4). In addition, we observed

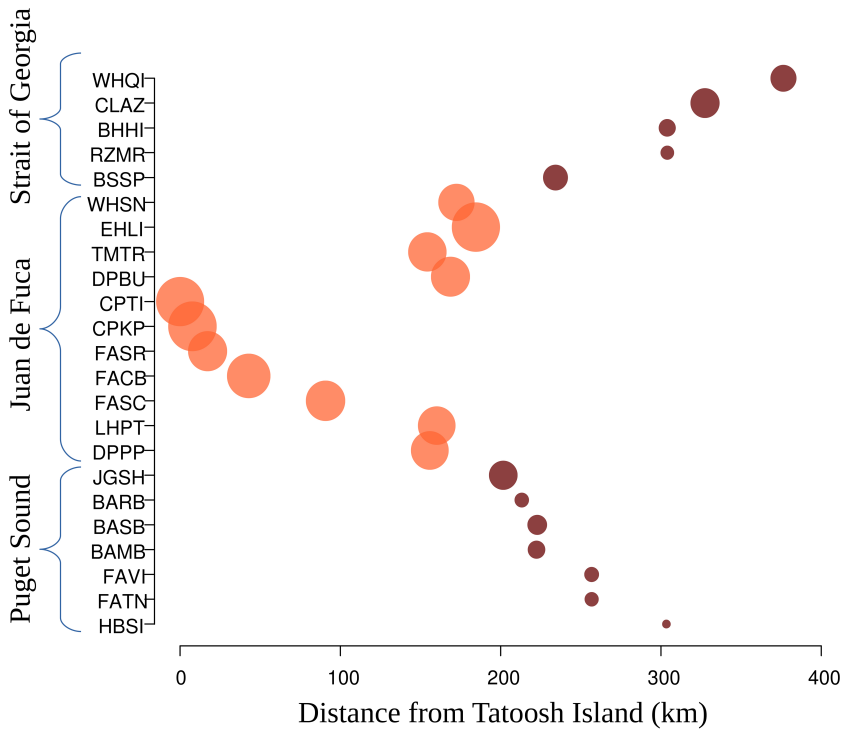

FIGURE 2
Loss of microsatellite allelic richness (circle area), across *Nereocystis luetkeana* Salish Sea sites, with increasing site distance from the ocean. Population names are ordered by latitude on the y-axis. Distances on the x-axis are measured over the water from Tatoosh Island, located at the entry of the Strait of Juan de Fuca. Circle colors represent the dominant STRUCTURE group of genetic co-ancestry for each population (see Figure 3). In Puget Sound, allelic richness decreases with increasing distance into the system to reach a minimum (across all sampled populations) in Squaxin Island. In the Strait of Georgia, allelic richness is lowest in the middle region and recovers in the northernmost sites, likely due to the open connectivity with the ocean provided by Discovery Passage.

two other groups of genetic co-ancestry, one with all sampled Alaska sites and another with sites from Oregon and California. This southernmost group span over 1,000 km across areas of discontinuous habitat. An admixture of genetic co-ancestry was apparent from Haida Gwaii Island to northern Vancouver Island (Figure 1).

To test the isolation by environment model, we used CCA to explore associations between environmental predictors and membership to genetic co-ancestry groups as determined by STRUCTURE analysis for k=4 co-ancestry groups (Figure 5). Model selection resulted in latitude, longitude, PAR, light attenuation, and Chl *a* as significant predictors associated with

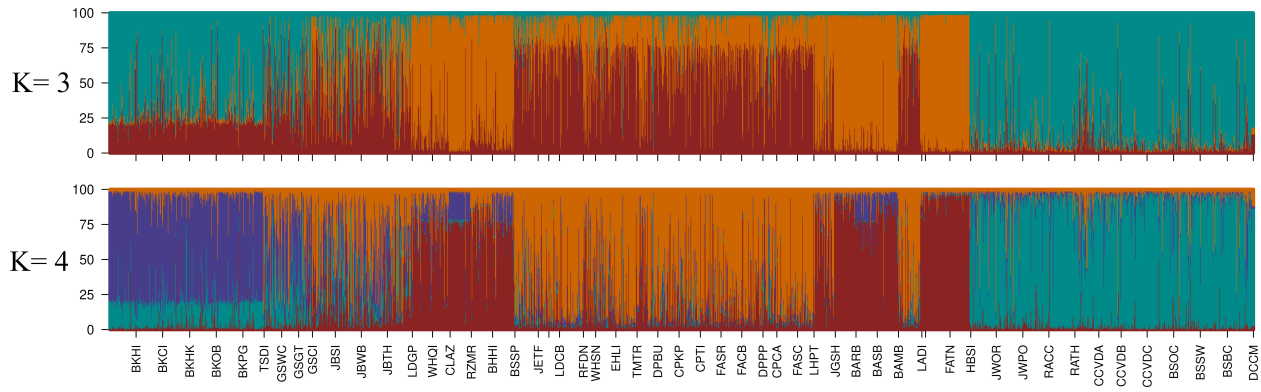

FIGURE 3
STRUCTURE plots for k=3 and k=4 where k is the number of co-ancestry groups, each represented by a different color. Each specimen genotyped has a stacked vertical bar indicating the proportion of its genome assigned to the different co-ancestry groups. Sites are ordered left to right according to their latitude. The Puechmaille method (see methods) provided support for k=4 co-ancestry groups. Each bar represents genetic co-ancestry membership for an individual, and the solid bar at the bottom indicates the co-ancestry group with the maximum mean individual assignment for each site.

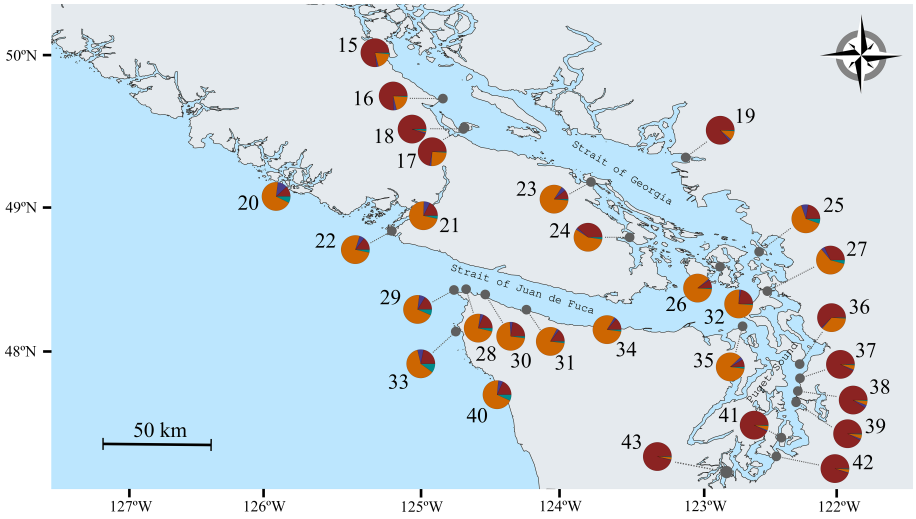

FIGURE 4
Detail of sampling locations of *Nereocystis luetkeana* in the Salish Sea and adjacent areas. For each sample site, a pie chart shows the average proportions of individual assignment to the four groups of genetic co-ancestry estimated with STRUCTURE. A pattern of genetic differentiation between the inner regions of the Salish Sea and the areas adjacent, or belonging to, the Strait of Juan de Fuca and the outer coast was apparent.

mean population proportion assignments to groups of genetic co-ancestry. Light attenuation was not associated with latitude and longitude, while PAR was. However, when spatial auto-correlation (latitude and longitude) was controlled for, light attenuation, PAR, and POC were important variables separating the two STRUCTURE clusters from the Salish Sea and outer coastal area. Variance partitioning showed that environmental predictors and geography explained 70% of the variance. Of this explained variance, 3% was explained by geography, 19% by environmental variables, and 75% was jointly explained by both. When geography was controlled, POC, PAR, light attenuation, and Chl *a* remained significant predictors of population assignment to the different clusters. Under the same model controlling for spatial auto-correlation, Alaska and Oregon/California co-ancestry groups clustered closer to each other, despite being the most geographically separated groups, whereas the inner Salish Sea and outer coastal Washington/British Columbia remained separated (Figure 5B). The relative genetic relatedness between Alaska and the Oregon/California groups, the two groups with the highest *AR*, was also apparent in a genetic distance network (Figure 6).

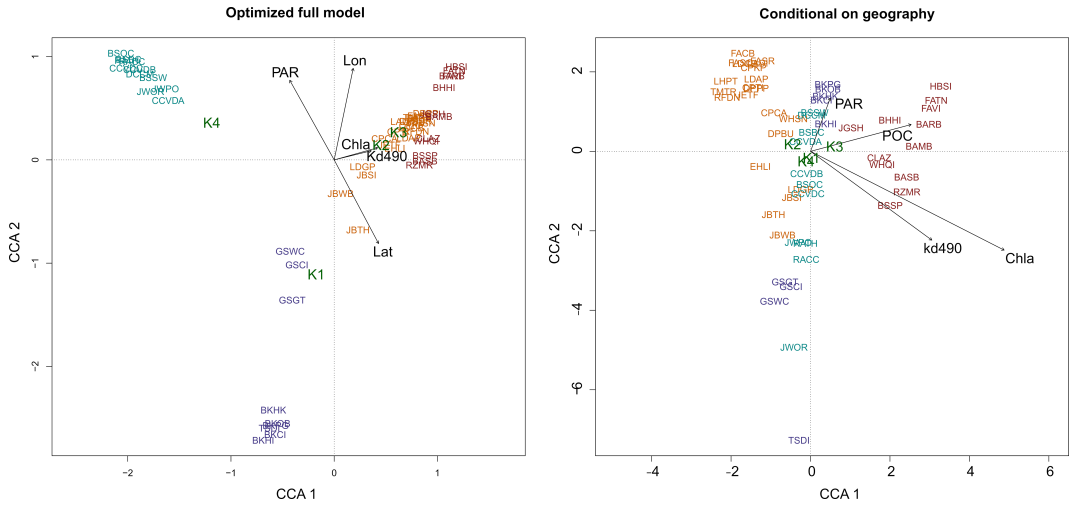

FIGURE 5
Canonical correspondence analysis showing the association of STRUCTURE assignments to the four groups of bull kelp genetic co-ancestry (response variable) and the following predictor variables: photosynthetically active radiation (PAR), particulate organic carbon (POC), summer sea surface temperature (SST), spring SST, fall SST, winter SST, light attenuation (kd490) and chlorophyll-a (chl a). Site names are colored by the dominant group of STRUCTURE assignment: Alaska (purple), outer coastal Washington, British Columbia, Strait of Juan de Fuca, and adjacent areas of Salish Sea (orange), inner Salish Sea (red); and Oregon and California (teal). Site name abbreviations are found in Table 1, and information on predictor variables is found in the Methods.

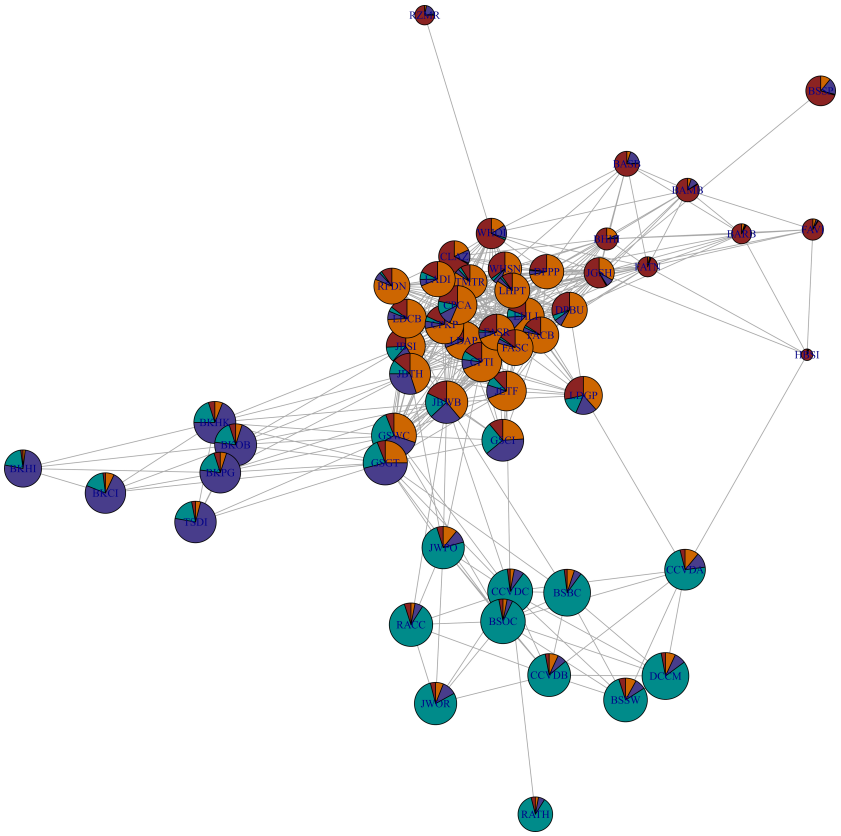

FIGURE 6
Genetic differentiation network for *Nereocystis luetkeana* sites sampled across the species distribution range. Network topology representing pair-wise Cavalli-Sforza and Edwards chord distance between sites. The network was pruned (removal of edges with higher genetic distances) until one step before two clusters of connected sites would be formed. Pie charts for each site show the mean individual assignment to four groups of genetic co-ancestry (same colors as used in other figures). The pie-chart area represents site allelic richness (Figure 1). Genetic distances were calculated with R package adegenet and network produced with R package igraph.

Seascape genetics in the Salish Sea and adjacent areas

Multiple regression analysis identified oceanographic connectivity, spatial distances, and environmental variables as predictors of genetic differentiation within the Salish Sea (Table 2). Temporal variability in oceanographic connectivity revealed slight differences between the different 14-day periods evaluated (Supplementary Table S1). The final optimized multiple regression model included spatial and oceanographic (from July 15th to the 29th period) pairwise distances between sites as predictors of F_{ST}. Likewise, light attenuation (kd490); Chl-*a;* summer, fall and winter SST; PIC; and POC were the environmental distances retained in the final model (Figure 7). Hierarchical partitioning of the model explained variance showed that the largest contributions were made by oceanographic distance (21.4%), PIC (16.7%), summer SST (13.6%), spatial distance (12.2%), POC (10.5%) and light penetration (9.3%). These predictors were positively associated with increased genetic differentiation (F_{ST}), whereas PAR, fall SST and winter SST were negatively associated. The predictors with negative partial regression slopes explained small % of the total variance (< 6%). There was no multicollinearity among the predictors retained in the final model (VIF ranged from 1.2 to 2.5). The final multiple

TABLE 2 Optimized multiple regression model for *Nereocystis luetkeana* pair-wise genetic differentiation (F_{ST}).

Predictor	Std. slope	% independent effects	*t*-test p value
Oceanographic distance	0.27	21.4	***
Spatial Distance	0.32	12.2	***
Light penetration	0.16	9.3	***
PAR	-0.21	6.0	***
POC	0.15	10.5	***
PIC	0.20	16.7	***
SST in summer	0.32	13.6	***
SST in fall	-0.21	5.5	***
SST in winter	-0.10	4.7	*

All predictors below were kept in the final model. Indicated are the standardized partial regression slopes, the percentage of independent effects from each predictor explaining the variance in F_{ST}, and the significance for the test that the slope of each predictor was different from zero.

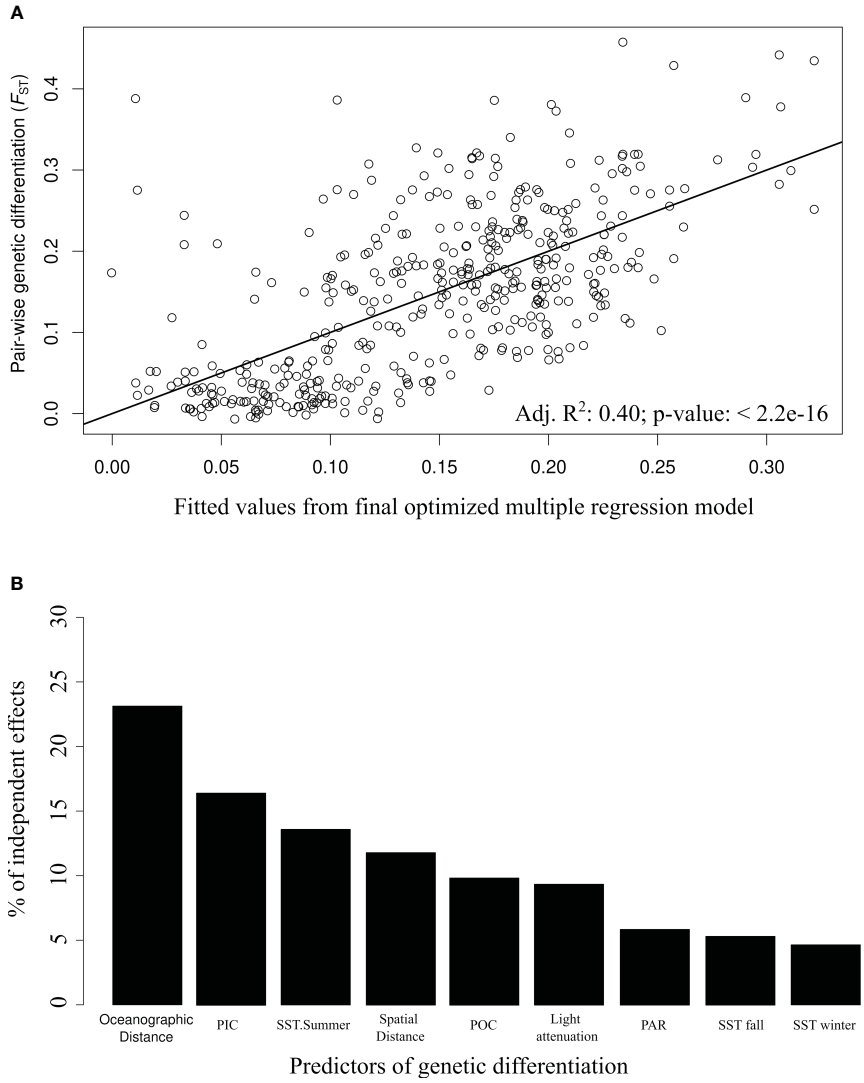

FIGURE 7
Optimized regression model for *Nereocystis luetkeana* pair-wise genetic differentiation (*FST*) in the Salish Sea and adjacent areas **(A)**. Only predictors with significant associations remained in the final model. Their percentage of independent effects on the response variable was estimated using R package hier.part **(B)**.

regression model explained 40% of the genetic differentiation in pairwise F_{ST} between sites in the Salish Sea and adjacent areas.

Discussion

Range-wide genetic structure and diversity

The species distribution level analysis of *Nereocystis luetkeana* revealed four genetic co-ancestry groups with coherent geographic distribution across the species range. Maximum allelic and private allele richness were observed within the southernmost of these groups, at the southern range of the distribution in central California. However, high allelic and private allele richness were also found in the northern part of the species range in Prince of Wales Island (southern Alaska) and Haida Gwaii. These patterns of genetic structure and diversity support the hypothesis that during the last glacial maximum (LGM) *N. luetkeana* had both southern and northern glacial refugia. During this period, much of the coastal Pacific Northwest was glaciated (Mann and Hamilton, 1995; Jacobs et al., 2004) aside from small areas of glacial refugia where species could persist (Blanchette et al., 2008; Shafer et al., 2010; Ager, 2019). At the southern edge of the Alaska group, Haida Gwaii had close to maximum values of allele richness, while the relatively close Prince of Wales Island site of Dasani Island had the highest private allele diversity in the northern group and second highest across all sites. Similar patterns have been recorded in other species and used to support the hypothesis of a northern refugium (Warner et al., 1982; Byun et al., 1997; Soltis et al., 1997; Jacobs et al., 2004; Carrara et al., 2007; Lindstrom, 2009; Shafer et al., 2010). This hypothesis is supported by the likelihood of ice-free conditions (Warner et al., 1982; Mann and Hamilton, 1995) and animal and plant morphological characteristics distinct from those of mainland counterparts (Clarke et al., 2001). The northern part of

Vancouver Island also showed high allelic richness. The continental shelf between Haida Gwaii and Vancouver Island remained ice-free and terrestrial (Guilbault et al., 2003) up until the late Pleistocene when glaciers retreated, and sea level rise filled the area between Haida Gwaii and Vancouver Island. The documented ice-free conditions (Mann and Hamilton, 1995) and similar genetic admixture found in our study between these two islands suggested historic connectivity and a potential recolonization pathway originating in Haida Gwaii and extending into the Salish Sea. Higher allelic richness found further north in the Alaskan Kenai Peninsula, could have resulted from an earlier deglaciation (16,000 ybp) of this area when compared to Washington (14,000-13,000 ybp), allowing for an earlier range expansion north from the Prince of Wales Island and Haida Gwaii refugia (Mann and Hamilton, 1995). Based on molecular evidence, northern refugia for other kelp species have been recently proposed further north in the Gulf of Alaska Bay (Grant and Bringloe, 2020; Grant et al., 2020; Grant and Chenoweth, 2021).

The highest allelic richness values observed in central California just north of Point Conception, at the southern limit of the species distribution, are likely due to a southern glacial refugium resulting from the extension and contraction of species distribution during the glacial-interglacial cycles. This pattern of maximum genetic diversity at the southern ranges of species distribution is well documented in the Northern Hemisphere across many taxa (Bennett et al., 1991; Hewitt, 1996), including seaweed species, such as *Fucus serrat*us (Hoarau et al., 2007), *Macrocystis pyrifera* (Johansson et al., 2015), *Saccorhiza polyschides* (Assis et al., 2016), and across taxa that maintained southern refugia during the LGM (Maggs et al., 2008). A single genetic co-ancestry group was estimated for California and Oregon sites. Interestingly, the separation between this group and Washington sites matches the southern limit of continental glaciation (Dyke, 2004). On land, a secondary biogeographic transition zone, the "Soltis line", has been found across many taxa (Soltis et al., 1997; Wilke and Duncan, 2004; Miller et al., 2006; Jaramillo-Correa et al., 2009). The possible causes for this discontinuity have been proposed to be northwards dispersal during the interglacial and the existence of genetically distinct glacial populations, including the Haida Gwaii islands (Shafer et al., 2010).

When the number of STRUCTURE co-ancestry groups was constrained to three (one below the most supported number of four), Alaska, Oregon and California sites all grouped together. This higher genetic relatedness between the southern and northernmost groups, than between them separately with the Washington groups, was also evident from the CCA, and network analyses. Allelic richness was higher in the California-Oregon and the Alaska-northern British Columbia groups than in Washington, where the inner Salish Sea had the poorest allelic richness observed across the distribution range. Private allele richness was also the lowest in the Salish Sea with an exception found for Stanley Park site (Vancouver). This pattern supports that outer and inner Salish Sea bull kelp descend from a post-glaciation colonization event and thus only represent a subset of the historical diversity (a founder's effect). The high private allele richness at Stanley Park could be evidence that the overall genetic diversity representative of the post-glacial colonization might have been higher and has since been lost due to the small population size and isolation in the Salish Sea.

The coastal extent covered by bull kelp populations sharing the same dominant group of genetic co-ancestry was around ~1,000km for both Alaska and Oregon-California groups. We note that these represent groups sharing a more recent common ancestor, not present-day panmictic populations. The giant kelp, *Macrocystis pyrifera*, a species with similar life history characteristics (e.g., haplodiplontic with spore dispersal) and northern hemisphere distribution, is also characterized by long swats of coast where a single dominant ancestral genetic group dominates (Johansson et al., 2015). These spatially extensive genetic co-ancestry groups spanning discontinuous habitat suggest that multiple-generation, stepping-stone dispersal distances are sufficient to balance the effects of genetic drift that otherwise further isolate populations (Reed et al., 1988; Alberto et al., 2010). This extended dispersal capability may be due to the rafting of adult sporophytes – a mechanism proposed for several kelps that could also occur in *N. luetkeana* (Macaya et al., 2005; Hernández-Carmona et al., 2006; Waters et al., 2018; Fraser et al., 2022). Rafts of *N. luetkeana* have been found far from both the southern and northern edges of the species distribution (Miller and Estes, 1989; Selivanova and Zhigadlova, 1997). In *Macrocystis pyrifera*, adult sporophytes have viable sori after traveling over long distances (Reed, 1987; Hernández-Carmona et al., 2006), and sporophylls were found to maintain buoyancy for up to 21 days (Macaya et al., 2005). Raft dispersal has been suggested across other kelps (Waters et al., 2018; Fraser et al., 2022).

In general, patterns of genetic differentiation for intertidal species in the Pacific Northeast are associated with environmental variation and oceanographic transport. Modeling by Fenberg et al. (2015) identified biogeographic structure for rocky intertidal species, including a main biogeographic break where the North Pacific Current diverges into the California Current and Alaska Current just south of Haida Gwaii Island, which is consistent with data for the California sea cucumber (Xuereb et al., 2018). This diverging current does not appear to be a barrier to gene flow in *N. luetkeana*, as Haida Gwaii and Vancouver Island share similar genetic co-ancestry and are admixture centers, suggesting successful gene flow from multiple populations. Particle transport models by Robinson et al. (2005) found that sea surface currents would allow drifting individuals to be carried between the two islands.

Bull kelp dispersal and mating system

Bull kelp in Alaska and Oregon-California sustain high genetic diversity and low within-region genetic differentiation, suggesting an association between dispersal capacity, large effective population sizes, and outcrossing. At the same time, selfing was supported by significant heterozygote deficiencies at many sites (positive F_{IS}). Generally, there was no regional association with F_{IS}, except in the Salish Sea, where many non-significant values were observed. Given

the extremely low diversity in the inner sites within the Salish Sea, higher biparental selfing is expected in the region. However, the fact that many loci are fixed for dominant alleles at these sites precludes the detection of heterozygote deficiency. Selfing in this mixed mating system species was expected from the unique abscission of the entire ripe sori from blades when spore release starts and the fast rate at which spores are released compared to related species (Amsler and Neushul, 1989). However, this mechanism also makes it possible for spores to be released along a sporophyte's entire vertical distribution, which will maximize the dispersal distance of a fraction of spores. Amsler and Neushul (1989) suggested that bull kelp could disperse some propagules while maintaining others near the environment where the parents have successfully matured. This prediction is supported by the within and between-site genetic diversity pattern found here. The bull kelp sporophyte is largely annual, and its mixed mating system is likely a critical reproductive assurance trait important for species coping with high environmental and demographic variation (Bell et al., 2023; Cavanaugh et al., 2023).

The association between dispersal and mating system is often described between two opposite evolutionary syndromes. On the one hand, a selfing and not dispersing strategy is proposed for species with low or absent inbreeding depression and a predictable environment where locally adapted gene associations are maintained. On the other hand, an outcrossing and dispersing strategy is proposed for species facing inbreeding depression and environmental heterogeneity (Auld and Rubio de Casas, 2013, Cheptou, 2012). Additionally, a "bet-hedging" strategy has been proposed for species with intermediate levels of self-fertilization and predominant local dispersal but maintaining some long-distance dispersal (Cohen, 1966, Simons, 2011). Inbreeding depression is central to the theory behind the maintenance of mixed mating systems due to selection against reduced fitness (Charlesworth and Charlesworth, 1987). Thus, understanding the evolutionary advantages of the unique bull kelp sori abscission, maintenance of a mixed mating system, and long-distance dispersal will require studying inbreeding depression (Raimondi et al., 2004; Barner et al., 2011), as well as the pattern of local adaptation and reproductive assurance at the metapopulation scale (Dornier et al., 2008). In other related kelp species, contrasting results have been found regarding inbreeding depression. The sea palm *Postelsia palmaeformis* has strong genetic differentiation between populations, a mating system strongly reliant on selfing for reproductive assurance and no inbreeding depression (Kusumo et al., 2006; Barner et al., 2011). In giant kelp, *Macrocystis pyrifera*, the mating system is more reliant on outcrossing and dispersal capacity, as suggested by lower F_{IS} in most sites (Johansson et al., 2015) and evidence for inbreeding depression (Raimondi et al., 2004). Given our results and bull kelp life history traits we posit that its mating system is intermediate to *P. palmaeformis* and *M. pyrifera*. Future studies on the species inbreeding depression will inform our fundamental understanding of kelp life history variation and directly apply to the growing restoration and breeding efforts targeting this kelp.

Patterns of genetic differentiation within the Salish Sea

In the Salish Sea, we observed a disjunct population structure where the inner Puget Sound and Strait of Georgia sites were genetically differentiated (and had lower genetic diversity) from those in the outer coast, Strait of Juan de Fuca, and adjacent Salish Sea region. This pattern does not follow a simple isolation by distance (IBD) model of genetic differentiation because some sites directly adjacent (e.g., Admiralty Inlet and Suan Juan Islands) transition sharply between co-ancestry groups. This disjunctive pattern within the Salish Sea is inconsistent with similar studies on fish species that have mobile larval stages, such as the Pacific hake, *Merluccius productus* (Iwamoto et al., 2015) and copper rockfish, *Sebastes caurinus* (Buonaccorsi et al., 2002). These studies support the hypothesis that currents in the Strait of Juan de Fuca are a barrier to gene flow between these inner waterways. The Strait of Juan de Fuca is a highly dynamic environment with large fluxes of water movement each day (Khangaonkar et al., 2018) that could limit gene flow between the Strait of Georgia and the inner regions of Puget Sound.

The inconsistency between fish models and *N. luetkeana* is that within the Puget Sound and Strait of Georgia bull kelp colonization post-glaciation resulted in a founder's effect and reduction of genetic diversity. This hypothesis is supported by allelic richness values that show a stepwise reduction from Alaska southward and into the Salish Sea. There is a further reduction of diversity with distance from the outer coast moving inward within the Salish Sea, with the lowest values found in the southernmost site, Squaxin Island (Figure 2). Founder effects have been suggested for other species with distributions that span the outer coast of Washington and the Salish Sea, such as the Pacific hake *M. productus* (Iwamoto et al., 2015). A founder effect for bull kelp in the Salish Sea is likely accentuated by increased isolation and habitat fragmentation further into Puget Sound and parts of the Strait of Georgia. In the inner regions of the Puget Sound, bull kelp has declined dramatically over the past few decades, more so recently. In south Puget Sound, bull kelp canopy decreased 63% basin-wide from the 1870s to 2017, with up to 96% loss in smaller sub-basins (Berry et al., 2021). Several factors, including increased temperature, may be causing the recent declines and increased fragmentation (Pfister et al., 2017; Beas-Luna et al., 2020; Supratya et al., 2020; Starko et al., 2022). Recent bottlenecks could be why a single Salish Sea site (Stanley Park) had high private allele richness.

The genetic similarity between the inner regions of the Strait of Georgia and Puget Sound found with this set of microsatellite markers might mask some differentiation across the entire genome. When only looking at a limited number of microsatellite markers, the two regions could have been assigned to the same genetic co-ancestry group simply due to the chance of fixing the same dominant alleles in a common ancestor population during the population bottleneck. Any further divergence between the Strait of Georgia and Puget Sound might go undetectable if populations are highly homozygous or may require scanning a larger region of the genome (e.g., SNP analysis).

Oceanographic distance was a better predictor of genetic differentiation between sites than over-the-water spatial distance. The Salish Sea is influenced by coastal oceanographic currents predominantly through the Strait of Juan de Fuca and less so by the northern limit of the Strait of Georgia. Khangaonkar et al. (2018) showed that less than 12% of the water that flows from the Pacific into the Strait of Juan de Fuca makes it into the Puget Sound; in comparison, up to 42% reaches the Strait of Georgia, and the remaining 46% is returned into the Pacific Ocean. This suggests that ocean currents affect the Salish Sea more directly in the Juan de Fuca and Georgia Straits than in Puget Sound. The importance of oceanographic currents as a driver of gene flow has been found across a variety of marine dispersed taxa, including other kelps (White et al., 2010; Alberto et al., 2011; Truelove et al., 2017; Wesselmann et al., 2018; Xuereb et al., 2018; Gouvêa et al., 2023).

The multiple regression model and the CCA showed an association between environmental and genetic variation within the Salish Sea. Light attenuation, chl *a*, summer SST and POC were all significant predictors of genetic differentiation in the region. Despite a vigorous exchange flow with the Ocean (Khangaonkar et al., 2018), the Salish Sea is a region with substantial environmental variation from the outer Ocean, with the largest gradients for the above variables (in addition to PIC and light penetration) across the species range. In addition, other interacting sources of environmental variation are associated with anthropogenic factors (Sobocinski et al., 2018). For example, the major cities of Seattle and Vancouver provide a high influx of pollutants, such as sewage and other runoff, often in the form of suspended sediment in the water column. Sedimentation reduces light penetration in the water column and negatively affects the recruitment of *N. luetkeana* zoospores and juvenile sporophytes (Carney, 2003).

Temperatures above 19°C inhibit the formation of germ tubes in *N. luetkeana* zoospores, effectively halting the life cycle before gametophyte development (Schiltroth et al., 2018). Other experiments on the effects of temperature on bull kelp production of gametophytes and embryonic sporophytes suggest that adverse effects might start at temperatures as low as 15°C (Korabik et al., 2022). The observed association of genetic differentiation with Summer SST is therefore expected under a model of localized adaptation to a warmer environment. However, such a model will require validation from direct fitness measurements from reciprocal transplant studies. We are currently using a genome-wide molecular approach combined with reciprocal transplants to investigate if the isolation by environment (IBE) found within the Salish Sea has an adaptive basis.

Bull kelp conservation

We observed that near maximum *N. luetkeana* allelic richness persisted in northern California despite the recent dramatic population declines (Rogers-Bennett and Catton, 2019). Samples in this study from this region were collected in 2016, two years after the documented decline, while the sporophyte density was still extremely low. A recent study using high-resolution CubSats imagery showed that despite the regional kelp forest collapse, there were small remnant pockets where bull kelp sporophytes could survive (Cavanaugh et al., 2023). Therefore, despite near-complete canopy loss, genetic diversity was still comparable to maximal values recorded further south in California, where these declines were not observed (Bell et al., 2023). A future study using population genetics simulations, guided by satellite-derived population size census (Cavanaugh et al., 2023; Saccomanno et al., 2023) and dispersal estimates obtained from oceanographic transport models (Gaylord et al., 2006) can inform if the high genetic diversity found in the region could have been maintained by these remnant populations. A non-mutual exclusive explanation for genetic diversity resilience is the presence of a bank of gametophytes with delayed development, acting as a reservoir of the effective population size while the sporophyte generation is down (Carney, 2013, Edwards, 2022). More species-specific studies on delayed development of gametophytes are needed (Veenhof et al., 2022); new eDNA methods could assist in this regard (Schoenrock et al., 2021).

The reduction in genetic diversity within the inner regions of the Salish Sea, combined with environmental stressors due to proximity to metropolitan areas, raises concerns for the future of bull kelp in this region. Low genetic diversity is associated with decreased resilience to increasing temperatures in seagrasses (Reusch et al., 2005; Hughes et al., 2008; Duarte et al., 2018). Currently, we hold ex-situ collections of gametophytes from California and Puget Sound that are sufficiently large (> 1,800 haploid genotypes) to contain a large fraction of the extant genetic diversity and can be used to restore threatened areas (Wade et al., 2020).

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://datadryad.org/stash, DOI: 10.5061/dryad.g4f4qrfvt and https://github.com/falberto73/NereoFMSpaper.

Author contributions

FA: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Visualization, Writing – review & editing. LG: Formal Analysis, Investigation, Methodology, Software, Writing – original draft. NC: Methodology, Project administration, Resources, Writing – review & editing. TK: Funding acquisition, Investigation, Methodology, Resources, Software, Writing – review & editing. TM: Funding acquisition, Methodology, Project administration, Resources, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1275905/full#supplementary-material

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