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The *5th World Conference on Marine Biodiversity Collection* - published in the *PeerJ Life & Environment journal* - collates research presented at the 2020 edition of the WCMB series, which was held virtually by the University of Auckland, New Zealand in December of that year.

The WCMB series first started in 2008, and has become a major focal assembly for sharing research outcomes, management and policy issues, as well as discussions on the role of biodiversity in sustaining ocean ecosystems. This meeting brings together scientists, practitioners, and policy makers to discuss and advance our understanding of the importance and current state of biodiversity in the marine environment.
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At launch, this Conference Collection is formed of four published articles: the discovery of extensive fields of cyanobacteria-like mats that threaten coral health off Rapa Nui (Easter Island); a study into the distribution of 71,108 amphipods from 355 species across the Icelandic seabed; a model to predict the distribution of sponge and coral species in unexplored seamounts off South America; and an investigation into a marine national park which is important for the dispersal and connectivity of coral reef-dwelling species in the South China Sea.

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Biogeography, diversity and environmental relationships of shelf and deep-sea benthic Amphipoda around Iceland

Anne-Nina Lörz[1], Stefanie Kaiser[2], Jens Oldeland[3], Caroline Stolter[4], Karlotta Kürzel[5] and Saskia Brix[6]

[1] Institute for Marine Ecosystems and Fisheries Science, Universität Hamburg, Hamburg, Germany
[2] Faculty of Biology and Environmental Protection, Department of Invertebrate Zoology and Hydrobiology, University of Łódź, Lodz, Poland
[3] Eco-Systems, Hamburg, Germany
[4] Department Biology, Zoological Institute, Universität Hamburg, Hamburg, Germany
[5] Department Biology, Universität Hamburg, Hamburg, Germany
[6] Deutsches Zentrum für Marine Biodiversität, Senckenberg Nature Research Society, Hamburg, Germany

ABSTRACT

The waters around Iceland, bounding the Northern North Atlantic and the Nordic seas, are a region characterized by complex hydrography and seabed topography. This and the presence of the Greenland-Iceland-Faroe-Scotland ridge (GIFR) are likely to have a major impact on the diversity and distribution of the benthic fauna there. Biodiversity in this region is also under increasing threat from climate-induced changes, ocean warming and acidification in particular, affecting the marine realm. The aim of the present study was to investigate the biodiversity and distributional patterns of amphipod crustaceans in Icelandic waters and how it relates to environmental variables and depth. A comprehensive data set from the literature and recent expeditions was compiled constituting distributional records for 355 amphipod species across a major depth gradient (18–3,700 m). Using a 1° hexagonal grid to map amphipod distributions and a set of environmental factors (depth, pH, phytobiomass, velocity, dissolved oxygen, dissolved iron, salinity and temperature) we could identify four distinct amphipod assemblages: A Deep-North, Deep-South, and a Coastal cluster as well as one restricted to the GIFR. In addition to depth, salinity and temperature were the main parameters that determined the distribution of amphipods. Diversity differed greatly between the depth clusters and was significantly higher in coastal and GIFR assemblages compared to the deep-sea clusters north and south of the GIFR. A variety of factors and processes are likely to be responsible for the perceived biodiversity patterns, which, however, appear to vary according to region and depth. Low diversity of amphipod communities in the Nordic basins can be interpreted as a reflection of the prevailing harsh environmental conditions in combination with a barrier effect of the GIFR. By contrast, low diversity of the deep North Atlantic assemblages might be linked to the variable nature of the oceanographic environment in the region over multiple spatio-temporal scales. Overall, our study highlights the importance of amphipods as a constituent part of Icelandic benthos. The strong responses of amphipod communities to certain water

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Corresponding author
Anne-Nina Lörz, Anne-Nina.Loerz@uni-hamburg.de

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mass variables raise the question of whether and how their distribution will change due to climate alteration, which should be a focus of future studies.

Subjects Biodiversity, Biogeography, Ecology, Marine Biology, Zoology
Keywords Amphipoda, Biodiversity, Biogeography, Deep sea, North Atlantic, Arctic, Water masses, Benthic

INTRODUCTION

Human impacts on the world's oceans are fundamentally altering the biogeography and biodiversity of marine communities (*Lotze et al., 2006*; *Halpern et al., 2008*). Cumulating effects of climate change, resource exploitation and pollution are particularly pronounced in the Northern Hemisphere, and some of these changes have already evoked significant biotic responses, such as shifts in distribution and abundance (*e.g*., *Harley et al., 2006*; *Jones et al., 2014*; *Birchenough et al., 2015*; *Hiddink, Burrows & García Molinos, 2015*). The pace and strength of global warming and increased atmospheric CO_2 may be faster and greater in the ocean than in the terrestrial realm (*Burrows et al., 2011*), but our knowledge of the consequences for the marine biota is limited (*Richardson & Poloczanska, 2008*). Uncovering distribution patterns of species and the identification of the ecological and evolutionary factors and processes responsible for them is therefore vital for predicting biodiversity responses to global change.

A complex array of mechanisms have been identified to determine the distribution of species on multiple spatial and temporal scales (*Leibold et al., 2004*). Abiotic variables confine the space that species occupy according to their physiological limits (*Chase & Leibold, 2003*). Species' dispersal capacity alongside their evolutionary heritage defines the size of their realized distribution (*Grantham, Eckert & Shanks, 2003*; *Hilário et al., 2015*; *Baco et al., 2016*). Finally, biological relationships are known to structure spatial patterns of species in many ways, such as those associated with competitors, consumers, and facilitators (*Jablonski, 2008*; *Bascompte, 2009*).

Environmental differences may be less obvious in the deep sea (>200 m) than in the shallows. It is now clear, though, that there is considerable spatial and temporal variation in the physical and biological properties to which species are exposed and which determine their distribution. Processes associated with sediment properties, temperature, salinity, nutrient input and dissolved oxygen are among the main drivers for structuring biodiversity and its geographical distribution (*Levin et al., 2001*; *Schnurr et al., 2018*). However, there is still a lack of understanding of distribution boundaries in the marine realm and even less so in the deep sea (*Lourie & Vincent, 2004*; *Rex et al., 2005*), making it difficult to predict how communities will respond in the wake of a changing ocean.

The waters around Iceland and adjoining seas represent a spatially heterogeneous environment with steep gradients that promote distinct habitats and related communities. As a boundary region between temperate North Atlantic, and polar waters, they are also considered to be very susceptible to climatic changes (*Astthorsson, Gislason & Jonsson, 2007*; *Eiríksson et al., 2011*). Iceland is located on top of the mid-Atlantic ridge and is criss-crossed by several topographic barriers that determine the flow of water masses and ultimately the distribution of species. At the forefront is the Greenland-Iceland-Faroe ridge (GIFR), which stretches from Scotland and the Faroes *via* Iceland to Greenland, and and restricts the exchange of water masses between the warm, salty North Atlantic waters and the cold and less salty Nordic Seas (*Hansen et al., 2008*). As a result, seabed temperature and salinity differ strongly between areas north and south of the GIFR, which, in turn, can lead to marked differences in species compositions (*Weisshappel & Svavarsson, 1998*; *Weisshappel, 2000*; *Bett, 2001*; *Weisshappel, 2001*; *Brix & Svavarsson, 2010*; *Dauvin et al., 2012*; *Jochumsen, Schnurr & Quadfasel, 2016*; *Schnurr et al., 2018*). Alterations of the physicochemical environment, including temperature rise, ocean acidification, and salinity, have already been observed around Iceland (*Astthorsson, Gislason & Jonsson, 2007*; *Olafsson et al., 2009*; *Seidov et al., 2015*; *Jochumsen, Schnurr & Quadfasel, 2016*). Knowledge on the most important environmental parameters structuring deep-sea benthic communities would therefore allow prediction of future changes for those communities.

Amphipod crustaceans are very common and diverse across marine benthic habitats (*Just, 1980*; *De Broyer & Jazdzewski, 1996*; *Lörz, 2010*; *Stransky & Brandt, 2010*; *Brix et al., 2018*; *Jażdżewska et al., 2018*), and also in Icelandic waters (*Weisshappel, 2000*; *Weisshappel, 2001*; *Dauvin et al., 2012*; *Brix et al., 2018*). Their occurrence in a wide variety of marine environments, in turn translates into a diverse feeding types that comprise detritivores, suspension-feeders, predators, and scavengers amongst others (*Guerra-García et al., 2014*). But they also play a central role in the marine food web (*e.g.*, *Lörz, 2010*; *Nyssen et al., 2002*). Amphipods, as a member of the crustacean superorder Peracarida, have a brooding life style, from which a limited dispersal capacity is derived for most species making them potentially very susceptible to environmental change (*e.g.*, *Jablonski & Roy, 2003*; but see *Lucey et al., 2015*). Exceptions are purely pelagic species (*e.g.*, within the Hyperiidea) or species of the highly mobile scavenging guild.

The aim of this study was to identify the main factors influencing the distribution and biodiversity of marine amphipods in the waters around Iceland. This could provide hints as to which variables could most importantly affect distribution changes as a result of climate change. For this purpose, a comprehensive data—set from the literature and recent expeditions was compiled constituting distributional records for 355 species across a major depth gradient (18–3,700 m). These come from historical missions, in particular the Danish Ingolf expedition (1895 and 1896), which carried out sampling in Icelandic and West Greenlandic waters (*Stephensen, 1944b*), but mainly from sampling as part of BIOICE (Benthic Invertebrates of Icelandic Waters) and IceAGE (Icelandic marine Animals: Genetics and Ecology) projects (*e.g.*, *Brix et al., 2014*). Earlier community analyses of the Icelandic amphipod fauna identified depth as a strong driver of species distributions, but water mass properties were also important (*Dauvin et al., 2012*; *Brix et al., 2018*). In this regard, the GIFR appears to act as a major, albeit surmountable distributional barrier (*Weisshappel & Svavarsson, 1998*; *Weisshappel, 2000*; *Weisshappel, 2001*; *Dauvin et al., 2012*; *Brix et al., 2018*). Therefore, we tested whether geographical distinctions of Iceland, mainly determined by the GIFR and depth, are mirrored by the distribution of benthic amphipods.

MATERIALS & METHODS

Amphipoda data

We compiled data on occurrences and abundance of 355 amphipod species for 532 localities from the literature. The following expeditions and respective data sources were used: extensive literature search, data from BIOICE and IceAGE expeditions. The assembled dataset was highly heterogenous regarding sampling effort and method, time, location and date of the different expeditions. Many only listed one or two species, in particular the historic data from *e.g.*, *Boeck (1861)*, *Hansen (1887)* and *Stephensen (1933*, *1938*, *1942*, *1944a*, *1944b)* only providing occurrence data. However, other had high abundances of individuals (max: 2,709) and high species richness (max: 72). Due to this high heterogeneity, we aggregated the data at a coarser spatial resolution.

A common approach is to construct a coarse rectangular grid in which species occurrences are joined. We constructed a hexagonal grid using QGIS (*QGIS Development Team, 2019*) with a horizontal diameter of 1° per grid cell. Within each grid cell, the occurrence and abundance information were pooled, so that a grid cell contained information from multiple localities but species were not double counted, yet the sum of the abundances per species could be calculated. Hexagonal grids have several advantages over rectangular grids, *e.g.*, symmetric neighbourhood relations or reduced edge effects (*Birch, Oom & Beecham, 2007*). For our study the most compelling reason to favour a hexagonal grid was the match of the polygons to the coastlines of Iceland and Greenland. Hexagonal grids provided a much better fit to this jagged pattern with an appropriate size, whereas rectangular grid cells would have to be much smaller and would then be too small for the purposes of our sampling. Given the case that many of our samples were near the coast, the hexagonal design clearly improved our sampling design.

Environmental layers

We extracted twelve variables from the Bio-Oracle 2.0 database (*Assis et al., 2018*) using the *sdmpredictors* package (*Bosch, Tyberghein & De Clerck, 2018*). Variables were chosen to represent major environmental deep-sea gradients (Table 1). All variables, except minimum depth, represented long-term maximum values modelled at minimum depths on a raster with 7 km^2 resolution per cell. In order to use the parameters on the same spatial scale as the species data, we aggregated the raster data to the scale of the hexagonal grid cells by calculating the mean raster value for each grid cell. Hexagons then represented the summed species abundances and averaged environmental data.

We analysed the environmental data for multicollinearity on the level of the hexagons. We calculated a Pearson correlation matrix (AppS1) for all environmental layers and removed all layers with a Pearson's r above 0.75. As expected, we found strong correlation between parameters of the same information type, *i.e.*, Chl-*a* and primary productivity or all nutrient related parameters. Finally, we retained the following parameters: depth, pH, phytobiomass, velocity, dissolved oxygen, dissolved iron, salinity and temperature.

Table 1 **Environmental parameters.**

Acronym	Parameter	Units	Source
depth	Bathymetry	meters	GEBCO URL: http://gebco.net Bathymetry URL: http://www.emodnet-bathymetry.eu/
chla	Chlorophyll concentration	mg/m^2	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
vel	Current velocity	m/s	Global Ocean Physics Reanalysis ECMWF ORAP5.0 (1979–2013) URL: http://marine.copernicus.eu/
dO_2	Dissolved oxygen concentration	µmol/m^2	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
dFe	Dissolved iron concentration	µmol/m^2	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
dP	Phosphate concentration	µmol/m^2	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
dNO_3	Nitrate concentration	µmol/m^2	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
temp	Sea water temperature	degrees Celcius	Global Ocean Physics Reanalysis ECMWF ORAP5.0 (1979–2013) URL: http://marine.copernicus.eu/
phybio	Carbon phytoplankton biomass	µmol/m^2	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
prod	Primary production	g/m^2/day	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
Salinity	Sea water salinity	PSS	Global Ocean Physics Reanalysis ECMWF ORAP5.0 (1979–2013) URL: http://marine.copernicus.eu/
SiO_4	Silicate concentration	µmol/m^2	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/

Note:
Environmental parameters initially extracted from the BIO-ORACLE 2.0 database. All parameters are long-term maxima at minimum depth, except bathymetry, which represents the deepest (=minimum) depth measured.

We kept salinity although it was correlated with temperature as it is an important parameter to structuring deep-sea communities around Iceland (*e.g.*, *Weisshappel & Svavarsson, 1998*).

Environmental cluster analysis

We hypothesized that deep-sea regions with similar environmental conditions would have a similar benthic fauna. Hence, we clustered the hexagonal grid cells based on the reduced set of the averaged environmental layers into a small set of environmentally homogenous regions. We used the *mclust* package (*Scrucca et al., 2016*) to conduct model-based hierarchical clustering using finite Gaussian Mixtures. The clustering algorithm compares 14 differently shaped types of Gaussian covariance structures representing different kinds of elliptical shapes ordered by an increasing complexity. The different models are compared using the Bayesian Information Criterion (*Burnham & Anderson, 2002*) choosing the model with the lowest complexity. Based on the plot of the different BIC models for possible cluster sizes from 2 to 10 (S3), we identified the optimal cluster as that one with highest regionalization capacity, *i.e.*, having a low number of clusters but already touching the plateau of the curve, signalling little differences in the model fit. We further confirmed the optimal number of clusters using a bootstrapped sequential likelihood ratio test (*Scrucca et al., 2016*) by comparing an increasing number of cluster sizes. Finally, we calculated mean, standard deviation, minimum and maxima for each parameter and cluster combination. This was done to allow an interpretation of the environmental conditions representing the clusters.

Taxonomic data

To interpret the overlap between clusters in terms of species composition, we first performed a constrained analysis of principal coordinates (CAP) (*Anderson & Willis, 2003*) with presence absence information and the Jaccard distance measure. CAP is an ordination technique, that allows to visualize similarities in sites based on species composition and environmental correlates. The ordination diagram was visually inspected by plotting the sites encircled by hulls on the first two axes. We further calculated the ANOSIM statistic on presence/absence transformed species data. ANOSIM is a non-parametric method to measure the community-wise overlap between different clusters (*Clarke, 1993*). It yields a statistic called R that is in the range from 0 to 1 with values of R below 0.5 indicating strong overlap. The statistic is tested for significance using a permuted p-value (n = 9,999). R-values above 0.75 indicate largely non-overlapping clusters with strongly different species composition. Both analyses were performed using the vegan package (*Oksanen et al., 2019*).

To identify characteristic species for each cluster, we identified all species being positively associated with one specific cluster or combinations of clusters using the *multipatt* function of the *indicspecies* package (*Cáceres & Legendre, 2009*). We used the group-size corrected Indicator Value (IndVal.g) as a measure of association. The null hypothesis tested is that the association of a species is not higher in a specific cluster than in the other clusters. This function calculates a p-value based on 9,999 permutations, which is not corrected for multiple testing. However, as we are not interested in the number of indicator species, but in whether a species has a high association to a cluster or not, the p-values do not have to be adjusted (*De Cáceres, Legendre & Moretti, 2010*). After the analysis, species with high association values were extracted as lists for each cluster combination. The resulting species-cluster relationship was compared with literature and information from the World Register of Marine Species (WoRMS) database (*Horton et al., 2021*).

Diversity

We aimed to compare amphipod diversity between the different clusters. However, due to different numbers of samples (n = 136), *i.e.*, hexagonal cells, that contained the species data, clusters were not directly comparable in terms of diversity. Hence, we conducted a combined rarefaction-extrapolation analysis based on Hill numbers (*Chao, Chiu & Jost, 2014*). The concept of comparing species diversity using Hill numbers stems from the fact that most diversity indices are measures of entropy, such as Shannon or Simpson and do not translate directly into a diversity measure although often applied in such a way (*Jost, 2006*). Yet three well known measures of diversity *i.e.*, species richness, Shannon and Simpson diversity (*Shannon & Weaver, 1949*; *Simpson, 1949*) can be generalized by a formula derived by Hill (*Jost, 2006*; *Chao, Chiu & Jost, 2014*) which orders the indices along an order of q, *i.e.*, q = 0, 1, 2 translating to richness, Shannon and Simpson, respectively. This order reflects an increasing importance of the evenness component of diversity, while the richness component becomes less effective. This means that for richness, there is no effect of abundance on the diversity measure, while for the Simpson index, rare species only have little effect on the estimated diversity values. Hence, the Simpson index is often thought to be the most robust index, when number of individuals strongly differ, as is the case here. The diversity information is transformed into a common measure of diversity, the effective number of species, which is the number of species having equal abundances that would be required to reach *e.g.*, the Shannon entropy value of the sample. This measure allows comparisons of all three different indices having the same unit, the effective number of species. We performed the analysis using the iNEXT package (*Hsieh, Ma & Chao, 2016*) based on the summed abundance vectors per species and cluster.

When studying deep-sea organisms, the most important indirect environmental gradient is depth in meters. In order to evaluate the diversity pattern related to depth we studied the original data from the different stations (n = 532) and expeditions. First, we calculated a Poisson Generalized Linear Model (GLM) to quantify the relationship between the number of species per station and depth in meters. Then we split the depth gradient in 100-m intervals to study the trend of the maximum number of species across the depth gradient.

RESULTS

General

The total number of amphipod individuals analyzed is n = 71,108. The assembled dataset contained 355 species from 141 genera and 44 families (Tab. 2). From these, 101 species were only be identified to the genus level, where species were given a numerical code. The original number of stations from the expeditions (n = 532) were reduced to a set of 136 one-degree wide hexagonal cells in order to reduce the heterogeneity in the dataset. These hexagonal cells were clustered according to their environmental conditions. The entire dataset is available *via* Peer J supplement as well as Pangaea (GfBIO) https://doi.pangaea.de/10.1594/PANGAEA.931959 (*Lörz et al., 2021*).

Environmental clusters

The *mclust* algorithm identified six clusters to be the optimal configuration according to BIC and the likelihood ratio tests. However, when aggregating the species data to six clusters, this would result in clusters with disproportionally large differences in samples per cluster. Hence, we reduced the final number of clusters to four (Fig. 1). As the clustering is hierarchical, and the four-cluster solution is not much worse in terms of BIC we were confident that this aggregation is more informative with regard to the species than the six-cluster solution which would have split the northern and southern clusters into separate regions for the specific basins (the six cluster map is shown in the Supplementary Data). The four-cluster solution also provides a good overview of the large-scale spatial

Table 2 **Amphipoda species.**

Nr	Species	Authority	Family
1	*Abludomelita gladiosa*	(Spence Bate, 1862)	Melitidae
2	*Abludomelita obtusata*	(Montagu, 1813)	Melitidae
3	*Acanthonotozoma cristatum*	(Ross, 1835)	Acanthonotozomatidae
4	*Acanthonotozoma serratum*	(O. Fabricius, 1780)	Acanthonotozomatidae
5	*Acanthostepheia malmgreni*	(Goës, 1866)	Oedicerotidae
6	*Aceroides latipes*	(G.O. Sars, 1883)	Oedicerotidae
7	*Aeginella spinosa*	Boeck, 1861	Caprellidae
8	*Aeginina longicornis*	(Krøyer, 1843)	Caprellidae
9	*Ambasia atlantica*	(H. Milne Edwards, 1830)	Ambasiidae
10	*Ampelisca aequicornis*	Bruzelius, 1859	Ampeliscidae
11	*Ampelisca amblyops*	G.O. Sars, 1891	Ampeliscidae
12	*Ampelisca compacta*	Norman, 1882	Ampeliscidae
13	*Ampelisca eschrichtii*	Krøyer, 1842	Ampeliscidae
14	*Ampelisca gibba*	G.O. Sars, 1883	Ampeliscidae
15	*Ampelisca islandica*	Bellan-Santini & Dauvin, 1996	Ampeliscidae
16	*Ampelisca macrocephala*	Liljeborg, 1852	Ampeliscidae
17	*Ampelisca odontoplax*	G. O. Sars, 1879	Ampeliscidae
18	*Ampelisca* sp. A	Krøyer, 1842	Ampeliscidae
19	*Ampelisca* sp. B	Krøyer, 1842	Ampeliscidae
20	*Ampelisca uncinata*	Chevreux, 1887	Ampeliscidae
21	*Amphilochoides boecki*	G.O. Sars, 1892	Amphilochidae
22	*Amphilochoides serratipes*	(Norman, 1869)	Amphilochidae
23	*Amphilochus anoculus*	Tandberg & Vader, 2018	Amphilochidae
24	*Amphilochus hamatus*	(Stephensen, 1925)	Amphilochidae
25	*Amphilochus manudens*	Spence Bate, 1862	Amphilochidae
26	*Amphilochus* sp. A	Spence Bate, 1862	Amphilochidae
27	*Amphilochus* sp. B	Spence Bate, 1862	Amphilochidae
28	*Amphilochus* sp. C	Spence Bate, 1862	Amphilochidae
29	*Amphilochus tenuimanus*	Boeck, 1871	Amphilochidae
30	*Amphithopsis longicaudata*	Boeck, 1861	Calliopiidae
31	*Andaniella pectinata*	G.O. Sars, 1883	Stegocephalidae
32	*Andaniexis abyssi*	(Boeck, 1871)	Stegocephalidae
33	*Andaniexis lupus*	Berge & Vader, 1997	Stegocephalidae
34	*Andaniexis* sp. A	Stebbing, 1906	Stegocephalidae
35	*Andaniopsis nordlandica*	(Boeck, 1871)	Stegocephalidae
36	*Andaniopsis pectinata*	(G.O. Sars, 1883)	Stegocephalidae
37	*Anonyx* sp. A	Krøyer, 1838	Uristidae
38	*Apherusa glacialis*	(Hansen, 1888)	Calliopiidae
39	*Apherusa sarsii*	Shoemaker, 1930	Calliopiidae
40	*Apherusa* sp. A	Walker, 1891	Calliopiidae
41	*Apherusa* sp. B	Walker, 1891	Calliopiidae

Table 2 **(continued)**

Nr	Species	Authority	Family
42	*Apherusa* sp. C	Walker, 1891	Calliopiidae
43	*Apherusa* sp. D	Walker, 1891	Calliopiidae
44	*Argissa hamatipes*	(Norman, 1869)	Argissidae
45	*Arrhinopsis* sp. A	Stappers, 1911	Oedicerotidae
46	*Arrhis phyllonyx*	(Sars, 1858)	Oedicerotidae
47	*Arrhis* sp. A	Stebbing, 1906	Oedicerotidae
48	*Astyra abyssi*	Boeck, 1871	Stilipedidae
49	*Astyra* sp. A	Boeck, 1871	Stilipedidae
50	*Austrosyrrhoe septentrionalis*	Stephensen, 1931	Synopiidae
51	*Austrosyrrhoe* sp. A	K.H. Barnard, 1925	Synopiidae
52	*Autonoe borealis*	(Myers, 1976)	Aoridae
53	*Bathymedon longimanus*	(Boeck, 1871)	Oedicerotidae
54	*Bathymedon obtusifrons*	(Hansen, 1883)	Oedicerotidae
55	*Bathymedon saussurei*	(Boeck, 1871)	Oedicerotidae
56	*Bathymedon* sp. A	G.O. Sars, 1892	Oedicerotidae
57	*Bruzelia* sp. A	Boeck, 1871	Synopiidae
58	*Bruzelia tuberculata*	G.O. Sars, 1883	Synopiidae
59	*Byblis crassicornis*	Metzger, 1875	Ampeliscidae
60	*Byblis erythrops*	G.O. Sars, 1883	Ampeliscidae
61	*Byblis gaimardii*	(Krøyer, 1846)	Ampeliscidae
62	*Byblis medialis*	Mills, 1971	Ampeliscidae
63	*Byblis minuticornis*	Sars, 1879	Ampeliscidae
64	*Byblis* sp. A	Boeck, 1871	Ampeliscidae
65	*Byblisoides bellansantiniae*	Peart, 2018	Ampeliscidae
66	*Calliopius laeviusculus*	(Krøyer, 1838)	Calliopiidae
67	*Camacho faroensis*	Myers, 1998	Aoridae
68	*Caprella ciliata*	G.O. Sars, 1883	Caprellidae
69	*Caprella dubia*	Hansen, 1887	Caprellidae
70	*Caprella microtuberculata*	G. O. Sars, 1879	Caprellidae
71	*Caprella rinki*	Stephensen, 1916	Caprellidae
72	*Caprella septentrionalis*	Krøyer, 1838	Caprellidae
73	*Chevreuxius grandimanus*	Bonnier, 1896	Aoridae
74	*Cleippides bicuspis*	Stephensen, 1931	Calliopiidae
75	*Cleippides quadricuspis*	Heller, 1875	Calliopiidae
76	*Cleippides tricuspis*	(Krøyer, 1846)	Calliopiidae
77	*Cleonardo* sp. A	Stebbing, 1888	Eusiridae
78	*Cleonardopsis* sp. A	K.H. Barnard, 1916	Amathillopsidae
79	*Corophiidira* sp. A	Leach, 1814 (*sensu* Lowry & Myers, 2013)	Corophiidira
80	*Cressa carinata*	Stephensen, 1931	Cressidae
81	*Cressa jeanjusti*	Krapp-Schickel, 2005	Cressidae
82	*Cressa minuta*	Boeck, 1871	Cressidae

(Continued)

Table 2 (continued)

Nr	Species	Authority	Family
83	*Cressa quinquedentata*	Stephensen, 1931	Cressidae
84	*Cressina monocuspis*	Stephensen, 1931	Cressidae
85	*Deflexilodes norvegicus*	(Boeck, 1871)	Oedicerotidae
86	*Deflexilodes rostratus*	(Stephensen, 1931)	Oedicerotidae
87	*Deflexilodes subnudus*	(Norman, 1889)	Oedicerotidae
88	*Deflexilodes tenuirostratus*	(Boeck, 1871)	Oedicerotidae
89	*Deflexilodes tesselatus*	(Schneider, 1883)	Oedicerotidae
90	*Deflexilodes tuberculatus*	(Boeck, 1871)	Oedicerotidae
91	*Dulichia sp. A*	Krøyer, 1845	Dulichiidae
92	*Dulichia spinosissima*	Krøyer, 1845	Dulichiidae
93	*Dulichiopsis* sp. A	Laubitz, 1977	Dulichiidae
94	*Dyopedos porrectus*	Spence Bate, 1857	Dulichiidae
95	*Dyopedos* sp. A	Spence Bate, 1857	Dulichiidae
96	*Epimeria (Epimeria) loricata*	G.O. Sars, 1879	Epimeriidae
97	*Epimeria (Epimeria)* sp. A	Costa in Hope, 1851	Epimeriidae
98	*Ericthonius megalops*	(Sars G.O., 1879)	Ischyroceridae
99	*Eusirella elegans*	Chevreux, 1908	Eusiridae
100	*Eusirogenes* sp. A	Stebbing, 1904	Eusiridae
101	*Eusirogenes* sp. B	Stebbing, 1904	Eusiridae
102	*Eusirus bathybius*	Schellenberg, 1955	Eusiridae
103	*Eusirus biscayensis*	Bonnier, 1896	Eusiridae
104	*Eusirus holmii*	Hansen, 1887	Eusiridae
105	*Eusirus longipes*	Boeck, 1861	Eusiridae
106	*Eusirus minutus*	G.O. Sars, 1893	Eusiridae
107	*Eusirus propinquus*	Sars, 1893	Eusiridae
108	*Eusirus* sp. A	Krøyer, 1845	Eusiridae
109	*Eusirus* sp. B	Krøyer, 1845	Eusiridae
110	*Eusirus* sp. C	Krøyer, 1845	Eusiridae
111	*Eusirus* sp. D	Krøyer, 1845	Eusiridae
112	*Eusyrophoxus* sp. A	Gurjanova, 1977	Phoxocephalidae
113	*Gammaropsis* sp. A	Lilljeborg, 1855	Photidae
114	*Gitana abyssicola*	G.O. Sars, 1892	Amphilochidae
115	*Gitana rostrata*	Boeck, 1871	Amphilochidae
116	*Gitana sarsi*	Boeck, 1871	Amphilochidae
117	*Gitana* sp. A	Boeck, 1871	Amphilochidae
118	*Gitanopsis arctica*	G.O. Sars, 1892	Amphilochidae
119	*Gitanopsis bispinosa*	(Boeck, 1871)	Amphilochidae
120	*Gitanopsis inermis*	(G.O. Sars, 1883)	Amphilochidae
121	*Gitanopsis sp. A*	G.O. Sars, 1892	Amphilochidae
122	*Glorandaniotes eilae*	(Berge & Vader, 1997)	Stegocephalidae
123	*Gronella groenlandica*	(Hansen, 1888)	Tryphosidae

Table 2 **(continued)**

Nr	Species	Authority	Family
124	*Halice abyssi*	Boeck, 1871	Pardaliscidae
125	*Halice* sp. A	Boeck, 1871	Pardaliscidae
126	*Halicoides* sp. A	Walker, 1896	Pardaliscidae
127	*Halicoides tertia*	(Stephensen, 1931)	Pardaliscidae
128	*Halirages fulvocinctus*	(M. Sars, 1858)	Calliopiidae
129	*Halirages qvadridentatus*	G.O. Sars, 1877	Calliopiidae
130	*Halirages* sp. A	Boeck, 1871	Calliopiidae
131	*Haliragoides inermis*	(G.O. Sars, 1883)	Calliopiidae
132	*Haploops carinata*	Liljeborg, 1856	Ampeliscidae
133	*Haploops dauvini*	Peart, 2018	Ampeliscidae
134	*Haploops islandica*	Kaïm-Malka, Bellan-Santini & Dauvin, 2016	Ampeliscidae
135	*Haploops kaimmalkai*	Peart, 2018	Ampeliscidae
136	*Haploops setosa*	Boeck, 1871	Ampeliscidae
137	*Haploops similis*	Stephensen, 1925	Ampeliscidae
138	*Haploops* sp. A	Liljeborg, 1856	Ampeliscidae
139	*Haploops tenuis*	Kanneworff, 1966	Ampeliscidae
140	*Haploops tubicola*	Liljeborg, 1856	Ampeliscidae
141	*Hardametopa nasuta*	(Boeck, 1871)	Stenothoidae
142	*Harpinia abyssi*	G.O. Sars, 1879	Phoxocephalidae
143	*Harpinia antennaria*	Meinert, 1890	Phoxocephalidae
144	*Harpinia crenulata*	(Boeck, 1871)	Phoxocephalidae
145	*Harpinia crenuloides*	Stephensen, 1925	Phoxocephalidae
146	*Harpinia laevis*	Sars, 1891	Phoxocephalidae
147	*Harpinia mucronata*	G. O. Sars, 1879	Phoxocephalidae
148	*Harpinia pectinata*	Sars, 1891	Phoxocephalidae
149	*Harpinia propinqua*	Sars, 1891	Phoxocephalidae
150	*Harpinia* sp. A	Boeck, 1876	Phoxocephalidae
151	*Harpinia* sp. B	Boeck, 1876	Phoxocephalidae
152	*Harpinia* sp. C	Boeck, 1876	Phoxocephalidae
153	*Harpinia* sp. D	Boeck, 1876	Phoxocephalidae
154	*Harpinia* sp. E	Boeck, 1876	Phoxocephalidae
155	*Harpinia* sp. F	Boeck, 1876	Phoxocephalidae
156	*Harpinia* sp. G	Boeck, 1876	Phoxocephalidae
157	*Harpinia* sp. H	Boeck, 1876	Phoxocephalidae
158	*Harpinia truncata*	Sars, 1891	Phoxocephalidae
159	*Harpiniopsis similis*	Stephensen, 1925	Phoxocephalidae
160	*Hippomedon gorbunovi*	Gurjanova, 1929	Tryphosidae
161	*Hippomedon propinqvus*	G.O. Sars, 1890	Tryphosidae
162	*Idunella aeqvicornis*	(G.O. Sars, 1877)	Liljeborgiidae
163	*Idunella* sp. A	G.O. Sars, 1894	Liljeborgiidae
164	*Ischyrocerus anguipes*	Krøyer, 1838	Ischyroceridae

(Continued)

Table 2 (continued)

Nr	Species	Authority	Family
165	*Ischyrocerus latipes*	Krøyer, 1842	Ischyroceridae
166	*Ischyrocerus megacheir*	(Boeck, 1871)	Ischyroceridae
167	*Ischyrocerus megalops*	Sars, 1894	Ischyroceridae
168	*Jassa* sp. A	Leach, 1814	Ischyroceridae
169	*Kerguelenia borealis*	G.O. Sars, 1891	Kergueleniidae
170	*Laetmatophilus* sp. A	Bruzelius, 1859	Podoceridae
171	*Laetmatophilus tuberculatus*	Bruzelius, 1859	Podoceridae
172	*Laothoes meinerti*	Boeck, 1871	Calliopiidae
173	*Laothoes pallaschi*	Coleman, 1999	Calliopiidae
174	*Laothoes* sp. A	Boeck, 1871	Calliopiidae
175	*Lepechinella arctica*	Schellenberg, 1926	Lepechinellidae
176	*Lepechinella grimi*	Thurston, 1980	Lepechinellidae
177	*Lepechinella helgii*	Thurston, 1980	Lepechinellidae
178	*Lepechinella skarphedini*	Thurston, 1980	Lepechinellidae
179	*Lepechinella victoriae*	Johansen & Vader, 2015	Lepechinellidae
180	*Lepechinelloides karii*	Thurston, 1980	Lepechinellidae
181	*Lepidepecreum* sp. A	Spence Bate & Westwood, 1868	Tryphosidae
182	*Leptamphopus sarsi*	Vanhöffen, 1897	Calliopiidae
183	*Leptophoxus falcatus*	(G.O. Sars, 1883)	Phoxocephalidae
184	*Leucothoe lilljeborgi*	Boeck, 1861	Leucothoidae
185	*Leucothoe* sp. A	Leach, 1814	Leucothoidae
186	*Leucothoe spinicarpa*	(Abildgaard, 1789)	Leucothoidae
187	*Leucothoe vaderotti*	Krapp-Schickel, 2018	Leucothoidae
188	*Liljeborgia fissicornis*	(Sars, 1858)	Liljeborgiidae
189	*Liljeborgia pallida*	(Spence Bate, 1857)	Liljeborgiidae
190	*Liljeborgia* sp. A	Spence Bate, 1862	Liljeborgiidae
191	*Lysianella petalocera*	G.O. Sars, 1883	Tryphosidae
192	*Megamoera dentata*	(Krøyer, 1842)	Melitidae
193	*Megamphopus raptor*	Myers, 1998	Photidae
194	*Melphidippa borealis*	Boeck, 1871	Melphidippidae
195	*Melphidippa goesi*	Stebbing, 1899	Melphidippidae
196	*Melphidippa macrura*	G.O. Sars, 1894	Melphidippidae
197	*Melphidippa* sp. A	Boeck, 1871	Melphidippidae
198	*Melphidippa* sp. B	Boeck, 1871	Melphidippidae
199	*Metacaprella horrida*	(Sars G.O., 1877)	Caprellidae
200	*Metandania wimi*	Berge, 2001	Stegocephalidae
201	*Metopa abyssalis*	Stephensen, 1931	Stenothoidae
202	*Metopa boeckii*	Sars, 1892	Stenothoidae
203	*Metopa bruzelii*	(Goës, 1866)	Stenothoidae
204	*Metopa leptocarpa*	G.O. Sars, 1883	Stenothoidae
205	*Metopa norvegica*	(Liljeborg, 1851)	Stenothoidae

Table 2 (continued)

Nr	Species	Authority	Family
206	*Metopa palmata*	Sars, 1892	Stenothoidae
207	*Metopa robusta*	Sars, 1892	Stenothoidae
208	*Metopa rubrovittata*	G.O. Sars, 1883	Stenothoidae
209	*Metopa sinuata*	Sars, 1892	Stenothoidae
210	*Metopa* sp. A	Boeck, 1871	Stenothoidae
211	*Metopa* sp. B	Boeck, 1871	Stenothoidae
212	*Metopa* sp. C	Boeck, 1871	Stenothoidae
213	*Metopa* sp. D	Boeck, 1871	Stenothoidae
214	*Metopa* sp. E	Boeck, 1871	Stenothoidae
215	*Monoculodes latimanus*	(Goës, 1866)	Oedicerotidae
216	*Monoculodes latissimanus*	Stephensen, 1931	Oedicerotidae
217	*Monoculodes packardi*	Boeck, 1871	Oedicerotidae
218	*Monoculodes* sp. A	Stimpson, 1853	Oedicerotidae
219	*Monoculodes* sp. B	Stimpson, 1853	Oedicerotidae
220	*Monoculodes* sp. C	Stimpson, 1853	Oedicerotidae
221	*Monoculodes* sp. D	Stimpson, 1853	Oedicerotidae
222	*Monoculodes* sp. E	Stimpson, 1853	Oedicerotidae
223	*Monoculodes* sp. F	Stimpson, 1853	Oedicerotidae
224	*Monoculodes* sp. G	Stimpson, 1853	Oedicerotidae
225	*Monoculopsis longicornis*	(Boeck, 1871)	Oedicerotidae
226	*Neopleustes boecki*	(Hansen, 1888)	Pleustidae
227	*Neopleustes pulchellus*	(Krøyer, 1846)	Pleustidae
228	*Neopleustes* sp. A	Stebbing, 1906	Pleustidae
229	*Nicippe tumida*	Bruzelius, 1859	Pardaliscidae
230	*Nototropis smitti*	(Goës, 1866)	Atylidae
231	*Nototropis* sp. A	Costa, 1853	Atylidae
232	*Odius carinatus*	(Spence Bate, 1862)	Ochlesidae
233	*Oedicerina ingolfi*	Stephensen, 1931	Oedicerotidae
234	*Oedicerina* sp. A	Stephensen, 1931	Oedicerotidae
235	*Oediceropsis brevicornis*	Lilljeborg, 1865	Oedicerotidae
236	*Oediceropsis* sp. A	Lilljeborg, 1865	Oedicerotidae
237	*Oediceros borealis*	Boeck, 1871	Oedicerotidae
238	*Onisimus plautus*	(Krøyer, 1845)	Uristidae
239	*Orchomene macroserratus*	Shoemaker, 1930	Tryphosidae
240	*Orchomene pectinatus*	G.O. Sars, 1883	Tryphosidae
241	*Orchomene* sp. A	Boeck, 1871	Tryphosidae
242	*Pacifoculodes pallidus*	(G.O. Sars, 1892)	Oedicerotidae
243	*Paradulichia typica*	Boeck, 1871	Dulichiidae
244	*Paramphilochoides odontonyx*	(Boeck, 1871)	Amphilochidae
245	*Paramphithoe hystrix*	(Ross, 1835)	Paramphithoidae
246	*Parandania gigantea*	(Stebbing, 1883)	Stegocephalidae

(Continued)

Table 2 **(continued)**

Nr	Species	Authority	Family
247	*Paraphoxus oculatus*	(G. O. Sars, 1879)	Phoxocephalidae
248	*Parapleustes assimilis*	(G.O. Sars, 1883)	Pleustidae
249	*Parapleustes bicuspis*	(Krøyer, 1838)	Pleustidae
250	*Pardalisca abyssi*	Boeck, 1871	Pardaliscidae
251	*Pardalisca cuspidata*	Krøyer, 1842	Pardaliscidae
252	*Pardalisca* sp. A	Krøyer, 1842	Pardaliscidae
253	*Pardalisca* sp. B	Krøyer, 1842	Pardaliscidae
254	*Pardalisca* sp. C	Krøyer, 1842	Pardaliscidae
255	*Pardalisca tenuipes*	G.O. Sars, 1893	Pardaliscidae
256	*Pardaliscoides tenellus*	Stebbing, 1888	Pardaliscidae
257	*Paroediceros curvirostris*	(Hansen, 1888)	Oedicerotidae
258	*Paroediceros lynceus*	(M. Sars, 1858)	Oedicerotidae
259	*Paroediceros propinquus*	(Goës, 1866)	Oedicerotidae
260	*Perioculodes longimanus*	(Spence Bate & Westwood, 1868)	Oedicerotidae
261	*Phippsia gibbosa*	(G.O. Sars, 1883)	Stegocephalidae
262	*Phippsia roemeri*	Schellenberg, 1925	Stegocephalidae
263	*Photis reinhardi*	Krøyer, 1842	Photidae
264	*Phoxocephalus holbolli*	(Krøyer, 1842)	Phoxocephalidae
265	*Pleustes (Pleustes) panoplus*	(Krøyer, 1838)	Pleustidae
266	*Pleustes tuberculatus*	Spence Bate, 1858	Pleustidae
267	*Pleusymtes pulchella*	(G.O. Sars, 1876)	Pleustidae
268	*Pleusymtes* sp. A	J.L. Barnard, 1969	Pleustidae
269	*Pontocrates arcticus*	G.O. Sars, 1895	Oedicerotidae
270	*Pontocrates* sp. A	Boeck, 1871	Oedicerotidae
271	*Proaeginina norvegica*	(Stephensen, 1931)	Caprellidae
272	*Proboloides gregaria*	(G.O. Sars, 1883)	Stenothoidae
273	*Protellina ingolfi*	Stephensen, 1944	Caprellidae
274	*Protoaeginella muriculata*	Laubitz & Mills, 1972	Caprellidae
275	*Protomedeia fasciata*	Krøyer, 1842	Corophiidae
276	*Pseudo bioice*	(Berge & Vader, 1997)	Stegocephalidae
277	*Pseudotiron* sp. A	Chevreux, 1895	Synopiidae
278	*Rhachotropis aculeata*	(Lepechin, 1780)	Eusiridae
279	*Rhachotropis arii*	Thurston, 1980	Eusiridae
280	*Rhachotropis distincta*	(Holmes, 1908)	Eusiridae
281	*Rhachotropis gislii*	Thurston, 1980	Eusiridae
282	*Rhachotropis gloriosae*	Ledoyer, 1982	Eusiridae
283	*Rhachotropis helleri*	(Boeck, 1871)	Eusiridae
284	*Rhachotropis inflata*	(G.O. Sars, 1883)	Eusiridae
285	*Rhachotropis kergueleni*	Stebbing, 1888	Eusiridae
286	*Rhachotropis leucophthalma*	G.O. Sars, 1893	Eusiridae
287	*Rhachotropis macropus*	G.O. Sars, 1893	Eusiridae

Table 2 **(continued)**

Nr	Species	Authority	Family
288	*Rhachotropis northriana*	d'Udekem d'Acoz, Vader & Legezinska, 2007	Eusiridae
289	*Rhachotropis oculata*	(Hansen, 1887)	Eusiridae
290	*Rhachotropis palporum*	Stebbing, 1908	Eusiridae
291	*Rhachotropis proxima*	Chevreux, 1911	Eusiridae
292	*Rhachotropis* sp. A	S.I. Smith, 1883	Eusiridae
293	*Rhachotropis* sp. B	S.I. Smith, 1883	Eusiridae
294	*Rhachotropis* sp. C	S.I. Smith, 1883	Eusiridae
295	*Rhachotropis* sp. D	S.I. Smith, 1883	Eusiridae
296	*Rhachotropis thordisae*	Thurston, 1980	Eusiridae
297	*Rhachotropis thorkelli*	Thurston, 1980	Eusiridae
298	*Rostroculodes borealis*	(Boeck, 1871)	Oedicerotidae
299	*Rostroculodes kroyeri*	(Boeck, 1870)	Oedicerotidae
300	*Rostroculodes longirostris*	(Goës, 1866)	Oedicerotidae
301	*Scopelocheirus* sp. A	Spence Bate, 1857	Scopelocheiridae
302	*Sicafodia iceage*	Campean & Coleman, 2017	Sicafodiidae
303	*Sicafodia* sp. A	Just, 2004	Sicafodiidae
304	*Siphonoecetes typicus*	Krøyer, 1845	Ischyroceridae
305	*Socarnes bidenticulatus*	(Spence Bate, 1858)	Lysianassidae
306	*Socarnes vahlii*	(Krøyer, 1838)	Lysianassidae
307	*Stegocephalina wagini*	(Gurjanova, 1936)	Stegocephalidae
308	*Stegocephaloides auratus*	(G.O. Sars, 1883)	Stegocephalidae
309	*Stegocephaloides barnardi*	Berge & Vader, 1997	Stegocephalidae
310	*Stegocephaloides christianiensis*	Boeck, 1871	Stegocephalidae
311	*Stegocephalus ampulla*	(Phipps, 1774)	Stegocephalidae
312	*Stegocephalus inflatus*	Krøyer, 1842	Stegocephalidae
313	*Stegocephalus similis*	Sars, 1891	Stegocephalidae
314	*Stegocephalus* sp. A	Krøyer, 1842	Stegocephalidae
315	*Stegocephalus* sp. B	Krøyer, 1842	Stegocephalidae
316	*Stegonomadia biofar*	(Berge & Vader, 1997)	Stegocephalidae
317	*Stegonomadia idae*	(Berge & Vader, 1997)	Stegocephalidae
318	*Stegoplax longirostris*	G.O. Sars, 1883	Cyproideidae
319	*Stegoplax* sp. A	G.O. Sars, 1883	Cyproideidae
320	*Stenopleustes latipes*	(M. Sars, 1858)	Pleustidae
321	*Stenopleustes malmgreni*	(Boeck, 1871)	Pleustidae
322	*Stenopleustes nodifera*	(G.O. Sars, 1883)	Pleustidae
323	*Stenopleustes* sp. A	G.O. Sars, 1893	Pleustidae
324	*Stenothoe marina*	(Spence Bate, 1857)	Stenothoidae
325	*Stenothoe megacheir*	(Boeck, 1871)	Stenothoidae
326	*Stenothoe* sp. A	Dana, 1852	Stenothoidae
327	*Stenothoe* sp. B	Dana, 1852	Stenothoidae
328	*Stenothoe* sp. C	Dana, 1852	Stenothoidae

(Continued)

Table 2 **(continued)**

Nr	Species	Authority	Family
329	*Stenothoe* sp. D	Dana, 1852	Stenothoidae
330	*Stephobruzelia dentata*	(Stephensen, 1931)	Synopiidae
331	*Synchelidium haplocheles*	(Grube, 1864)	Oedicerotidae
332	*Synchelidium intermedium*	Sars, 1892	Oedicerotidae
333	*Synchelidium* sp. A	G.O. Sars, 1892	Oedicerotidae
334	*Syrrhoe crenulata*	Goës, 1866	Synopiidae
335	*Syrrhoe* sp. A	Goës, 1866	Synopiidae
336	*Syrrhoites pusilla*	Enequist, 1949	Synopiidae
337	*Syrrhoites serrata*	(G.O. Sars, 1879)	Synopiidae
338	*Syrrhoites* sp. A	G.O. Sars, 1893	Synopiidae
339	*Themisto gaudichaudii*	Guérin, 1825	Hyperiidae
340	*Thorina elongata*	Laubitz & Mills, 1972	Caprellidae
341	*Thorina spinosa*	Stephensen, 1944	Caprellidae
342	*Tiron spiniferus*	(Stimpson, 1853)	Synopiidae
343	*Tmetonyx cicada*	(Fabricius, 1780)	Uristidae
344	*Tmetonyx* sp. A	Stebbing, 1906	Uristidae
345	*Tryphosella schneideri*	(Stephensen, 1921)	Tryphosidae
346	*Tryphosella* sp. A	Bonnier, 1893	Tryphosidae
347	*Unciola laticornis*	Hansen, 1887	Unciolidae
348	*Unciola leucopis*	(Krøyer, 1845)	Unciolidae
349	*Unciola planipes*	Norman, 1867	Unciolidae
350	*Urothoe elegans*	Spence Bate, 1857	Urothoidae
351	*Westwoodilla brevicalcar*	Goës, 1866	Oedicerotidae
352	*Westwoodilla caecula*	(Spence Bate, 1857)	Oedicerotidae
353	*Westwoodilla megalops*	(G.O. Sars, 1883)	Oedicerotidae
354	*Westwoodilla* sp. A	Spence Bate, 1862	Oedicerotidae
355	*Xenodice* sp. A	Boeck, 1871	Podoceridae

Note:
Amphipoda species, authorities and family.

pattern. There is a "Coastal" cluster ($n = 34$ cells) which is always close to the coastline and is characterized by shallow depth, high amounts of dissolved iron and phytobiomass and warm, oxygen-rich waters with a high current speed (Fig. 2). The second cluster resembles the GIFR ($n = 55$), which spreads from west to east and separates the northern and southern basis. In many points it is similar to the coastal cluster but is deeper and with less dissolved iron, oxygen, and phytobiomass. The other two clusters are called "Deep South" ($n = 19$) and "Deep North" ($n = 28$) as they represent the deep-sea regions around Iceland. They differ strongly from the first two clusters by having very low values for many parameters. "Deep North" differs from "Deep South" by being much colder, with almost no current velocity. Further, "Deep North" has a much higher amount of dissolved oxygen and pH. The lowest depths of around 3,400 m are observed in the Aegir ridge. These four

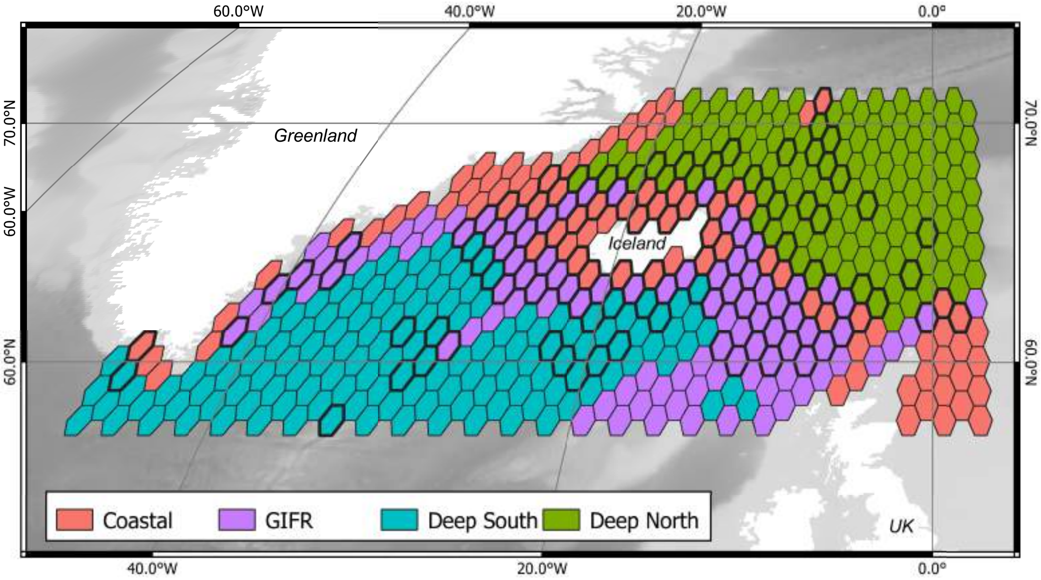

Figure 1 **Four environmental clusters.** Map of the outlines for four identified environmental clusters in the North Atlantic. The Greenland-Faroe-Iceland ridge (GIFR) extends from west to east and is, like the coastal cluster, partly interrupted due to the coarse resolution of the hexagonal cells of 1° in east-west direction, (n = 469). Full-size DOI: 10.7717/peerj.11898/fig-1

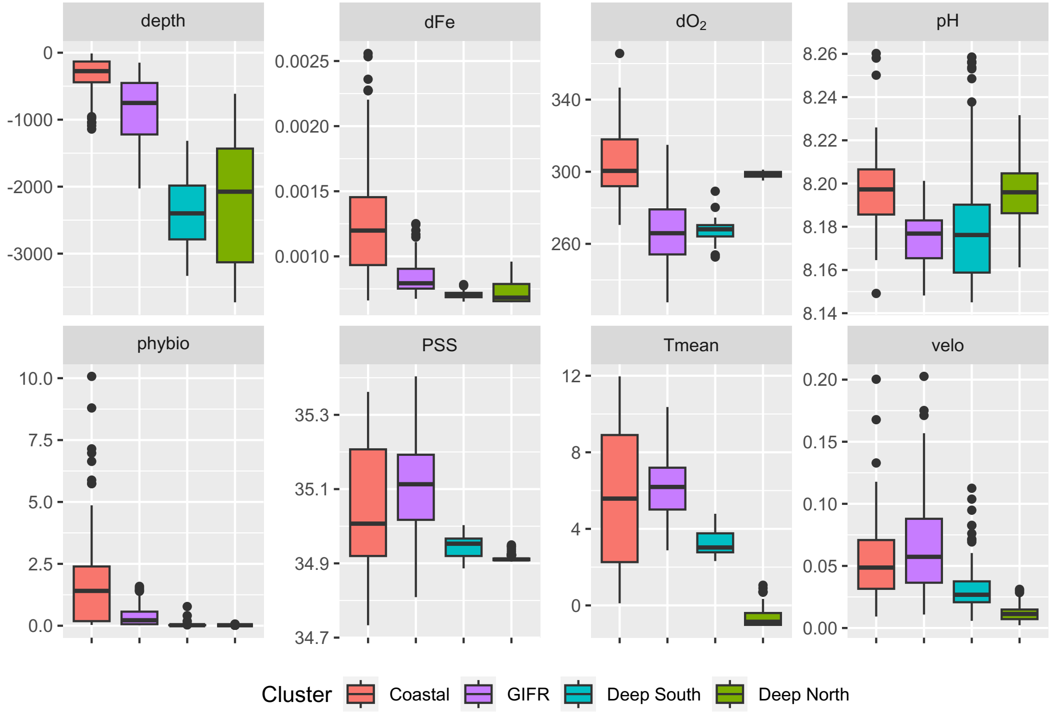

Figure 2 **Environmental parameters.** Characterization of the four environmental clusters by the environmental parameters with box-whisker plots. For abbreviations refer to Table 1. An extended table with numeric information can be found in the appendix. Full-size DOI: 10.7717/peerj.11898/fig-2

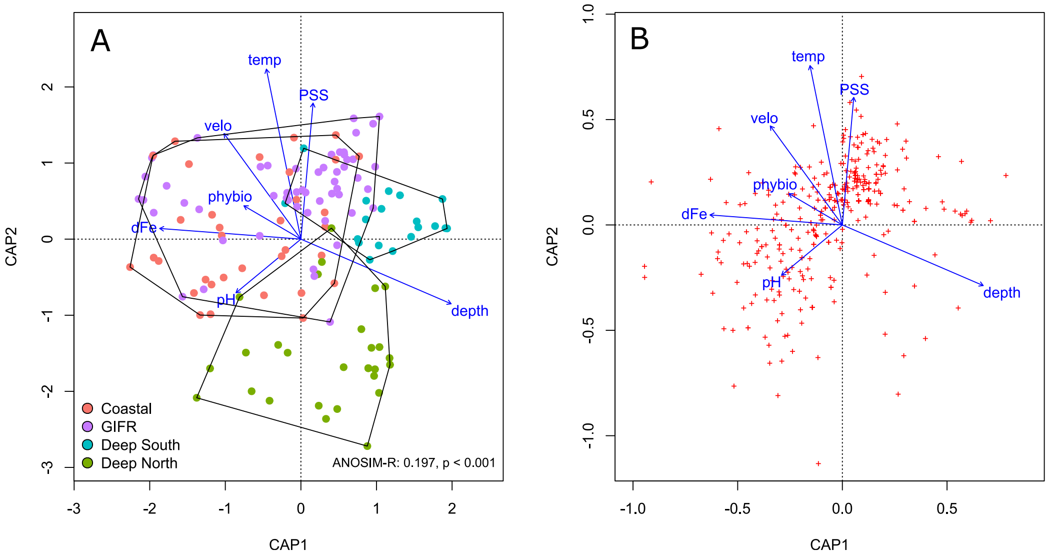

Figure 3 **Constrained analysis of principal coordinates.** Constrained analysis of principal coordinates (CAP) based on Jaccard distances. (A) Scaling is based on site scores, (B) scaling is based on species scores (red dots)—note the differences of the axes. Arrows point into the direction of largest correlation with species and site scores. The 0,0 coordinate reflects the centroid of each variable. The environmental clusters still overlap considerably in their species composition as reflected by the low ANOSIM-R statistic. Full-size DOI: 10.7717/peerj.11898/fig-3

clusters thus characterize the environmental conditions around Iceland on a regional spatial scale.

Constrained ordination

We conducted a constrained ordination to verify the amount of variation explained in the species data by the environmental information contained at the level of the hexagonal cells. The constrained axes of the ordination explained 11% of the total variation, while 89% is explained by the 357 unconstrained axes. According to a permutation test of the marginal effects of each environmental variable carried out using the *anova.cca* function of the *vegan* package, the most important environmental variables were temperature (F = 2.34, $p < 0.001$), depth (F = 2.123, $p < 0.001$), and salinity (F = 2.01, $p < 0.001$).

The four different clusters strongly overlapped in ordination space (Fig. 3A). The ANOSIM-R value of 0.197 signals considerable similarity in species composition between the clusters. All clusters overlap in the centre of the diagram; their large spread indicates strong heterogeneity. The deep-sea clusters overlapped less than the coastal and GIFR-cluster. In general, the first constrained axis represented the depth gradient, which was in contrast to all other variables. Salinity, temperature and pH characterized the second constrained axes, with pH being in contrast to temperature and salinity (Fig. 3A). The species pattern clumped near the centroid of the ordination diagram (Fig. 3B) indicating that many species are found in intermediate environmental conditions. Fewer species have a clear centroid in deeper waters, instead many species favour higher temperatures and an above average salinity. Large variation appears in the direction of pH and dissolved iron, as indicated by the strong scatter of species centroids (Fig. 3B).

Indicator species analysis

To characterize the different clusters with regard to faithful species, *i.e.*, so-called indicator species we conducted a multipattern indicator species analysis. We compared 15 different combinations with an increasing number of clusters. From 355 species, we identified 56 to have a strong association to one or more clusters. Fourty-three species were associated to one cluster only, while twelve and one species were associated to two and three clusters, respectively (Table 3). Only two species were found for the GIFR cluster, but more species from GIFR appear in combination with other clusters.

Three of the clusters, the Deep North, the Deep South and the Coastal have indicator species belonging to the genus *Rhachotropis*. While different species of a genus might be specialized on different diets, all *Rhachotropis* species are very good swimmers (*Lörz, 2010*). The Deep South cluster has four *Rhachotropis* as indicator species. While the GIFR cluster only had two endobenthic species, belonging to the family Ampeliscidae, which are not considered strong swimmers (*Peart, 2018*), the combined GIFR and coastal cluster indicate *Rhachotropis aculeata* (*Lepechin, 1780*) as an indicator—a species that is known to have a circum-Arctic distribution (*Lörz et al., 2018*). *Caprella microtuberculata* G. O. *Sars, 1879* and *Aeginella spinosa Boeck, 1861* are indicator species of the combined coastal and GIFR cluster. These two species belong to the amphipod group Caprellidae, skeleton or ghost shrimps, which are known for their clinging lifestyle. The indicator species with the highest values, over 0.5, are *Cleippides quadricuspis Heller, 1875* from the Deep North, *Eusirus holmi Hansen, 1887* from the combined Coastal and Deep North cluster and *Rhachotropis thordisae Thurston, 1980* from the Deep South cluster—these three species are all large amphipods of several cm body length and known as predators (*Lörz et al., 2018*).

Diversity

The number of aggregated hexagonal cells differed for each cluster, hence we had to apply a rarefaction and extrapolation analysis to make the three diversity measures comparable. The rarefaction of the summed abundances revealed that the two clusters “coastal” and “GIFR” have about twice the number of species than the deep-sea clusters (Fig. 4A). This even holds when only the lowest comparable value of approximate 10,000 individuals is considered. Although there were so many individuals per cluster, the curves do not level off, indicating that still more sampling would be required to reach a plateau in species richness. The Shannon diversity (Fig. 4B) considers the richness-abundance component of diversity. The “coastal” and “GIFR” clusters are at the same level of 60 effective species; the deep-sea clusters again have a much lower diversity, *i.e.*, almost three times lower. All curves reach a plateau, indicating that there is little more diversity to expect when abundances are considered. Hence, only rare species might be added by future sampling. Considering the Simpson diversity (Fig. 4C), *i.e.*, when no rare species but only dominant species have an influence on the diversity measure, then the “coastal” cluster becomes the most diverse cluster while the “GIFR” is only half as diverse as the coastal cluster.

The richness pattern across the depth gradient showed high variation at depths above 1,500 m with richness values up to 79 species per station (Fig. 5A). Most of the stations

Table 3 **Indicator value analysis for all combinations of the environmental clusters.** The group-size corrected Indicator Value (IndVal.g) represent the association value of a species with a given cluster. The *p*-value is based on 999 permutations. Asterisks code for *p*-values at signifcance levels of 5% (*) and 1% (**).

Cluster	Nr.	Species	IndVal.g	*p*-value	
Coastal	1	*Rhachotropis oculata*	0.400	0.005	
	2	*Westwoodilla caecula*	0.383	0.015	
	3	*Ampelisca macrocephala*	0.368	0.010	**
	4	*Deflexilodes tesselatus*	0.368	0.035	*
	5	*Harpinia* sp. E	0.343	0.020	*
	6	*Monoculodes* sp. A	0.343	0.015	*
	7	*Westwoodilla megalops*	0.343	0.030	*
	8	*Harpinia pectinata*	0.328	0.020	*
	9	*Bathymedon obtusifrons*	0.319	0.035	*
	10	*Monoculodes latimanus*	0.297	0.045	*
Deep North	1	*Cleippides quadricuspis*	0.642	0.005	**
	2	*Bruzelia dentata*	0.463	0.005	**
	3	*Rhachotropis* sp. A	0.392	0.005	**
	4	*Paroediceros curvirostris*	0.375	0.015	*
	5	*Deflexilodes tenuirostratus*	0.349	0.040	*
	6	*Halirages quadridentata*	0.344	0.025	*
	7	*Monoculopsis longicornis*	0.344	0.025	*
	8	*Oedicerina* sp.	0.327	0.025	*
Deep South	1	*Rhachotropis thordisae*	0.559	0.005	**
	2	*Rhachotropis proxima*	0.499	0.010	**
	3	*Eusirus bathybius*	0.459	0.010	**
	4	*Lepechinelloides karii*	0.459	0.005	**
	5	*Rhachotropis gislii*	0.459	0.005	**
	6	*Protoaeginella muriculata*	0.401	0.010	**
	7	*Cleonardopsis* sp.	0.397	0.005	**
	8	*Lepechinella grimi*	0.397	0.005	**
	9	*Lepechinella helgii*	0.397	0.010	**
	10	*Lepechinella skarphedini*	0.397	0.010	**
	11	*Rhachotropis thorkelli*	0.397	0.010	**
	12	*Neopleustes boecki*	0.365	0.010	**
	13	*Neopleustes* sp.	0.324	0.010	**
	14	*Sicafodia* sp.	0.324	0.010	**
	15	*Eusirus* sp. C	0.300	0.020	*
	16	*Rhachotropis aislii*	0.300	0.040	*
	17	*Rhachotropis gloriosae*	0.300	0.035	*
GFIR	1	*Ampelisca odontoplax*	0.348	0.03	*
	2	*Haploops tenuis*	0.302	0.05	*
Coastal + Deep North	1	*Eusirus holmi*	0.509	0.005	**
	2	*Halirages fulvocincta*	0.490	0.050	*
	3	*Arrhis phyllonyx*	0.458	0.005	**
	4	*Andaniella pectinata*	0.430	0.005	**
	5	*Paroediceros propinquus*	0.372	0.040	*
	6	*Halirages elegans*	0.359	0.030	*
	7	*Harpiniopsis similis*	0.347	0.035	*

Table 3 (continued)

Cluster	Nr.	Species	IndVal.g	*p*-value	
Coastal + GFIR	1	*Aeginella spinosa*	0.559	0.005	**
	2	*Rhachotropis aculeata*	0.467	0.025	*
	3	*Caprella microtuberculata*	0.462	0.010	**
	4	*Harpinia propinqua*	0.459	0.030	*
Deep South + Deep North	1	*Liljeborgia pallida*	0.349	0.045	*
	2	*Ampelisca islandica*	0.329	0.025	*
Coastal + Deep South + Deep North	1	*Amphilochus anoculus*	0.424	0.035	*

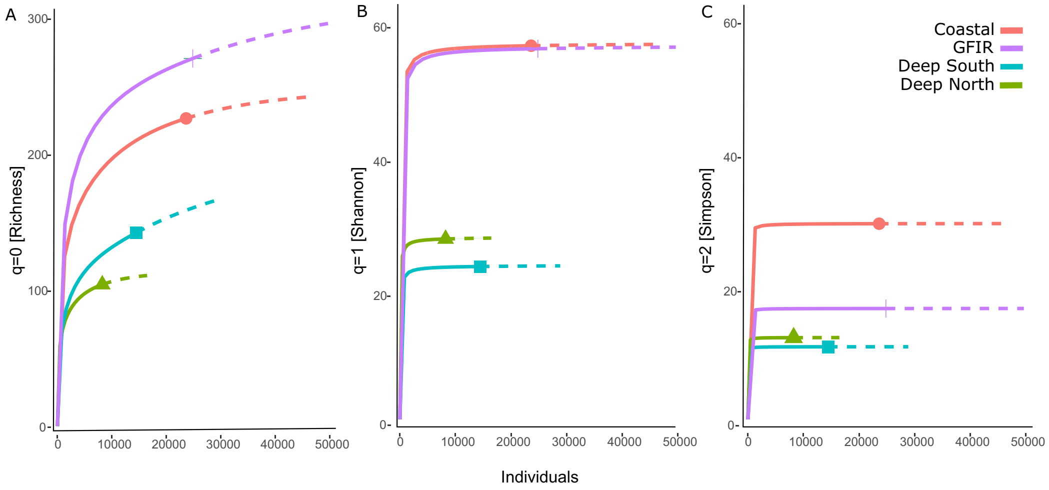

Figure 4 Rarefaction-extrapolation of diversity indices per cluster. The diversity indices (A) richness, (B) Shannon, and (C) Simpson, represent an increasing importance of abundant species. The unit of the y-axis is the effective number of species. Full-size DOI: 10.7717/peerj.11898/fig-4

recorded rather few species *i.e.*, up to 10 species with an average of 20 species at the shallowest parts (18 m) and an estimated richess of eight species at the lowest depths. The trend for the maximum number of species aggregated per 100-m interval showed an unimodal pattern with a peak at depths around 500 m and a much lower richness at depths lower than 1,000 m (Fig. 5B). These figures support the finding that the Coastal and GIFR clusters are much more diverse than the deep-sea clusters (Fig. 5C).

DISCUSSION

Environmental and historical imprints on amphipod distributions

Distributional groupings given in the present study corresponded to earlier findings, in which distinctive boundaries between a northern and a southern deep-sea fauna were inferred, while the composition of the shallow-water fauna (<500 m) around Iceland was very similar (*Weisshappel & Svavarsson, 1998*; *Weisshappel, 2000*; *Bett, 2001*; *Weisshappel, 2001*). Unsurprisingly, the spatial distribution of amphipods appeared to be most strongly influenced by bathymetry, salinity and seafloor temperature. The latter two were interconnected and indicative of particular water masses (*Puerta et al., 2020*).

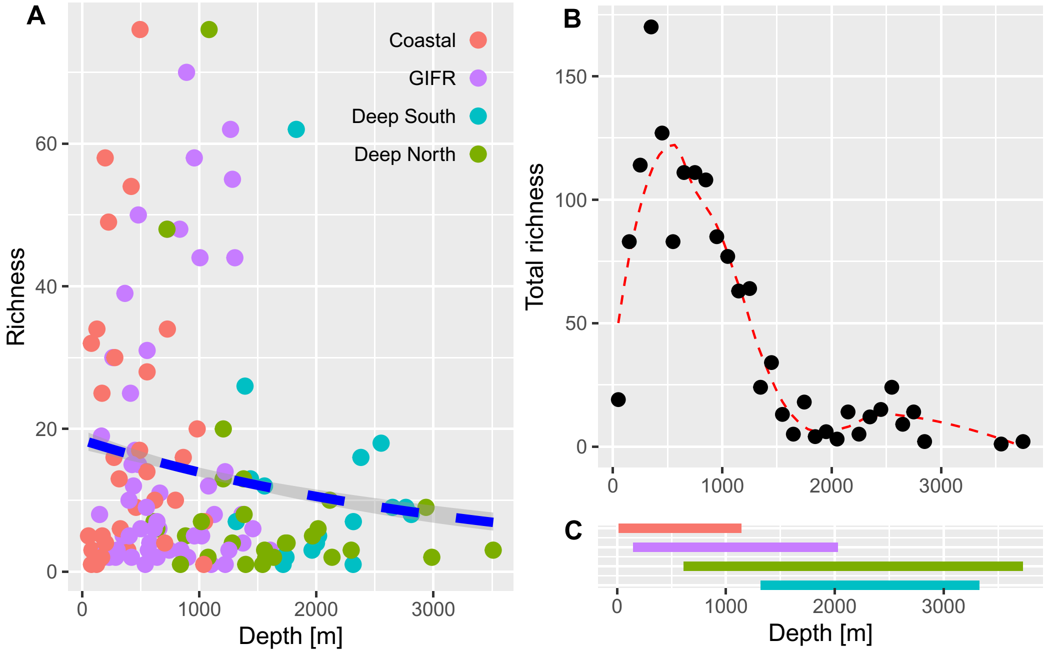

Figure 5 **Amphipod species diversity pattern along a depth gradient.** (A) Richness values per station and coloured according to the environmental clusters. The blue dashed line represents the Poisson GLM. (B) Maximum number of amphipod species per 100-m interval. A Loess smoother represented by the red dashed line is plotted to better visualize the pattern. (C) Bars show the depth ranges in meters for each of the four environmental clusters. Colours according to the legend in (A).

Full-size DOI: 10.7717/peerj.11898/fig-5

The presence of the GIFR is known as an effective barrier to disrupt the dispersal of benthic organisms between the North Atlantic and the Nordic seas (*Weisshappel & Svavarsson, 1998*; *Brix & Svavarsson, 2010*; *Schnurr et al., 2018*). With a saddle depth averaging 600 m in the Strait of Denmark and 480 m between Iceland and the Faroe Islands and a maximum depth of c. 840 m, the depth increases towards the abyssal basins on each side of the ridge exceeding 3,000 m. Depth, or rather ecological and environmental variables that change with depth, such as hydrostatic pressure, temperature, food availability, or competition, have been demonstrated to have a large impact on species distributions (*Rex & Etter, 2010*; *Brown & Thatje, 2011*; *Tittensor et al., 2011*).
In contrast, there are several examples of amphipod species, mostly within the more motile scavenger and predator guilds, with large depth distributions and thus at least the intrinsic capability to overcome topographical barriers (*Lacey et al., 2018*; *Lörz, Jażdżewska & Brandt, 2018*; *Weston et al., 2021*).

The GIFR also marks the transition between different bodies of water, and hence the effects of depth and water mass properties are intertwined. Generally, physical and chemical water mass attributes such as temperature, salinity, pH, organic matter, and dissolved oxygen play critical roles in structuring benthic communities including microbes, fish, crustaceans, corals, and sponges (*Koslow, 1993*; *Weisshappel & Svavarsson, 1998*; *Brix & Svavarsson, 2010*; *Schnurr et al., 2018*; *Puerta et al., 2020*; *Roberts et al., 2021*).
Reasons for this involve physiological tolerances of larvae, juveniles and adults towards

certain environmental conditions, dispersal constraints invoked by density differences or current shear, as well as enhanced nutrient input linked to hydrography (*Puerta et al., 2020*; *Roberts et al., 2021*).

Obviously, cold sub-zero temperatures in the Nordic sea basins restrict species distributions, as only few species are pre-adapted to such low temperatures while withstanding high hydrostatic pressures (*Svavarsson, Stromberg & Brattegard, 1993*; *Brown & Thatje, 2011*). This is supported by the fact that many amphipod species in our study prefer moderate conditions, at least in terms of temperature. Initially, however, species originating from the North Atlantic had to overcome the GIFR and enter the Nordic seas against the overflow water from the Denmark Strait and Faroe Bank Channel (*Yasuhara et al., 2008*), the latter being limited to species with broad bathymetric distributions or eurytherm "shallow"-water taxa. The presence of the GIFR is thereby inevitably linked to the opening of the North-east Atlantic about 55 Mya, representing a barrier between the Nordic seas and North Atlantic ever since (*Hjartarson, Erlendsson & Blischke, 2017*). Alternatively, species from the North Pacific had to cross the Bering Strait sill, and experience subsequent trans-Arctic migration (*Hardy et al., 2011*). While the shelf fauna represents a mixture of North Pacific, North Atlantic and to a lesser extent endemic Arctic fauna (*e.g.*, *Svavarsson, Stromberg & Brattegard, 1993*; *Hardy et al., 2011*), large parts of the contemporary deep-sea fauna of the Arctic and Nordic seas likely originate from the North Atlantic (*e.g.*, *Bluhm et al., 2011* and citations therein; *Svavarsson, Stromberg & Brattegard, 1993*).

In our indicator analysis, species were identified based on their predominant affiliation to certain oceanographic conditions. Identifying areas of endemicity, *Arfianti & Costello (2020)* defined our study area as part of a larger region that comprised North American boreal, Arctic and North Pacific areas. Our results, however, are consistent with the view that the deep-sea fauna of the Nordic seas appears to originate from shelf genera or less pronounced deep-sea taxa that were able to cross the GIFR (*Dahl, 1979*; *Just, 1980*; *Svavarsson, Stromberg & Brattegard, 1993*). The study by *Arfianti & Costello (2020)* contained data for the entire Arctic and sub-Arctic regions, encompassing both shelf and deep-sea areas, with the first reportedly representing a mixture of Atlantic, Arctic and Pacific elements (see above). Contrasting distribution patterns in hyperbenthic Eusiridae and Calliopiidae represent good examples to illustrate the barrier effect of the ridge; the family Eusiridae, which is more prevalent in deep water, has only a few species north of the GIFR, which is in contrast to the shallow water family Calliopiidae, whose species diversity is higher in the north (*Weisshappel, 2000*; *Weisshappel, 2001*). Overall, *Svavarsson, Stromberg & Brattegard (1993)* describe the deep-sea fauna of the Arctic and Nordic seas as very young, probably less than 100,000 yrs. old, due to the presence of the ridge and the adverse conditions prevailing in the northern regions ("topographic and environmental filtering"). Accordingly, little time remained for speciation and formation of endemic species (*Svavarsson, Stromberg & Brattegard, 1993*).

Our coastal amphipod assemblage, as well as the one associated with the GIFR, consisted of indicator species with broad North Atlantic distributions. Over the past millennia the biogeography of northern latitudes had been shaped by recurring glacial cycles (*Darby, Polyak & Bauch, 2006*). During the last glacial maximum (ending about 6,000 yrs ago; *Darby, Polyak & Bauch, 2006*) Arctic shelves were largely covered by grounded ice sheets forcing the fauna towards more southerly (North Atlantic) ice-free areas or deeper waters (*Dunton, 1992*; *Darby, Polyak & Bauch, 2006*). The latter may have become the ancestors of today's Nordic deep-sea fauna (*Nesis, 1984*). While evidence exists that at least parts of the shelf had remained ice-free and thus served as glacial refugia, notably here Iceland and the Faroe Islands (*Maggs et al., 2008*; *Hardy et al., 2011*), most species must have recolonized the previously ice-covered areas rather swiftly. Given the close overlap of coastal and GIFR fauna in our study, the ridge could have provided a potential shallow-water link for brooding taxa that has promoted the recolonization from suitable ice-free habitats.

Diversity trends

The comparison of the diversity between the environmental clusters showed that the diversity of the shallow clusters (coastal and GIFR) was higher than that of the deep clusters north and south of the ridge. While species richness had the highest number of effective species (Fig. 4A), its sole use is usually not encouraged as it is heavily affected by sample size and shows high sensitivity in recording rare species (*Jost, 2006*). There were some profound differences between Hill numbers—species richness, Shannon, and Simpson diversity—likely because each of these indices scales rarity differently (*Chao, Chiu & Jost, 2014*; *Roswell, Dushoff & Winfree, 2021*; Figs. 4B, 4C). The fact that none of the richness-based rarefaction curves has stabilized yet, could therefore be an artifact; many species have only been found once, either because they could not be identified to species level or because only a small number of individuals were sampled during the historical missions. The Simpson index, on the other hand, is considered as being most robust when sampling effort differs strongly between samples, since it largely reflects patterns in the most common species (*Jost, 2006*). Shannon diversity can be seen as a intermediate measure in terms of its responses to sample size and rarity (*Roswell, Dushoff & Winfree, 2021*). Overall, though, all estimates applied have their merits and pitfalls, and typically using all three indices provides the best representation of the diversity in a given area (*Roswell, Dushoff & Winfree, 2021*). Nevertheless, a consistent pattern of a higher diversity in the shallows—relative to the deep clusters—was evident in all three indices. In the same way, analysis of the entire data set showed an unimodal pattern, with richness peaking at around 500 m, and then a sharp decline in richness with increasing depth (Fig. 5). Compared to other studies that often show a peak between 2,000–3,000 m (cf. *Rex & Etter, 2010* and citations therein), maximum richness in amphipods of the Nordic Seas seems to be much shallower and to resemble patterns in isopods from the same area (*Brix et al., 2018*, but see *Svavarsson, 1997*). However, it should be noted here that differences in sampling intensity between grid cells and depth were a confounding factor in our study and the results therefore will have to be reassessed with additional future sampling.

Combined historical and ecological explanations have been utilized to interpret the overall low diversity of the Nordic basins compared to the other deep-sea regions

(*Svavarsson, Stromberg & Brattegard, 1993*; *Bluhm et al., 2011*). In general, it is believed that variation in energy supply (temperature and productivity) affect deep-sea diversity (*e.g.*, *Woolley et al., 2016*; *Yasuhara & Danovaro, 2016*; *Jöst et al., 2019*). However, cold temperatures *per se* do not seem to have a negative impact on diversity, since benthic communities at sub-zero temperatures in the Southern Ocean abyss appear to be extraordinarily rich (*Brandt et al., 2007*), but when coupled with the very low productivity and geographical isolation of the Nordic basins, the diversity of invertebrates is relatively low (*Svavarsson, Stromberg & Brattegard, 1993*; *Egilsdottir, McGinty & Gudmundsson, 2019*; *Jöst et al., 2019*). In addition, antagonistic effects of high hydrostatic pressure and low temperatures that prevail in the deep Nordic Sea basins could explain the low diversity there (*Brown & Thatje, 2011*, *2014*).

Notably, the diversity of the "Deep South" cluster in our study was as low as that of the Deep North, which contrasts with the perception of an impoverished Nordic deep-sea fauna (*Bouchet & Warén, 1979*; *Dahl, 1979*; *Rex et al., 1993*; *Svavarsson, 1997*; *Weisshappel & Svavarsson, 1998*; *Jöst et al., 2019*). Although amphipods are typically less well presented in the deep sea (*e.g.*, when compared to isopods; *Lörz, Kaiser & Bowden, 2013*), their 'deficiency' in Nordic waters was established earlier. For example, *Dahl (1979)* found that gammaridean species in the Norwegian Sea is a mere 20% of that in the North Atlantic. Yet, it is not clear whether this is a valid conclusion, since pure richness comparisons are very susceptible to differences in sample sizes and sample effort (see discussion above). In addition, different taxa north and south of the ridge can have different diversity patterns resulting *e.g.*, from their different evolutionary histories, lifestyles (brooding *vs*. broadcaster) or physiological scope. This becomes very evident in isopods, a sister group of the amphipods, where the diversity of the deep North Atlantic exceeds that of the Nordic seas (*Svavarsson, 1997*).

Although not strictly comparable, but in line with our results, *Egilsdottir, McGinty & Gudmundsson (2019)*, found local deep-sea diversity of bivalve and gastropod molluscs north and south of the GIFR to be equally low. They attributed this to specific oceanographic conditions prevailing at the deep southern stations. In addition, changes in environmental conditions in the course of past glacial maxima in the northern North Atlantic and in the North Sea were associated with cyclical changes of low (glacial) and relatively increased (interglacial) diversity (*Cronin & Raymo, 1997*; *Yasuhara et al., 2014*). The related environmental consequences of these climatic changes, in particular variation in bottom-water temperature, seasonality and meltwater runoff, evidently had a strong impact on deep-sea diversity, with recent deep-sea fauna still in the process of recovering from these events (*Rex et al., 1993*; *Cronin & Raymo, 1997*; *Wilson, 1998*; *Yasuhara et al., 2008*; *Yasuhara et al., 2014*; but see *Jöst et al., 2019* and citations therein).

Compared to the deep-sea cluster, the diversity of the shallower coastal and GIFR clusters was considerably higher (Fig. 4A). This is in stark contrast to an allegedly poor amphipod fauna, for example when compared to the South polar region (*Arfianti & Costello, 2020*). Although a direct comparison with other regions at complementary depth is still pending, it is already clear that the shelf and upper slope amphipod fauna on the border between the North Atlantic and North Sea, consisting of more than 300 effective species, is not depleted (Fig. 4A). In comparison, *De Broyer & Jazdzewska (2014)* counted ~560 amphipod species for the entire Antarctic region (south of the Polar front), which is considered to have a significantly higher amphipod diversity relative to high northern latitudes (*Arfianti & Costello, 2020*). In addition, through the application of molecular techniques, but also additional sampling, especially of the deeper and less frequently explored areas, more species are likely to be discovered for the northern region (*Bluhm et al., 2011*; *Jażdżewska et al., 2018*; *Lörz, Jażdżewska & Brandt, 2018*; *Schwentner & Lörz, 2020*). We admit the comparison is slightly misleading, as cryptic species are discovered across all environments at similar rates (*Pfenninger & Schwenk, 2007*), plus different geological histories, oceanographic settings, and the size of the Arctic *vs.* Antarctica, among other things represent additional confounders. We thus believe that the diversity of the northern regions should not be underestimated and presumably occupies globally at least a middle ranking.

CONCLUSIONS

In amphipods, water mass properties appear to be the main force in delineating species distributions at the boundary between the North Atlantic and the Nordic seas, with the GIFR additionally hindering the exchange of deep-sea species between northern and southern deep-sea basins. This pattern is largely congruent for all benthic but also hyperbenthic amphipod families. Different factors are likely responsible for driving deep-sea diversity on each side of the ridge. While impoverished amphipod communities in the Nordic basins are likely to be due to topographical and environmental barrier effects, the southern deep-sea assemblage shows similarly low diversity, presumably a response to variation in the oceanographic environment over a range of temporal and spatial scales. In addition, bathymetric sampling constraints need to be considered.

Since the Cenozoic Era (c. 65 mya) and more recently, the areas of the northern North Atlantic and the Nordic seas have undergone profound climatic changes, from greenhouse to icehouse conditions and vice versa, shaping the composition and distribution of the marine biota (*Piepenburg, 2005*; *Horton et al., 2020*). Distinct temperature thresholds for the Arctic and boreal benthic species point towards future range shifts (restrictions *vs.* extensions), which will have a strong impact on the diversity in the region (*Renaud et al., 2015*). Our data showed a high salinity and temperature-driven distribution of the amphipod assemblages, which also applies to a number of other taxa (*Brix & Svavarsson, 2010*; *Schnurr et al., 2018*; *Egilsdottir, McGinty & Gudmundsson, 2019*; *Jöst et al., 2019*). Additional environmental variables may prove important in explaining diversity and distribution, including seasonality in productivity, pH and ice cover (*Yasuhara et al., 2012*). These are especially the ones that are predicted to change first due to recent climate changes (*e.g.*, *Hoegh-Guldberg & Bruno, 2010*).

In our study, amphipods were highlighted as an important benthic component in Icelandic waters. Since climate change is supposed to have an impact on several organizational levels (populations, species, communities), in future studies, we aim to investigate the interaction of local and regional processes on amphipod diversity as well as species-specific responses to better understand potential effects of climate change in the Nordic seas.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare that they have no competing interests. Jens Oldeland is a freelancing environmental data scientist.

Author Contributions

- Anne-Nina Lörz conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Stefanie Kaiser analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Jens Oldeland performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Caroline Stolter performed the experiments, prepared figures and/or tables, and approved the final draft.
- Karlotta Kürzel performed the experiments, prepared figures and/or tables, and approved the final draft.
- Saskia Brix conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The data are available in the Supplemental Files.

The data is also available at Pangaea: Lörz, Anne-Nina; Brix, Saskia; Oldeland, Jens; Coleman, Charles Oliver; Peart, Rachel; Hughes, Lauren; Andres, Hans Georg; Kaiser, Stefanie; Stolter, Caroline; Kürzel, Karlotta; Vader, Wim; Tandberg, Anne Helene; Stransky, Bente; Svavarsson, Jörundur; Guerra-García, José-Manuel; Krapp-Schickel, Traudl (2021): Marine Amphipoda and environmental occurrence around Iceland. https://doi.pangaea.de/10.1594/PANGAEA.931959.

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A new threat to local marine biodiversity: filamentous mats proliferating at mesophotic depths off Rapa Nui

Javier Sellanes[1,2], Matthias Gorny[3], Germán Zapata-Hernández[1,2,4], Gonzalo Alvarez[5,6], Praxedes Muñoz[1] and Fadia Tala[1,6,7]

[1] Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Coquimbo, Chile
[2] Millennium Nucleus for Ecology and Sustainable Management of Oceanic Islands (ESMOI), Universidad Católica del Norte, Coquimbo, Coquimbo, Chile
[3] Oceana, Santiago, Chile
[4] Programa de Doctorado en Biología y Ecología Aplicada (BEA), Universidad Católica del Norte, Coquimbo, Coquimbo, Chile
[5] Departamento de Acuicultura, Universidad Católica del Norte, Coquimbo, Coquimbo, Chile
[6] Centro de Investigación y Desarrollo Tecnológico en Algas y otros Recursos Biológicos (CIDTA), Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Coquimbo, Chile
[7] Instituto Milenio en Socio-Ecología Costera (SECOS), Santiago, Chile

ABSTRACT

Mesophotic and deeper habitats (~40 to 350 m in depth) around Rapa Nui (Easter Island) were investigated using a remotely operated vehicle. We observed extensive fields of filamentous cyanobacteria-like mats covering sandy substrates and mostly dead mesophotic *Leptoseris* spp. reefs. These mats covered up to 100% of the seafloor off Hanga Roa, the main village on the island, located on its western side. The highest mortality of corals was observed at depths between 70 and 95 m in this area. Healthy *Leptoseris* reefs were documented off the northern and southeastern sides of the island, which are also the least populated. A preliminary morphologic analysis of samples of the mats indicated that the assemblage is composed of at least four filamentous taxa, including two cyanobacteria (cf. *Lyngbya* sp. and *Pseudoanabaena* sp.), a brown alga (*Ectocarpus* sp.), and a green alga (*Cladophora* sp.). An ongoing eutrophication process is suggested as a potential driver of the proliferation of these filamentous mats off Hanga Roa village.

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Corresponding author
Javier Sellanes, sellanes@ucn.cl

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INTRODUCTION

Mesophotic coral ecosystems are deep reef communities that typically occur at a depth range of 30 or 40 to over 150 m (*Baker et al., 2016*). They are formed mainly by coral taxa adapted to living in low-light conditions and often also include other structure-forming taxa, such as sponge and macroalgae species (*Baker et al., 2016*; *Slattery & Lesser, 2021*). These ecosystems are now recognized as ecologically distinct and independent from their shallower counterparts and contain a substantial diversity of unique biota that is still

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unexplored in most parts of the world (Rocha et al., 2018). The lack of knowledge about these deep coral ecosystems is a consequence of the difficulty of accessing the depths at which they occur, as technical diving (*e.g.*, rebreather diving using trimix) or sophisticated submarine equipment (*e.g.*, remotely operated vehicles, autonomous drop-cams, or manned submersibles) are required to carry out research. Mesophotic coral ecosystems are vulnerable to a series of anthropogenic stressors, such as fishing, thermal stress, diseases, pollution, invasive species, the marine aquarium trade, oil and gas exploration, cables, and pipelines (Andradi-Brown et al., 2016).

Rapa Nui (Easter Island; 27°07′S, 109°22′W), which formed ~0.8 Mya, is a remote island located at the westernmost end of the large chain of seamounts comprising the Salas y Gómez ridge, relatively close to the East Pacific Rise (Rodrigo, Díaz & González-Fernández, 2014). Located in the easternmost apex of the Polynesian triangle, it is recognized for the high overall endemism levels of its coastal marine fishes (~22%; Randall & Cea, 2010) and invertebrate taxa (4% to 34%; see Fernandez et al., 2014). However, this unique marine biodiversity is severely threatened by several anthropogenic impacts, including overfishing (Zylich et al., 2014), plastic pollution (Hidalgo-Ruz et al., 2021), exacerbated tourism (Figueroa & Rotarou, 2016), coastal erosion and terrestrial runoff (Mieth & Bork, 2005), and potential pollution from the percolation of domestic sewage and landfill contaminants into aquifers (Rosa, 2013).

Recently (2015–2018), through the use of a remotely operated vehicle (ROV), we have been able to access unexplored marine habitats (from ~40 to 350 m deep) around the island, as well as at nearby seamounts, allowing for a first assessment of the biodiversity of mesophotic ecosystems and deeper sites (Easton et al., 2019), generation of new records of fauna, including fishes (*e.g.*, Easton et al., 2017) and echinoderms (Mecho et al., 2019), and reports of vast fields of the solitary mesophotic mushroom coral *Cycloseris vaughani* (Hoeksema, Sellanes & Easton, 2019). In these surveys, a chance discovery was the presence of dense and extensive fields of filamentous mats, covering the seafloor and nearby reefs at mesophotic depths at several locations around the island. It is known that cyanobacteria are a common constituent of coral reef ecosystems (Stal, 2000) and play an important role in nitrogen fixation and primary production (Charpy et al., 2012). However, under certain conditions, they can undergo massive proliferation, affecting the health of the ecosystem (Bakker et al., 2017; Ford et al., 2017). These events have been associated with variation in irradiance, nutrient supply, and other natural and anthropogenic disturbances (Ford et al., 2018). These proliferation events seem to be increasing at a global scale because of alterations in local biogeochemical cycles related to climate change (Paul, 2008; Paerl & Paul, 2012). These filamentous mats could develop into such dense blooms that they could even wash ashore, producing a mass accumulation, as reported by Nagle & Paul (1999) for Guam. At this location, benthic marine cyanobacterial blooms often occur in the presence of diverse assemblages of herbivorous fishes and urchins, but the underlying factors causing these proliferations, as well as the interaction mechanisms between grazers and these mats (since cyanobacteria are known to produce feeding-deterrent compounds), are still poorly understood (Cissell, Manning & McCoy, 2019; Ford et al., 2021). In addition, cyanobacteria have been directly linked with ciguatera fish poisoning outbreaks (Laurent et al., 2008), and mats can create suitable habitats for other toxic microalgae, including toxin-producing dinoflagellates, thus generating co-occurring blooms (*Paerl & Otten, 2013*). Although several microalgae species are not toxic, their growth could produce low oxygen conditions as a consequence of organic matter accumulation and associated degradation processes in the bottom water, thus affecting the benthic communities (*Albert et al., 2012*). It is also possible that the rise of fixed nitrogen may modify its budget in the system, promoting the growth of macroalgae, further increasing the organic matter content within the sediments, and decreasing porewater oxygen content (*Brocke et al., 2015*; *Brocke et al., 2018*). In some environments, mats form associations with sulfate-reducing bacteria, producing sulfide, which is toxic for corals and establishes black band disease (*Myers & Richardson, 2009*; *Charpy et al., 2012*).

It has also been reported that in littoral reefs, green algae (chlorophytes) are common indicators of eutrophication (*Barile, 2004*). Most of the species in this group proliferate due to increased nutrient inputs, tolerate a wide range of environmental conditions, aggressively compete against sensitive corals, and have sub-lethal effects on several of the biological functions of corals (*Koop et al., 2001*; *Fabricius, 2005*; *Birrel et al., 2008*).

In this context, the aims of the present study were: (1) to provide a first approach to the spatial coverage of filamentous mats in the benthic ecosystem around Rapa Nui, (2) to evaluate the extent of the mesophotic coral reefs potentially impacted by these mats, and (3) to provide a preliminary description of the taxonomic composition of these mats.

MATERIALS AND METHODS

Rapa Nui is a triangular-shaped island, delimited by the volcanoes Rano Kau in the southwest, Terevaka in the north, and Poike in the east, with Hanga Roa, the main village, located on the western side (Fig. 1). Aiming to have a representative spatial and bathymetric (∼40 to 350 m deep) characterization of the mesophotic habitats on the three sides of the island, a remotely operated vehicle (ROV), controlled from local fishing boats, was deployed in 56 mostly independent sites around the island. There were 18 deployments each in January 2018 and 2019, and 20 during November and December 2019 (Fig. 1). The ROV, model Commander MKII (Mariscope Meerestechnik, Kiel, Germany), was equipped with two laser pointers, 10 cm apart, and a front-pointing HD video camera (Panasonic SD 909), angled at 45° and recording at 30 fps with a resolution of 1920 × 1080 pixels. The videos were analyzed at half their normal speed using GOM Player 2.3.19 (GOM & Company; https://www.gomlab.com/).

As mentioned in the Introduction, some of the results of these and previous ROV surveys have been presented elsewhere (*Easton et al., 2017*; *Easton et al., 2019*; *Hoeksema, Sellanes & Easton, 2019*; *Mecho et al., 2019*), for selected biotic components. For the present study, however, the focus was to evaluate the spatial coverage of filamentous mats in the benthic ecosystem, and the extent of mesophotic reefs potentially impacted by these mats, as well as their overall health conditions. The presence and coverage of filamentous mats were assessed semi-quantitatively by observing the seafloor in a stepwise manner as the ROV advanced over the ground along transects. Bottom-time varied between 10 and 42 min

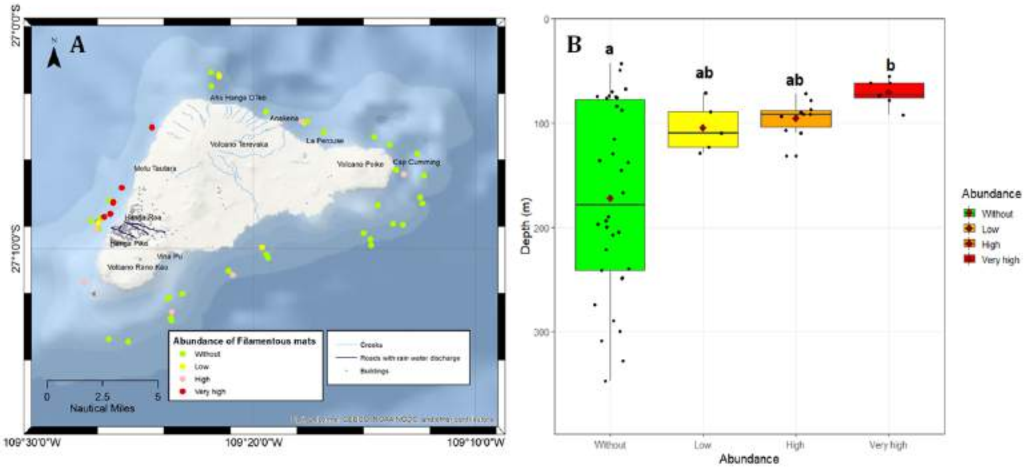

Figure 1 **Map of Rapa Nui showing the main features of the island, the sites surveyed in the present study, and the extent of coverage of filamentous mats at these sites.** (A) Abundance of filamentous mats in the benthic ecosystems at the survey sites. (B) Depth range of the remotely operated vehicle stations for each category of filamentous mat coverage used in this study. Green: no mats observed, yellow: low coverage, orange: high coverage, and red: very high coverage. The box plots show the mean (red diamonds), median (horizontal black line), and lower and upper quartiles; the whiskers indicate the depth range for each category. The letters (a, b) indicate homogenous groups identified using the Wilcoxon *post hoc* test.

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(mean: 25 min) per transect. In general, a portion of 10 to 20 min of video, considering mainly those segments in which the ROV was displaced at a steady velocity and a suitable distance from the bottom, was selected and analyzed per site. For each transect, we analyzed an area of at least 10 m^2, corresponding to ~15 non-overlapping frames. We exclusively analyzed those frames when the ROV was approximately 25 cm above the ground or in front of the reefs. As calibrated with the ROV on land, at these distances the images covered an area of ~0.65 m^2 (width ~117 cm × height ~65 cm).

According to the extent to which the bottom or the coral was covered by filamentous mats, the transects were cataloged into four groups: (1) without patches of filamentous mats, (2) low coverage (less than 50% coverage in at least five non-overlapping frames of the video of a transect), (3) high coverage (50% to 75% coverage in at least five frames of the video of a transect), and (4) very high coverage (100% coverage). Statistical comparisons of the mean depth between the four categories of filamentous mat coverage were evaluated using the Kruskal-Wallis test. *Post hoc* analyses were performed using pairwise comparisons with the Wilcoxon rank sum test and the *p*-value was adjusted using the Holm method (*Holm, 1979*). Before comparisons, normality and homogeneity of variance were tested using the Shapiro–Wilk and Levene tests, respectively. Statistical analyses were performed using RStudio (*R StudioTeam, 2020*), specifically the "car" package (*Fox & Weisberg, 2019*) and the "ggplot2" package for boxplots (*Wickham, 2016*).

We used the same ROV survey approximation to assess the extent of live coral coverage as a proxy for coral health status. Three categories were considered: (1) a healthy reef with >75% of the corals alive, (2) some damage with 25% to 75% of the corals alive, and (3) mostly damaged with <25% of the corals alive (mainly dead corals or fragments). Dead corals were easily identified by their generally greenish or darker colors. Some were also covered by filaments.

To characterize the taxonomic composition of the filamentous mat assemblage, in May 2019, a small benthic trawl with a horizontal aperture of 30 cm was deployed at a site off Hanga Roa, where patches with 100% coverage were frequent. Mat samples were fixed using a 4% aqueous solution of formaldehyde (ACS Reagent; Sigma-Aldrich, St. Louis, MO, USA). For morphological characterization, filaments were observed using an Olympus IX71 inverted microscope equipped with phase contrast and epifluorescence (Olympus Co., Tokyo, Japan). Micrographs were taken using a camera ProgRes C3 (JENOPTIK AG, Jena, Germany), and measurements of cells (length and width) were carried out using ProgRes® CapturePro (JENOPTIK AG) analytical software. Monographic publications, floristic studies, and systematic articles were used for taxonomic identification of the macroalgae composing the mats, at least to the genus level (*Santelices, 1989*; *Loiseaux-de Goër & Noailles, 2008*; *Cormaci, Furnari & Alongi, 2014*; *Ramirez et al., 2018*). Guides and systematic articles were used to identify the cyanobacteria inhabiting the mat samples (*Komarek & Anagnostidis, 2007*; *Yu et al., 2015*; *Brocke et al., 2018*; *Zubia et al., 2019*). The identification of taxa was performed at the genus or species complex level.

Sample collection was performed with permission Res. Ext No. 41/2016 and No. 3314/2017 from SUBPESCA (National Fishing Authority of Chile) granted to the Universidad Católica del Norte. This project was also presented to the local *Consejo del Mar de Rapa Nui* (Council of the Sea of Rapa Nui), which permitted the capture of underwater footage and sampling around the island.

RESULTS

The ROV transects around the island covered a depth range of 43 to 347 m. This allowed us to visualize the spatial and bathymetric distribution of sites with different levels of filamentous mat coverage (Figs. 1 and 2), and the distribution of mesophotic reefs and their health status around the island (Fig. 3). Mesophotic corals were represented by reef-forming *Porites lobata* and *Pocillopora* spp. at shallower depths (<60 m), *Leptoseris* spp., and *C. vaughani* at depths between 70 and 117 m, and sea-whips (*Stichopathes* spp.) between 127 and 327 m (Fig. 2). Other scleractinians were occasionally sighted deeper than 120 m (*e.g.*, cup corals), but they were too small to identify using ROV images.

Spatial distribution of filamentous mats and corals

Filamentous mats were absent (category: without) from 34 of the studied sites around Rapa Nui, and low to very high coverage was observed at the remaining 22 sites, commonly on the western side of the island (Fig. 1A) and in water shallower than ~130 m (Fig. 1B). Statistical comparisons confirmed the significant differences between the depths of the mat-coverage categories (Kruskal-Wallis, Ch $i^2 = 12.9$, $df = 3$, $p = 0.005$), in particular between the categories without and very high (Wilcoxon test, $p = 0.023$; Fig. 1B). Other comparisons between categories were not significant (Wilcoxon test, $p > 0.05$). Indeed, high coverage was observed in the northwest corner (close to Hanga O'teo) at a depth of

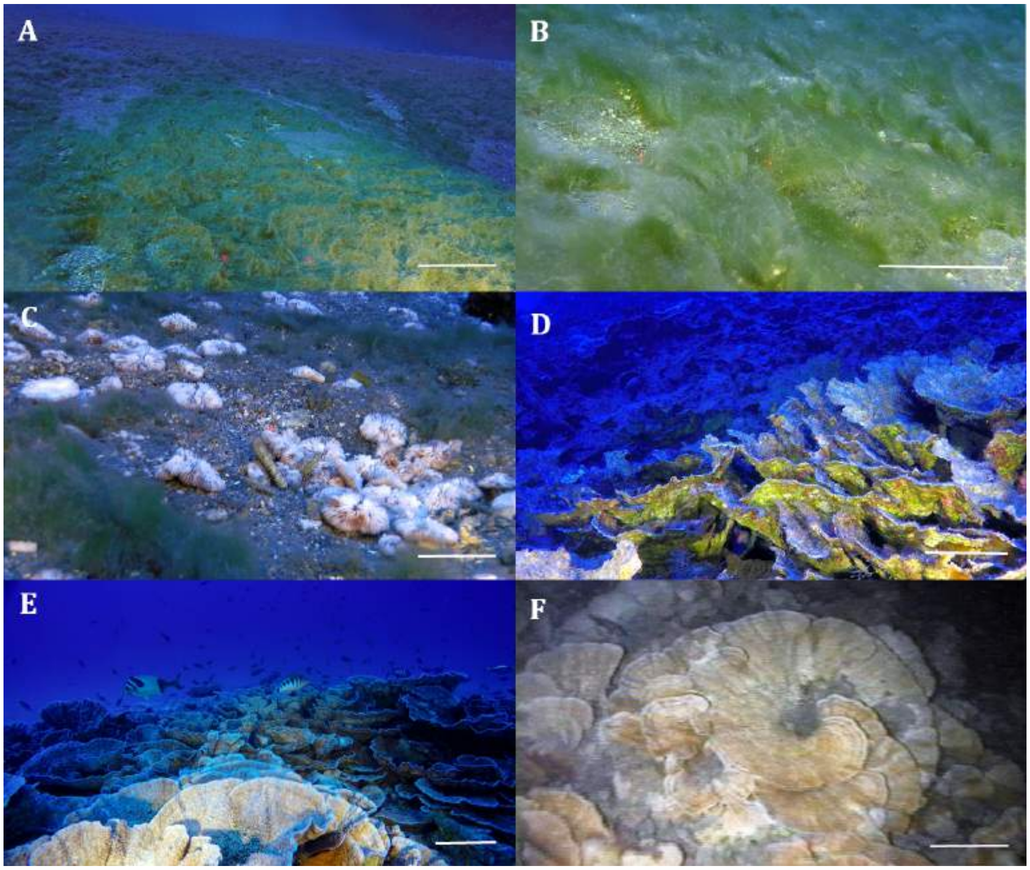

Figure 2 Remotely operated vehicle (ROV) images of the filamentous mats and mesophotic reefs off Rapa Nui. (A) Field of filamentous mats at ~80 m deep off Hanga Roa, Rapa Nui. (B) Close up view of the filaments. (C) Filaments among *Cycloseris vaughani* individuals. (D) Dead *Leptoseris* reef ~80 m deep overgrown by filaments. (E) Healthy *Leptoseris* reef off Anakena 80 m deep. (F) Healthy *Leptoseris* reef off Hanga Roa filmed during prospective ROV surveys during the "CIMAR-5 Islas" cruise conducted in 1999. Scale bars: 10 cm (A, B, C) and 25 cm (D, E, F). Images: Matthias Gorny, OCEANA.

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123 m, and high and very high coverages were observed mainly off Hanga Roa (Fig. 1B) from 70 to 95 m deep.

Corals were observed in 50% of the 56 transects (Fig. 3A), and *Leptoseris* was present in 11 of them. Off Hanga Roa, the location where filamentous mats were most frequent, they were observed covering the sediments (Figs. 2A, 2B), fringing fields of the zooxanthellate mushroom coral *C. vaughani* (Figs. 2C, 3A; see also *Hoeksema, Sellanes & Easton, 2019*), and close by dead *Leptoseris* reefs (~80 m deep), which were also overgrown by filamentous mats (Fig. 2D). Healthy *Leptoseris* reefs were documented mainly off the northern and southeastern parts of the island (*e.g.*, near Anakena, La Perouse, and Vinapú) at depths of 68 to 82 m (Fig. 3B). Of the six locations with the healthiest *Leptoseris* reefs, four of them had no filamentous mats, or a sporadic presence of them, whereas at the three sites where the reefs were completely dead, filamentous mat coverage was high or very high (see also Supplemental Information).

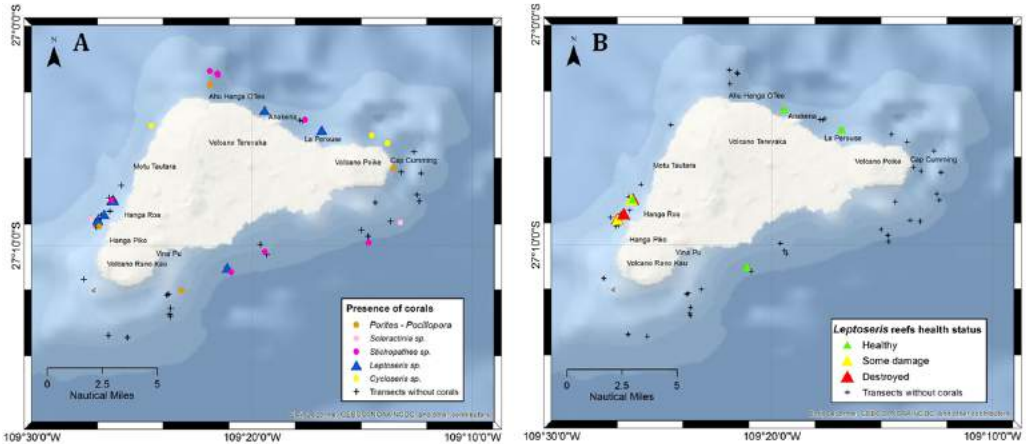

Figure 3 **Transects surveyed off Rapa Nui in the present study showing sites with mesophotic corals.** (A) Map showing the main mesophotic coral taxa at each site. (B) Health status of *Leptoseris* reefs indicated by color: green = healthy (no noticeable impact), yellow = some damage (25%–75% of corals damaged), and red = destroyed (only dead corals or fragments observed).

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Taxonomic characterization of the filamentous mat assemblage

Morphological analyses of samples of mats collected off Hanga Roa indicated that mats are an assemblage of at least four taxa: one Chlorophyta (*Cladophora* sp.), one Ochrophyta (*Ectocarpus* sp.), and two Cyanobacteria (*Lyngbya* s.l. ([sensu lato] and *Pseudoanabaena* sp.) (Fig. 4) as follows:

Cladophora sp. (Figs. 4A, 4B): thallus of green to light green branched uniseriate filaments with 2–3 cm in total length. Basal part of the filaments fixed to the substrate by a primary rhizoid. Presence of unilateral branches inserted laterally or obliquely on the filament. Principal axis constituted by cylindrical cells measuring of 998.9 ± 69.2 µm in length and 223.3 ± 9.5 µm in diameter. Apical cells cylindrical, round ended with a diameter of 250.0 ± 7.6 µm and length of 701.8 ± 76.0 µm. Zoosporangia were not observed.

Ectocarpus sp. (Figs. 4C, 4D): thallus of light brown to olive sparingly branched filament 0.1–0.5 cm in total length. Cells conform to uniseriate filaments ending in a rounded apical cell. Cells barrel-shaped, 50.0 ± 7.3 µm in length, and 14.1 ± 3.4 µm in diameter. Plurilocular sporangia were present, elongated with cylindroconical form, 80–130 µm in length and 20–30 µm in diameter.

Lyngbya s.l. (Figs. 4E, 4F): thallus caespitose, brownish-red, filaments slightly curved, sheet colorless, lamellated with apices not attenuated at the end. Trichome not constricted at the cross-wall, cylindrical cells very short 3.5 ± 0.3 µm in length and 7.1 ± 0.1 µm in diameter, sheath 1.6 ± 0.3 µm, end cells rotund, calyptra absent.

Pseudoanabaena sp. (Figs. 4G, 4H): trichomes solitary or crowded in clusters, straight or almost straight, pale blue–green. Cells barrel-shaped, 2.8 ± 0.8 µm in length and 1.2 ± 0.1 µm in diameter, intensely constricted at cross walls, no heterocysts or sheath, end cells round.

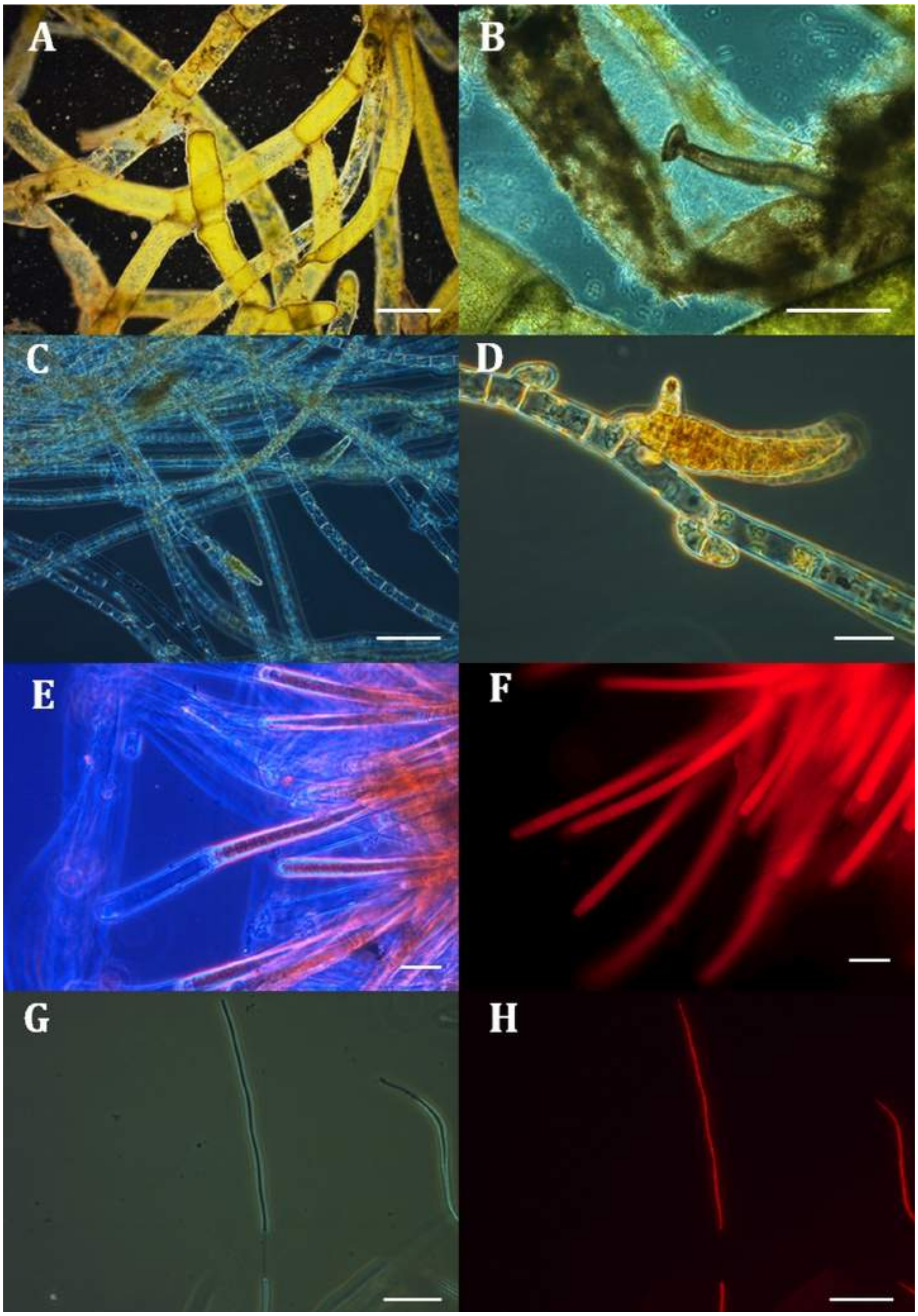

Figure 4 Micrographs of four filamentous taxa in samples from mats collected off Hanga Roa, Rapa Nui at mesophotic depths. A–E and G were photographed using phase-contrast and F and H using epifluorescence techniques. (A, B) *Cladophora* sp. (C, D) *Ectocarpus* sp. (E, F) *Lyngbya* s.l. (G, H) *Pseudoanabaena* sp. Scale bars represent (A): 500 µm, (B): 200 µm, (C): 100 µm, (D): 30 µm, (E and F): 20 µm, and (G) and H: 30 µm.

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DISCUSSION

Although we have provided only a preliminary taxonomic characterization of the filamentous mats covering sandy areas and dead mesophotic reefs off Rapa Nui, our findings indicate that these mats are composed of at least two cyanobacteria. We are aware of, and recognize the limitations associated with our approach to identifying mat taxa, based only on morphology. As indicated by *Komárek (2016)*, *Lyngbya*, *Okeania*, and *Moorea* cannot be distinguished from each other using light microscopy. Thus, we refer to *Lyngbya* s.l. ([sensu lato] and suggest that genetic analysis is needed to clarify this classification. Cyanobacteria-dominated microbial mats are known to be typical components of coral reef systems and often undergo massive proliferation (*Stal, 2000*). These events have been associated with natural processes (*e.g.*, variation in irradiance), but mostly with anthropogenic disturbances that increase nutrient concentrations in the marine environment (*Ford et al., 2017*). The highest coverage of mats was observed mainly off Hanga Roa village, which has the highest concentration of the island's human population (7,750 inhabitants; http://www.ine.cl) and where most tourists engage in recreational activities. *Figueroa & Rotarou (2016)* reported ~20,000 visitors per year in the late 1990s, whereas ~150,000 were reported during 2019 (http://www.sernatur.cl), representing an approximately eight-fold increase over the last two decades. Factors such as overtourism, the absence of a wastewater collection and treatment system (most of the residences have cesspools and a minor proportion have septic tanks), and the unlined landfill (*Rosa, 2013*) potentially pose a great threat to the marine environment off Hanga Roa village, owing to the potential input of organic matter, nutrients, and contaminants. Pollutants can reach the sea by runoff or percolation to aquifers that eventually discharge into the sea. On Rapa Nui, submarine groundwater discharges are ubiquitous in intertidal environments around the island (*Brosnan, Becker & Lipo, 2018*), and could hypothetically also seep through deeper sediments (*Montgomery EL & Associates INC, 2011*), potentially conducting nutrients of anthropogenic origin directly to mesophotic habitats. Indeed, very low salinities (4.7–16.8 psu) have been measured in the overlying water of unperturbed sediment cores obtained off Hanga Roa where filamentous mats proliferate, further suggesting percolation of pollutants to aquifers in the area (P. Muñoz, unpublished data). A similar situation has been observed at the western flank of Hawai'i Island, where freshwater from onshore aquifers can flow through permeable fractured basalts, mix with seawater to form freshened groundwater, and seep into offshore (mesophotic) benthic areas (*Attias et al., 2020*). Furthermore, the observation of low salinity bottom water is concomitant with relatively high NO_3^- concentrations (1.87 and 3.03 μM), compared to two other sites where nitrate concentrations were undetectable in overlying waters with normal salinities (~35 psu) (P. Muñoz, unpublished data). Therefore, it is feasible that the benthic fluxes and submarine groundwater discharges could channel nutrients to mesophotic depths, enhancing algal and cyanobacterial growth, to the detriment of corals. A similar situation, albeit caused by groundwater nutrients derived from bird guano, was observed in the coral reefs of Heron Island (Great Barrier Reef, Australia; *McMahon & Santos, 2017*). In addition to the potential impacts of pollutants, the permanent coastal erosion around Rapa Nui and terrestrial runoff during rainy seasons (May to October) could also increase nutrient inputs to the coastal environments, including ammonia, nitrate, and silicate, which are known to have negative consequences for corals (*D'Angelo & Wiedenman, 2014*). Furthermore, the volcanic origin of Rapa Nui, together with enhanced erosion could also increase the iron concentration in the marine ecosystem. Iron from shipwrecks has been found to directly drive cyanobacteria expansion in iron-limited reefs in the Pacific (*Kelly et al., 2012*; *Mangubhai & Obura, 2018*). Increased iron added to a decrease in the N:P ratio could even further stimulate the proliferation of cyanobacteria (*Ford et al., 2018*).

Regarding mesophotic reefs, two species of the genus *Leptoseris* have been reported for Rapa Nui, *L. scabra* and *L. solida*, both collected in 1999 off Hanga Roa at depths of 43 m and 80 to 100 m, respectively (*Glynn et al., 2007*). Given the depth of our observations as well as the plate-like structure of the colonies, as indicated by *Glynn et al. (2007)*, the damaged reef off Hanga Roa village was probably composed mainly of *L. solida*. A piece of evidence, also obtained in November 1999 during the first ROV survey ever done off Hanga Roa at ~80 m deep, suggests that the same *Leptoseris* reef that is currently dead was healthy ~20 years ago (Fig. 2D; *Gorny & Retamal, 2000*). In the present study, live *Leptoseris* reefs were documented mainly off the northern and southeastern sides of the island (*e.g.*, Anakena, La Perouse, and Vinapú).

Despite the circumstantial indication of the health status of the mesophotic reefs off Hanga Roa a few decades ago, the ecological impacts on the biodiversity and ecosystem functioning associated with anthropogenic causes are still unknown and need further investigation in the short term. Further research should address a more detailed taxonomic characterization of these mats, for example, through molecular techniques; assessment of the seasonal, spatial, and structural patterns of the assemblage; their eventual role in reef deterioration; recognition of eutrophication mechanisms; and long-term monitoring of dissolved organic matter and nutrient dynamics. These studies are encouraged to inform the implementation of effective and integrated land-sea management actions, including a wastewater treatment system. This information should also be key to inform the implementation of management strategies of the recently created Marine Protected Area of Multiple Uses (MPA-MU) of Rapa Nui, currently the largest in Latin America. This protected area encompasses ~579,000 km^2 (*Paredes et al., 2019*) and aims to protect this unique world biodiversity heritage site. In addition, this study will also serve as a baseline for future studies of changes in the mesophotic ecosystem off Rapa Nui after closure of the island to tourism, from March 2020 to date, due to the COVID-19 pandemic.

CONCLUSIONS

Based on opportunistic video observations, we provide the first report of filamentous mats covering sandy areas and dead mesophotic reefs (*Leptoseris* spp.) off Rapa Nui. A preliminary morphological analysis of mat samples suggested that the assemblage is constituted by at least four filamentous taxa, including two cyanobacteria (*Lyngbya* s.l. and *Pseudoanabaena* sp.), a brown alga (*Ectocarpus* sp.), and a green alga (*Cladophora* sp.). Whereas a highly damaged, even completely dead, *Leptoseris* reef was observed in the waters off the main village on the western side of the island, reefs in much healthier conditions were observed off the less populated northern and southeastern parts of the island (*e.g.*, Anakena, La Perouse, and Vinapú). Circumstantial evidence indicates that the *Leptoseris* reef off Hanga Roa was alive ~20 years ago. Our preliminary evidence suggests a link between ongoing eutrophication associated with human population expansion and deficient management of wastewater and urban runoff on the western side of the island, the proliferation of filamentous mats, and consequent damage to mesophotic *Leptoseris* reefs.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Javier Sellanes and Matthias Gorny conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Germán Zapata-Hernández and Gonzalo Alvarez performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

- Praxedes Muñoz conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Fadia Tala performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.

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Data Availability

The following information was supplied regarding data availability:

The raw data are available in the Supplementary File.

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Dongsha Atoll is an important stepping-stone that promotes regional genetic connectivity in the South China Sea

Shang Yin Vanson Liu[1,2], Jacob Green[3,4], Dana Briggs[3], Ruth Hastings[3], Ylva Jondelius[3], Skylar Kensinger[3,5], Hannah Leever[3], Sophia Santos[3], Trevor Throne[3], Chi Cheng[2], Hawis Madduppa[6], Robert J. Toonen[7], Michelle R. Gaither[8] and Eric D. Crandall[3,9]

[1] Dongsha Atoll Research Station, College of Marine Sciences, National Sun Yat-sen University, Kaohsiung City, Taiwan
[2] Department of Marine Biotechnology and Resources, National Sun Yat-Sen University, Kaohsiung City, Taiwan
[3] School of Natural Sciences, California State University, Monterey Bay, California, United States
[4] Department of Biological and Environmental Science, University of Rhode Island, Kingston, Rhode Island, United States
[5] Department of Molecular, Cellular and Developmental Biology, University of California, Santa Cruz, Santa Cruz, California, United States
[6] Department of Marine Science and Technology, Institut Pertanian Bogor, Bogor, Indonesia
[7] Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kane'ohe, Hawai'i, United States
[8] Department of Biology, University of Central Florida, Orlando, Florida, United States
[9] Department of Biology, Pennsylvania State University, University Park, Pennsylvania, United States

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Corresponding authors
Shang Yin Vanson Liu, syvliu@mail.nsysu.edu.tw
Eric D. Crandall, eric.d.crandall@gmail.com

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ABSTRACT

Background: Understanding region-wide patterns of larval connectivity and gene flow is crucial for managing and conserving marine biodiversity. Dongsha Atoll National Park (DANP), located in the northern South China Sea (SCS), was established in 2007 to study and conserve this diverse and remote coral atoll. However, the role of Dongsha Atoll in connectivity throughout the SCS is seldom studied. In this study, we aim to evaluate the role of DANP in conserving regional marine biodiversity.

Methods: In total, 206 samples across nine marine species were collected and sequenced from Dongsha Atoll, and these data were combined with available sequence data from each of these nine species archived in the Genomic Observatories Metadatabase (GEOME). Together, these data provide the most extensive population genetic analysis of a single marine protected area. We evaluate metapopulation structure for each species by using a coalescent sampler, selecting among panmixia, stepping-stone, and island models of connectivity in a likelihood-based framework. We then completed a heuristic graph theoretical analysis based on maximum dispersal distance to get a sense of Dongsha's centrality within the SCS.

Results: Our dataset yielded 111 unique haplotypes across all taxa at DANP, 58% of which were not sampled elsewhere. Analysis of metapopulation structure showed that five out of nine species have strong regional connectivity across the SCS such that their gene pools are effectively panmictic (mean pelagic larval duration (PLD) = 78 days, sd = 60 days); while four species have stepping-stone metapopulation structure, indicating that larvae are exchanged primarily between

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nearby populations (mean PLD = 37 days, sd = 15 days). For all but one species, Dongsha was ranked within the top 15 out of 115 large reefs in the South China Sea for betweenness centrality. Thus, for most species, Dongsha Atoll provides an essential link for maintaining stepping-stone gene flow across the SCS.
Conclusions: This multispecies study provides the most comprehensive examination of the role of Dongsha Atoll in marine connectivity in the South China Sea to date. Combining new and existing population genetic data for nine coral reef species in the region with a graph theoretical analysis, this study provides evidence that Dongsha Atoll is an important hub for sustaining connectivity for the majority of coral-reef species in the region.

Subjects Biodiversity, Conservation Biology, Evolutionary Studies, Marine Biology, Zoology
Keywords Indo-Pacific, Migration models, Larval dispersal, Marine connectivity, Phylogeography, Marine metapopulations, Stepping-stones

INTRODUCTION

With coral reefs and their communities in accelerating global decline (*Hughes et al., 2003*, *2018*), governments around the world have established Marine Protected Areas (MPAs) as a way to counteract this trend (*Selig & Bruno, 2010*). It is now quite clear that MPAs, especially when planned as part of a network, can increase biodiversity, enhance the biomass of fished species, and promote ecosystem resilience (*Emslie et al., 2015*; *Mellin et al., 2016*; *Sala et al., 2021*). When properly sized and spaced, a network of MPAs can protect coral reef populations, and an adequate fraction of their larval offspring that disperse to nearby MPAs, ensuring both long-term community persistence and fisheries spillover (*Gaines et al., 2010*; *Krueck et al., 2017*). However, while there are a few robust examples of MPA networks planned at the regional level (*Gleason et al., 2013*; *Emslie et al., 2015*), most MPAs are singletons implemented by regional governments for local benefit only (*Gaines et al., 2010*).

Singleton MPAs are still valuable for the conservation and resilience of local coral reef communities and maintaining local fisheries through larval export and adult spillover (*Lester et al., 2009*; *Mellin et al., 2016*). However, it remains crucial to evaluate, post hoc, their role in conserving regional marine biodiversity. Does the MPA serve as a useful intergenerational stepping-stone that can augment demographic and genetic connectivity among regional reefs (*McCook et al., 2009*)? Coalescent samplers are a family of population genetic models that allow a relatively quick and inexpensive way to make such an evaluation (*Crandall, Treml & Barber, 2012*; *Selkoe et al., 2016*; *Crandall et al., 2019b*). In a likelihood-based model selection framework, such methods can distinguish between models of effective panmixia (high regional gene flow) and metapopulation models in which larvae disperse only to nearby populations (stepping-stone model) or to all sampled populations (island model; *Beerli & Palczewski, 2010*).

Understanding the role of a given MPA in region-wide connectivity patterns requires genetic data from many species from inside the MPA and from the surrounding populations. Fortunately, a working group of the Diversity of the Indo-Pacific Network has

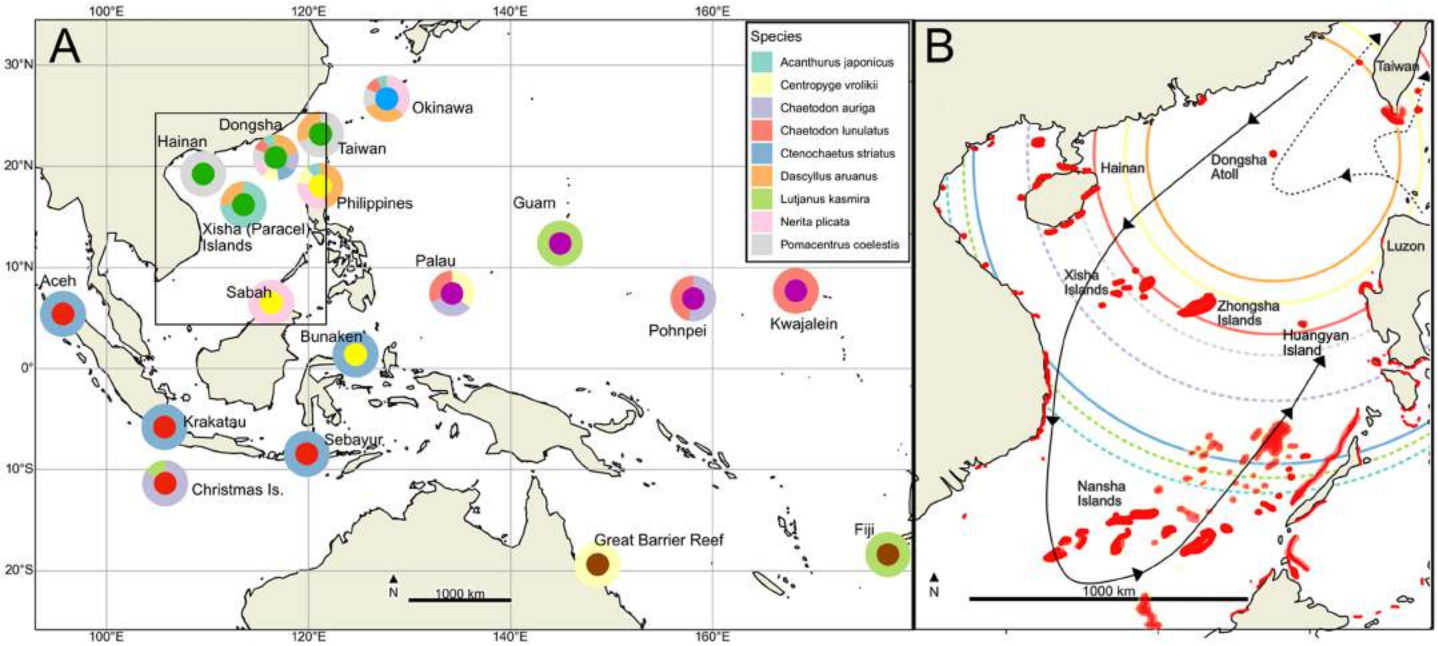

Figure 1 **Sampling map.** (A) Map of all sampled locations. Outer rings are colored by which species were sampled at a locality, while inner circles are keyed to regional colors in Fig. 3. (B) Inset of South China Sea showing coral reefs in red following *Zhao et al. (2016)* and *Dorman et al. (2016)*. Summer surface circulation patterns (solid line with arrows; winter circulation is roughly reversed) and Kuroshio Current intrusion (dotted line with arrows) follow *Hu et al. (2000)*. Open circles are colored by species, and give estimates of maximum larval dispersal distances given mean summer surface current speed of 18.7 km/day (*Hu et al., 2000*) and PLD s given in Table 1. Solid circles indicate species for which a stepping-stone model was selected, and dashed lines indicate species for which panmixia was selected. Maps were generated from the public domain Natural Earth raster with the Cartopy v0.11.2 package for Python (*Met Office, 2014*). Full-size DOI: 10.7717/peerj.12063/fig-1

compiled a genetic database comprising over 38,000 individuals from more than 230 species (DIPnet; *Crandall et al., 2019a*), stored within the Genomic Observatories Metadatabase (GEOME; *Deck et al., 2017*; *Riginos et al., 2020*). This open database provides the opportunity to test various biogeography, speciation, and connectivity hypotheses across a wide taxonomic swath of species comprising Indo-Pacific communities, without the need to sample every location and every species by a single research group.

Located 340 km southeast of Hong Kong and 850 km southwest of Taipei, Dongsha Atoll, with an area of about 600 km^2, is the largest and oldest atoll in the South China Sea (SCS; Fig. 1), (*Dai, 2004*). The atoll is of strategic political importance in that it sits in the Taiwan Strait, a major trade route between East and Southeast Asia. The atoll also hosts important coral reef habitats in the northern South China Sea, providing necessary fishing opportunities for the people of China, Taiwan, and Vietnam (*Dai, 2004*). For this reason, the Dongsha Atoll National Park (DANP) was established in 2004 by the Taiwanese government. The DANP encompasses 3,537 km^2 of marine habitat (*Cheng et al., 2020*), and its establishment has helped to mitigate the impact of massive bleaching events in 1998 and overfishing at the atoll, which were negatively impacting coral cover and biodiversity (*Fang, 1998*; *Soong, Dai & Lee, 2002*; *Dai, 2004*). With proper enforcement and regional cooperation in place since 2007, a general survey of marine resources in the

DANP in 2011 showed that both terrestrial and marine ecological resources are gradually recovering (*Dai, 2012*). Contradicting these results, *Cheng et al. (2020)* detected a dramatic 34% decrease in coral coverage since the DANP was established, with an alarming reduction in the abundance of branching corals indicating an overall simplification of habitat types. Although the effect of the establishment of the DANP on community biodiversity and health is still under debate, how these conservation efforts might have impacted other reefs in the South China Sea and beyond is poorly understood.

In the present study, we added sequence data from nine coral reef species sampled within the DANP to existing datasets in GEOME to test metapopulation hypotheses regarding the role of each species' Dongsha population in the greater context of the Indo-Pacific. We then used a graph theoretical analysis based on maximum dispersal distances to more closely examine Dongha's role as an intergenerational stepping-stone within the South China Sea.

MATERIALS & METHODS

Sampling and sequencing

We selected nine target species from the Genomic Observatories Metadatabase (GEOME; *Deck et al., 2017*) based on the availability of genetic data from nearby populations and their common occurrence at Dongsha Atoll, including eight reef fishes and the intertidal gastropod *Nerita plicata* (Table 1). In March of 2017, tissue samples for these nine species were collected at Dongsha by SCUBA divers using spears in the case of reef fish species, or by hand in the case of the gastropod. Tissues were preserved in 95% ethanol. The field sampling of the present study is under the permit number 0000691 which was approved by the Marine National Park Headquarters in Taiwan.

Mitochondrial DNA (mtDNA) amplification and sequencing were conducted at California State University Monterey Bay as part of the Molecular Ecology and Evolution capstone research course in Fall of 2017. Marker choice was made based on the data available in GEOME and included the mitochondrial Cytochrome Oxidase I, Cytochrome-B, and the Control Region. In each case, published primers were used (see Table 1 for details). DNA was extracted in a 10% Chelex® (Biorad) solution following *Walsh, Metzger & Higuchi (1991)*. Polymerase chain reactions (PCR) were conducted in 25 µL reactions with 2.5 µL of 10x PCR buffer, two µL $MgCl_2$ (25 mM), 2.5 µL dNTPs (8 mM), 1.25 µL of each 10 mM primer, one µL of DNA template, and 0.625 U of AmpliTaq (Applied Biosystems, Waltham, MA, USA). Thermocycling conditions were the same across species, only differing in annealing temperature: initial denature for 2 min at 95 °C; followed by 35 cycles of denaturation at 95 °C for 15 s; annealing at T °C for 30 s (where T is given in Table 1); and elongation at 72 °C for 1 min; with a final elongation step at 72 °C for 7 min. PCR products were checked on a 1% agarose gel using GelRed (Biotium, Fremont, CA, USA). Successful PCR products were sent to the MCLab (South San Francisco; mclab.com) for cleanup, cycle sequencing (both directions), and sequencing on an ABI 3730 DNA Sequencer. Forward and reverse reads for each sample were proofread and aligned using Geneious 9.1.8 software. Complementary sequence data from four or five nearby populations were downloaded for each species from the GEOME database (Fig. 1).

Table 1 **Species names, estimated pelagic larval durations, and primers and annealing temperatures used for PCR.**

Scientific name (dataset citation)	Common name	Maximum pelagic larval duration (days)	mtDNA Locus (base pairs) & Primers used	Annealing temp (°C)
Acanthurus japonicas (*DiBattista et al., 2016*)	Japanese surgeonfish	62 (for *A. triostegus*; *McCormick, 1999*)	Cytochrome-B (491) Cytb9/Cytb7 (*DiBattista et al., 2016*)	62
Centropyge vrolikii (*DiBattista et al., 2012*)	Pearlscale angelfish	29 (*Thresher & Brothers, 1985*)	Cytochrome-B (575) CLFM_FOR/CLFM_REV (*DiBattista et al., 2012*)	58
Chaetodon auriga (*DiBattista et al., 2015*)	Threadfin butterflyfish	48 (*Wilson & McCormick, 1999*)	Cytochrome-B (668) Cytb9/Cytb7 (*DiBattista et al., 2013*)	56
Chaetodon lunulatus (*Waldrop et al., 2016*)	Oval butterflyfish	35 (*Soeparno et al., 2012*)	Cytochrome-B (605) Cytb9/Cytb7 (*Waldrop et al., 2016*)	50
Ctenochaetus striatus	Striated surgeonfish	59 (*Wilson & McCormick, 1999*)	Control Region (316) CR-A/CR-E (*Lee et al., 1995*)	50
Dascyllus aruanus (*Liu et al., 2014*)	Whitetail dascyllus	26 (*Thresher, Colin & Bell, 1989*)	Cytochrome-B (1058) GluDG-L/H16460 (*Palumbi et al., 1991*)	56
Lutjanus kasmira (*Gaither et al., 2010*)	Bluestripe snapper	60 (*Baensch, 2014*)	Cytochrome-B (446) Cytb9/Cytb7 (*DiBattista et al., 2013*)	48
Nerita plicata (*Crandall et al., 2008*)	Whorled nerite	~180 (*Underwood, 1978*)	Cytochrome Oxidase I (613) LCO-1490/HCO-1498 (*Folmer et al., 1994*)	50
Pomacentrus coelestis (*Liu et al., 2012*)	Neon damselfish	39 (*Wilson & McCormick, 1999*)	Control Region (337) CR-A/CR-E (*Lee et al., 1995*)	50

Sequences for each species were aligned and trimmed to a common length using the muscle algorithm with default parameters implemented in Geneious v9 (Biomatters) and exported to FASTA format.

Population genetic analysis

We used the pegas (*Paradis, 2010*) and strataG (*Archer, Adams & Schneiders, 2017*) population genetic packages to read the FASTA-formatted data into R and identify unique haplotypes. We then utilized these packages to estimate standard genetic diversity statistics for the Dongsha population of each species. Haplotype diversity and the number of haplotypes unique to Dongsha were calculated using the *exptdHet*, *privateAlleles* functions in strataG. Fu's F_s, a statistic which identifies populations with an excess of recent substitution events caused by demographic growth, genetic hitchhiking, or background selection (*Fu, 1997*), was calculated using the *fusFS* functions in the same package.

Nucleotide diversity was measured using the *nuc.div* function in pegas. The significance of F_s was determined with 1,000 coalescent simulations of neutrality in Arlequin 3.5 (*Excoffier & Lischer, 2010*). Haplotype diversity, nucleotide diversity, and percentage of private haplotypes (unique to a given population) were also averaged across all nearby sampled populations, and a two-sided *t*-test was used to determine if the Dongsha populations' genetic diversity was significantly different from the nearest sampled populations.

Pairwise Φ_{ST}, a sequence analog of F_{ST} (*Excoffier, Smouse & Quattro, 1992*), was calculated with *pairwiseTest* in strataG with significance determined by 1,000 randomly drawn permutations of the data to represent the null hypothesis of no genetic structure. Finally, pairwise matrices were visualized in ggplot2 and as non-metric dimensional scaling (NMDS) plots to represent the distances in two-dimensional space using the *metaMDSiter* function in the R package vegan (*Oksanen et al., 2017*), using a hybrid model of monotone and linear regression for Φ_{ST} values lower than 0.1. For both visualizations, negative values were corrected to zero, and for NMDS, zero or negative values had a very small positive value added to them. To visualize whether there is a geographic pattern of haplotype distribution, we defined samples used in this study into six regional groups (Fig. 1). Median joining networks with these regional colors were created using PopArt (*Leigh & Bryant, 2015*). All analyses are detailed at https://github.com/ericcrandall/dongsha/.

We also estimated the marginal likelihood of three different metapopulation models for the nine species in Migrate-n 3.6.11 (*Beerli & Felsenstein, 2001*; *Beerli & Palczewski, 2010*; Fig. 2): (a) extremely high levels of larval dispersal (proportion of migrants (m) > 0.1) throughout the sampled range yielding effective panmixia, (b) slightly restricted larval dispersal ($m < 0.1$) represented by an n-island model with equal population sizes and equal migration between all population pairs, (c) restricted larval dispersal such that larvae are only exchanged between neighboring populations or regions as represented in a stepping-stone model (two populations were determined to be neighboring if no other sampled populations would serve as a likely intermediate stepping-stone).

Migrate-n analysis followed methods developed in *Crandall et al. (2019b)*. FASTA-formatted datasets were converted to Migrate-n format using PGDSpider 2.0.5.1 (*Lischer & Excoffier, 2012*). For each species, we found optimal parameters (gamma shape parameter, transition transversion ratio and base frequencies) for an HKY + G model of molecular evolution using the *modelTest* function in the R package phangorn (*Schliep, 2011*). The gamma shape parameter was discretized to four categories using the *discrete.gamma* function from the same package. All models had identical, windowed exponential priors on Θ (lower bound: 1×10^{-5}, upper bound: 1×10^{-1}, mean: 0.01) and m/μ (lower bound: 1×10^{-4}, upper bound: 1×10^{6}, mean: 1×10^{5}) parameters. We used four heated chains with temperatures of 1, 1.5, 3, and 1×10^{5} to ensure a thorough search of parameter space, thereby enabling an estimate of model marginal likelihood *via* path sampling (*Beerli & Palczewski, 2010*). Migrate-n was set to optimize on the m/μ parameter rather than the joint parameter N_em (to avoid correlations with the Θ (= N_e μ) parameters), and with an inheritance scalar that reflected the haploid, uniparental

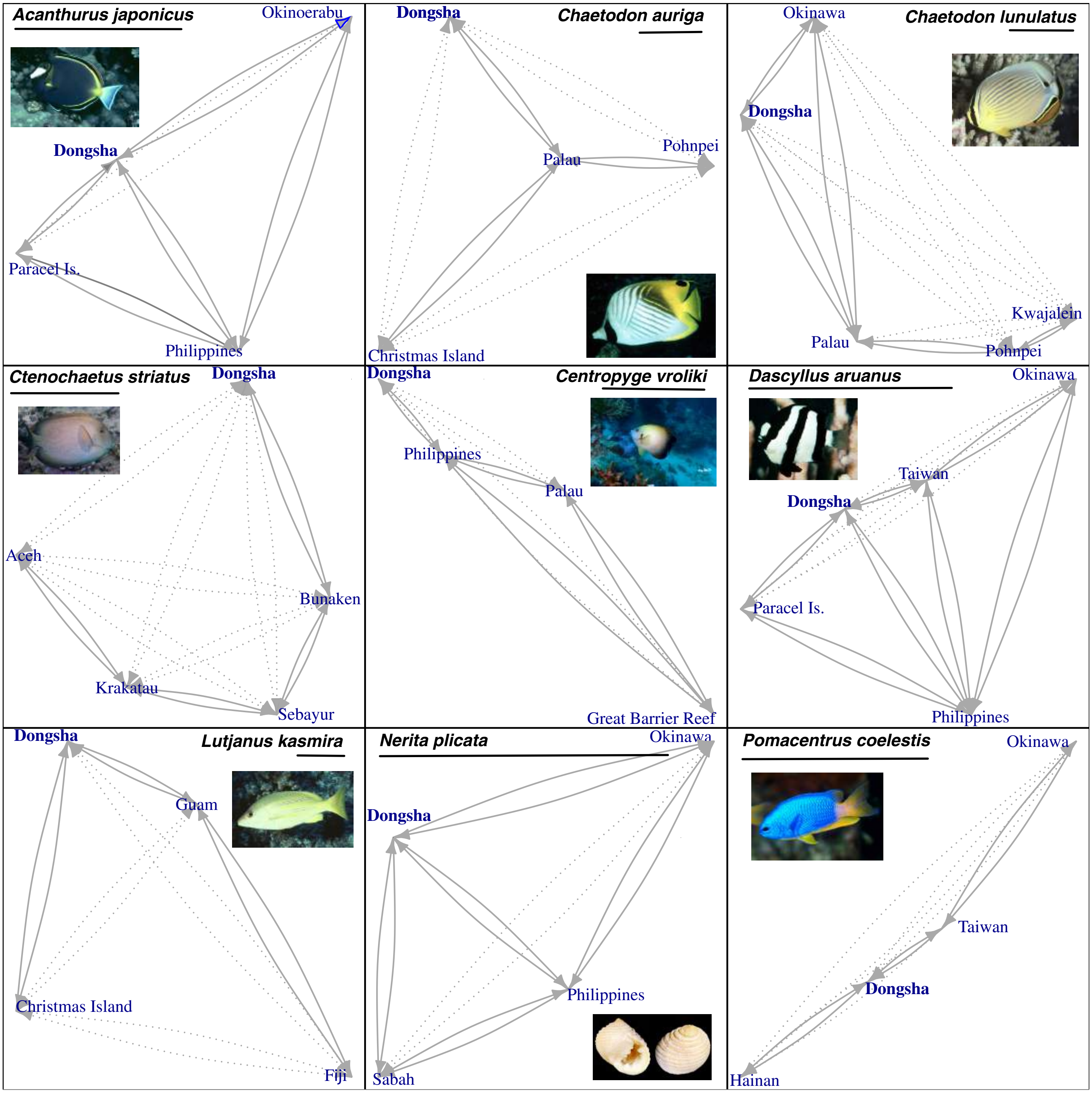

Figure 2 Visualization of all metapopulation models tested for each species. Visualization of all metapopulation models tested for each species. Black lines below each species name indicate a distance of 1,000 km. Blue text indicates sampled sites which are arranged in geographic space. Dotted lines with arrows connect every pair of sample sites and indicate directional migration (gene flow) parameters included in the n-island model while solid lines with arrows indicate directional migration parameters included in the stepping-stone model. The model of panmixia treated all sampled localities as a single population.

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transmission of mtDNA. For each model, the coolest chain explored fifty million genealogies, sampling every 500 iterations, and discarding the first five million genealogies as burn-in.

Each Migrate-n run comprised three replicates of fifty million genealogies to yield a single estimate of marginal likelihood. Each run was then repeated three times, to yield three independent estimates of metapopulation model marginal likelihood from nine replicate runs. The Bezier-corrected estimate of model marginal likelihood (which approximates the marginal likelihood from a larger number of heated chains) was harvested from each outfile and averaged across the three independent replicate runs. Mean Bezier-corrected marginal likelihoods were converted to relative model probabilities and Bayes factors following *Johnson & Omland (2004)*. To account for variance in mean marginal likelihoods across the three replicate runs, a permutation *t*-test was run to compare the mean marginal likelihoods of the first and second ranked models, following *Crandall et al. (2019b)*. Parameter files for each species and each model, as well as code for interpreting the output, are available in the Github repository, within the migrate_analysis directory.

We then asked to what extent the models selected for each species by Migrate-n were a product of the maximum pelagic larval duration (PLD), especially given the spatially heterogeneous sampling of surrounding populations. Because only two of three possible models were selected by all nine species, we constructed a logistic regression model using values for maximum PLDs from the literature (Table 1) and great-circle distances from Dongsha Atoll to both the nearest and furthest sampled populations for each species, calculated with the Raster package (*Hijmans, 2021*) in R: (p(Migrate Model) ~ Maximum PLD + Closest Distance + Furthest Distance). We used backward BIC model selection in the R package MASS (*Venables & Ripley, 2002*) to select the best model.

Graph theoretical analysis

To better place our results in the geographical context of the South China Sea, we undertook a graph theoretical analysis of the potential for larval dispersal in this region. We developed two rasters (Fig. 1B) representing (1) coral reef areas and (2) land areas of continents and islands of the South China Sea from Fig. 1 of *Zhao et al. (2016)* and Fig. 1A of *Dorman et al. (2016)*, and projected both rasters into UTM coordinates (zone 50N) with 1 km resolution using the raster package. We then imported these rasters into Graphab 2.6 (*Foltête, Clauzel & Vuidel, 2012*), defining the reef areas with at least 25 hectares as habitat patches, and the land areas as a cost raster with each pixel costing 10,000. Graphab then generated a linkset between reef patches for each species using a maximum dispersal distance calculated as the product of maximum PLD (Table 1) and the mean current speed of 18.7 km/day given by *Hu et al. (2000)*. The basic binary simple (undirected) graph generated by Graphab from this linkset was then imported into the igraph package for R (*Csardi & Nepusz, 2006*), which we used to measure betweenness centrality, defined as the fraction of shortest paths between all patches which pass through a given reef patch. *Estrada & Bodin (2008)* have shown that betweenness centrality is an important measure of the overall importance of a patch to the large-scale connectivity of a

Table 2 **Genetic diversity statistics including haplotype diversity (h), nucleotide diversity (π) and Fu's FS for each sampled Dongsha population in comparison to regional means.**

Species	**Dongsha *N***	**# Haplotypes**	**Private haplotypes**	**% Private**	**Regional mean % private**	**h**	**Regional mean h**	**π**	**Regional mean π**	**F_s**
A. japonicus	14	9	3	21.43	12.96	0.88	0.86	0.006	0.004	**−3.53**
C. auriga	28	6	2	7.14	7.06	0.51	0.56	0.001	0.001	−4.16
C. lunulatus	19	4	1	5.26	13.92	0.56	0.66	0.004	0.005	2.19
C. striatus	26	24	21	80.77	75.03	0.99	0.99	0.025	0.023	**−15.44**
C. vrolikii	24	12	9	37.50	29.37	0.79	0.80	0.003	0.003	**−7.45**
D. aruanus	44	13	5	11.36	14.63	0.79	0.75	0.002	0.002	−5.19
L. kasmira	6	6	4	66.67	16.20^{**}	1^{*}	0.59	0.007^{**}	0.002	**−3.03**
N. plicata	24	22	19	79.17	77.98	0.99	1.00	0.011	0.013	**−14.99**
P. coelestis	21	15	9	42.86	63.94^{**}	0.90^{**}	1.00	0.010^{**}	0.014	**−10.07**

Note:

Significant deviations from regional means are noted at $^{*}p < 0.05$ (*) and $^{**}p < 0.01$. Significantly low F_S values (compared to neutral coalescent simulations) at $p < 0.02$ are denoted in bold.

landscape. We also used igraph to measure the diameter of each species' graph, as the minimum number of larval-dispersal steps connecting the two most distant points. It is important to emphasize that this approach is not equivalent to a biophysical model of larval dispersal such as found in *Dorman et al. (2016)*, and most dispersal is expected to occur at much shorter distances (*Cowen et al., 2000*). However, since genetic structure is very sensitive to dispersal at the tails of the larval dispersal kernel (*Grosberg & Cunningham, 2001*), this approach might provide an approximate understanding of potential gene flow in the South China Sea.

RESULTS

We sequenced a total of 206 tissue samples from Dongsha across the nine species. Sequence length varied from 316 bp (Control Region, *Ctenochaetus striatus*) to 1,058 bp (Cytochrome-B, *Dascyllus aruanus*). A total of 111 unique haplotypes across all nine species were detected (Table 2). Within our dataset, 58% of these haplotypes were apparently private to Dongsha Atoll (at least within the local region sampled from GEOME), ranging from 5% in the oval butterflyfish *Chaetodon lunulatus* to ~80% in the whorled nerite *Nerita plicata* and the striated surgeonfish *Ctenochaetus striatus*.

The bluestripe snapper *Lutjanus kasmira* had significantly elevated genetic diversity (h, π and % private alleles) at Dongsha compared to the rest of the region; however, this may be an artifact of low sample size. The neon damselfish *Pomacentrus coelestis* had significantly lower genetic diversity (h, π, and % private alleles) at Dongsha than the surrounding populations. All but three species had Fu's F_S values that were significantly negative at the recommended alpha of $p < 0.02$ (*Fu, 1997*), indicating a departure from neutrality due to an excess of recent mutations at the tips of the genealogy. Median-joining haplotype networks showed no clear geographic pattern of haplotype distribution for any species (Fig. 3). In addition, all haplotype networks showed a star-like topology providing visual confirmation of the low Fu's F_S values and evidence of either recent

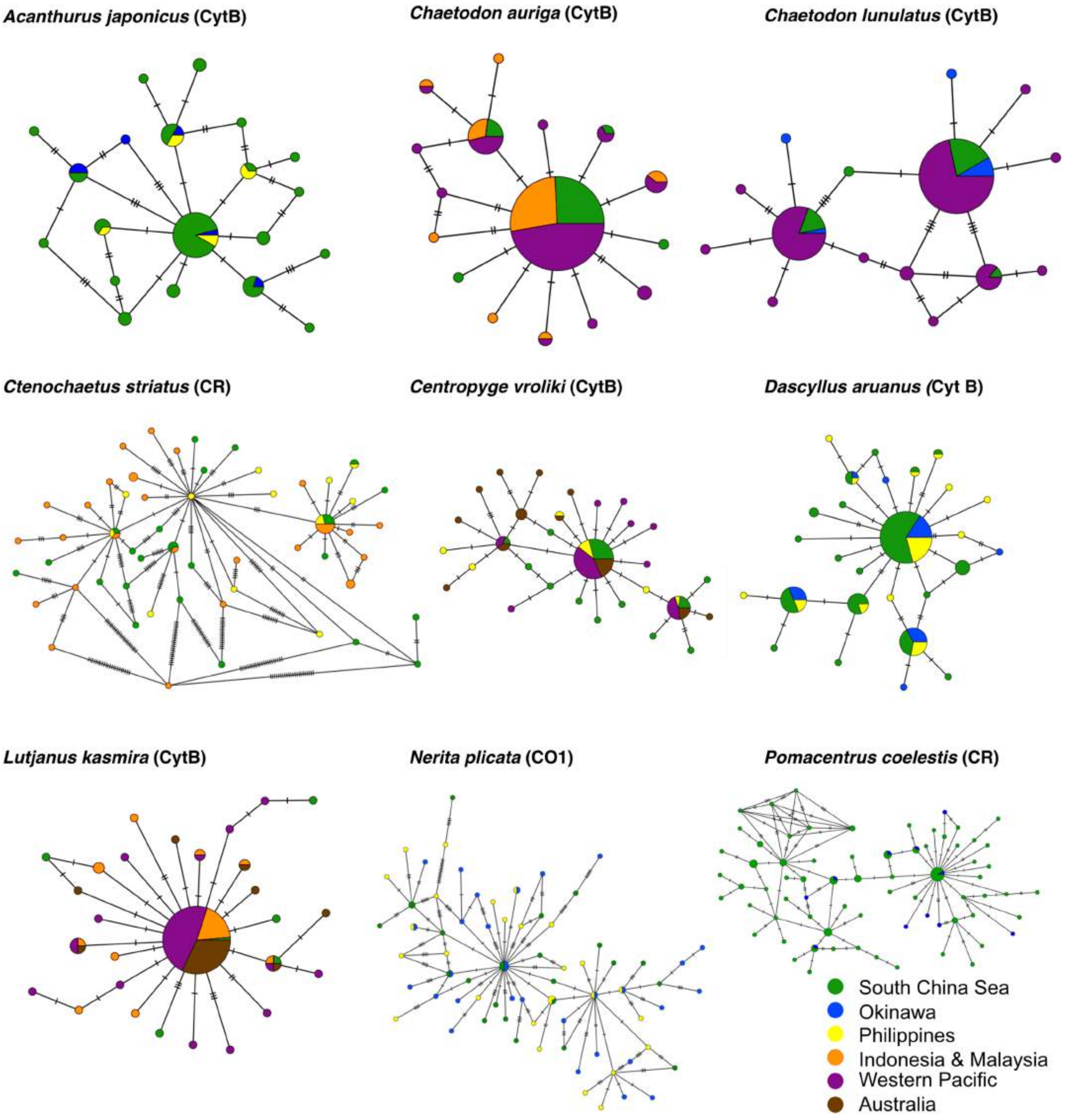

Figure 3 Haplotype networks of nine species. Median-joining networks for all nine species. Each circle represents a haplotype, with the frequency of the haplotype indicated by the circle's size (scale varies across species). Pie charts indicate each haplotype's distribution across sampling sites. Lines indicate possible mutational changes between haplotypes, with hash marks representing more than one change.

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natural selection or population expansion. The combined data set used in this study has been shared with location and date metadata in GEOME (geome-db.org) within the "Reef Species of Dongsha Atoll" expedition of the Diversity of the Indo-Pacific Project, with GUID: https://n2t.net/ark:/21547/Dos2. By clicking "Query All Reef Species of Dongsha Atoll Samples", the fasta file can be downloaded through the download option next to "map" option.

Pairwise Φ_{ST} values varied from 0 (found in every dataset) to 0.202 in different taxa across Indo-Pacific (Fig. S1). In the Japanese surgeonfish, *Acanthurus japonicas* significant genetic structures were found between Okinoerabu (near Okinawa Island), Philippines, and Xisha. In addition, the Dongsha population of *L. kasmira* was highly and significantly structured with all other populations. However, low sample size in the Okinoerabu population of *A. japonicus* ($n = 6$) and the Dongsha population of *L. kasmira* ($n = 6$) curtails our ability to interpret the significance of these observations of high Φ_{ST}. The only other significant value of Φ_{ST} (0.077) for a Dongsha population was with the Xisha Islands in the whitetail dascyllus, *Dascyllus aruanus*. On average, the Dongsha population of each species had 1.9 positive pairwise Φ_{ST} values out of a total of 3 or 4 populations that it was measured against. Due to the lack of co-sampling of each species at these other sites, there were no clear geographic patterns in Dongsha's genetic structuring with other populations. NMDS plots (Fig. S2) generally showed a similar lack of correlation with geography, except for perhaps *C. striatus* and *C. lunulatus*. This general lack of geographic signal in genetic structure is a common feature in the Indo-Pacific (*Gaither et al., 2011*; *Crandall et al., 2019a*) and marine population genetic datasets in general (*Selkoe & Toonen, 2011*; *Selkoe et al., 2016*).

Relative probabilities for each of three metapopulation models tested by Migrate-n are depicted in Fig. 4. Following guidelines laid out by *Kass & Raftery (1995)*, Migrate-n found strong support for a metapopulation model wherein the Dongsha population acts as an important regional stepping-stone for oval butterflyfish (*Chaetodon lunulatus*; 5.42×10^9: 1 odds against panmixia; see Table 3), striated surgeonfish (*Ctenochaetus striatus*; 1.78×10^8: 1 odds against panmixia; see Table 3, Fig. 4), and substantial support for a stepping-stone model in the pearlscale angelfish (*Centropyge vroliki*; 12:1 odds against panmixia). The whitetail damselfish (*Dascyllus aruanus*) had modest support for a stepping-stone model (4:1 odds against panmixia), but the mean log-likelihood for this model was not significantly higher than that for panmixia ($p = 0.15$), leaving this result ambiguous. Datasets from the five other species strongly and unambiguously supported a regional model of effective panmixia (Table 3).

Backward stepwise model selection found that maximal and minimal distances between Dongsha and other sampled populations were not important predictors of whether Migrate-n selected a stepping-stone model. Maximum PLD was the only important predictor in explaining when Migrate-n selected a stepping-stone model over panmixia, with an improvement of 4.12 units of log-likelihood between the full model and one with PLD only. The resultant model was significant ($p = 0.0473$), with the coefficient indicating that for every day increase in PLD, there is a 9.3% decrease in the odds of selecting a stepping-stone model (95% CI [0.002–23]; Fig. 5).

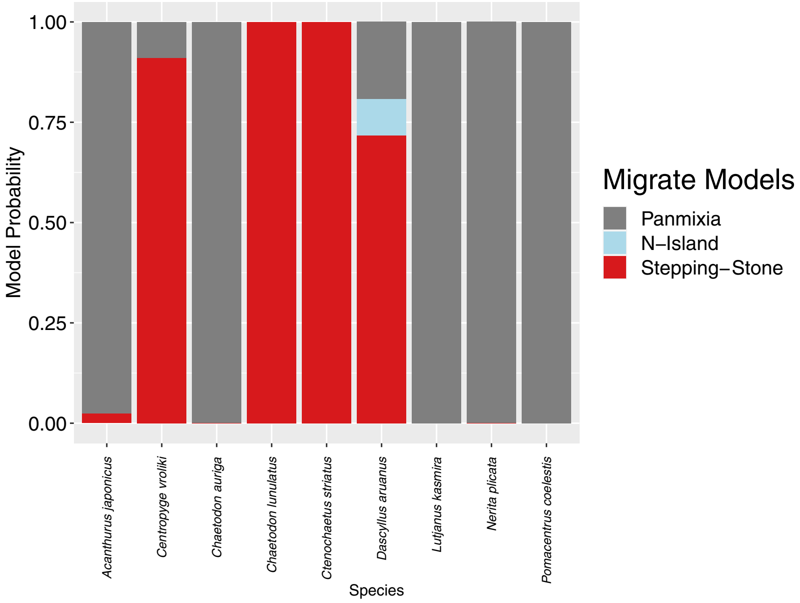

Figure 4 Relative probability of each of four metapopulation hypotheses. Relative probability of each of four metapopulation hypotheses depicted in Fig. 2 for each of nine species sampled at Dongsha as calculated from Migrate-n marginal likelihoods averaged across three replicate runs.

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Table 3 Most probable (1°) and second most probable (2°) models and their relative probabilities for each species, followed by the *P*-value of a one-tailed permutation *t*-test of the alternate hypothesis that the mean ln-likelihood of the 1° model is significantly higher than the mean of the 2° model.

Species	1° Model	1° Probability	2° Model	2° Probability	p 1° Mean > 2° Mean	2 Ln Bayes Factor 1°/2°	Odds 1°:2°
A. japonicus	Panmixia	0.992	Stepping-stone	0.008	0.05	**9.55***	118.4:1
C. auriga	Panmixia	1.000	Stepping-stone	0.000	0.05	**19.29***	1.54×10^4:1
C. lunulatus	Stepping-stone	1.000	Panmixia	0.000	0.05	**44.83***	5.42×10^9:1
C. striatus	Stepping-stone	1.000	Panmixia	0.000	0.05	**37.99***	1.78×10^8:1
C. vrolikii	Stepping-stone	0.921	Panmixia	0.079	0.05	**4.90**	11.6:1
D. aruanus	Stepping-stone	0.742	Panmixia	0.169	0.15	2.96	4.4:1
L. kasmira	Panmixia	1.000	Stepping-stone	0.000	0.05	**441.07***	6.0×10^{95}:1
N. plicata	Panmixia	1.000	Stepping-stone	0.000	0.05	**15.92***	2.86×10^3:1
P. coelestis	Panmixia	1.000	Stepping-stone	0.000	0.05	**123.10***	5.37×10^{26}:1

Note:
Loge Bayes Factor indicates the relative probability of the best model relative to the second best model, with values greater than six indicating a strong weight of evidence (odds > 20:1, indicated with *), and values greater than three indicating substantial support (bolded, *Kass & Raftery, 1995*). *P*-values indicate the outcome of a permutation *t*-test comparing the log-likelihoods of the two top-ranked models across three replicated Migrate-n runs, bolded at alpha of 0.05.

Graphab found 115 reef patches greater than 25 hectares in the South China Sea. These patches were connected with a minimum graph diameter of one larval dispersal step (*Nerita plicata*) or a maximum of seven generational steps for *Dascyllus aruanus* (Fig. 6). Graph diameter was highly correlated with PLD ($r^2 = 0.61$), so we do not present a separate logistic regression for its ability to predict whether a species had a stepping-stone model. Out of 115 reef patches, Dongsha was always ranked in the top 15 reef patches for

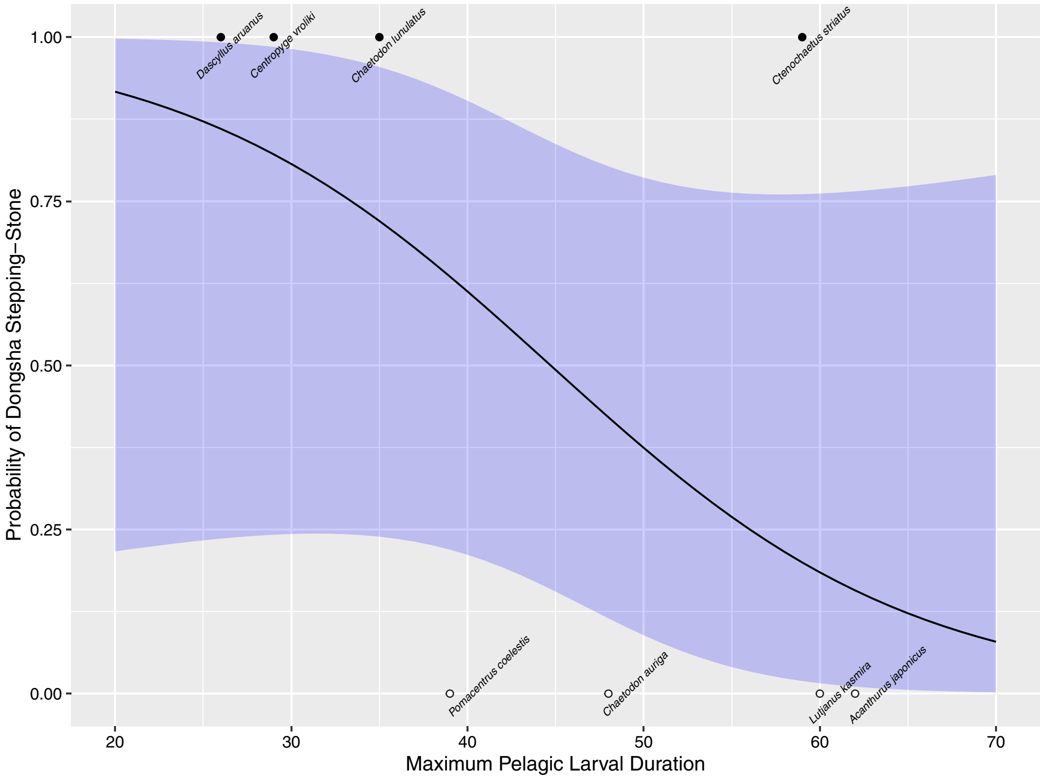

Figure 5 **Logistic regression model.** Logistic regression model for: Migrate-n model ~ maximum PLD, with 95% confidence intervals constructed as 1.96 × standard error. The model is shown between 20 and 70 days larval duration to avoid extrapolation. Black circles show species with datasets that selected a stepping-stone model, while open circles show species datasets that selected a model of effective panmixia.

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betweenness centrality, ranging from the 3rd most important reef (*Chaetodon lunulatus* and *Pomacentrus coelestis*) and the 14th most important reef (*Dascyllus aruanus*) for this metric. The only reefs with consistently higher rankings were found in the Xisha Islands, the Zhongsha Islands, and Huangyan Island (Fig. 6).

DISCUSSION

While this genetic analysis of nine coral reef species represents a relatively small proportion of the thousands of species comprising the Dongsha Atoll National Park community, it is also the most extensive analysis attempted to put a protected single reef community into the broader ecological and evolutionary context of the Indo-Pacific to date. Overall, our analysis indicates that over evolutionary timescales, Dongsha populations are well-connected with the rest of the South China Sea and indeed with the rest of the Indo-Pacific and maintain genetic diversities that do not significantly deviate from average (except for *P. coelestis*, see discussion below). Furthermore, for marine species with mean PLDs less than 40 days (the vast majority; *Strathman, 1987*; *Shanks, 2009*), Dongsha Atoll provides a valuable stepping-stone that is consistently within the top 15 reef patches for promoting regional genetic and demographic connectivity within the South China Sea (Figs. 5 and 6).

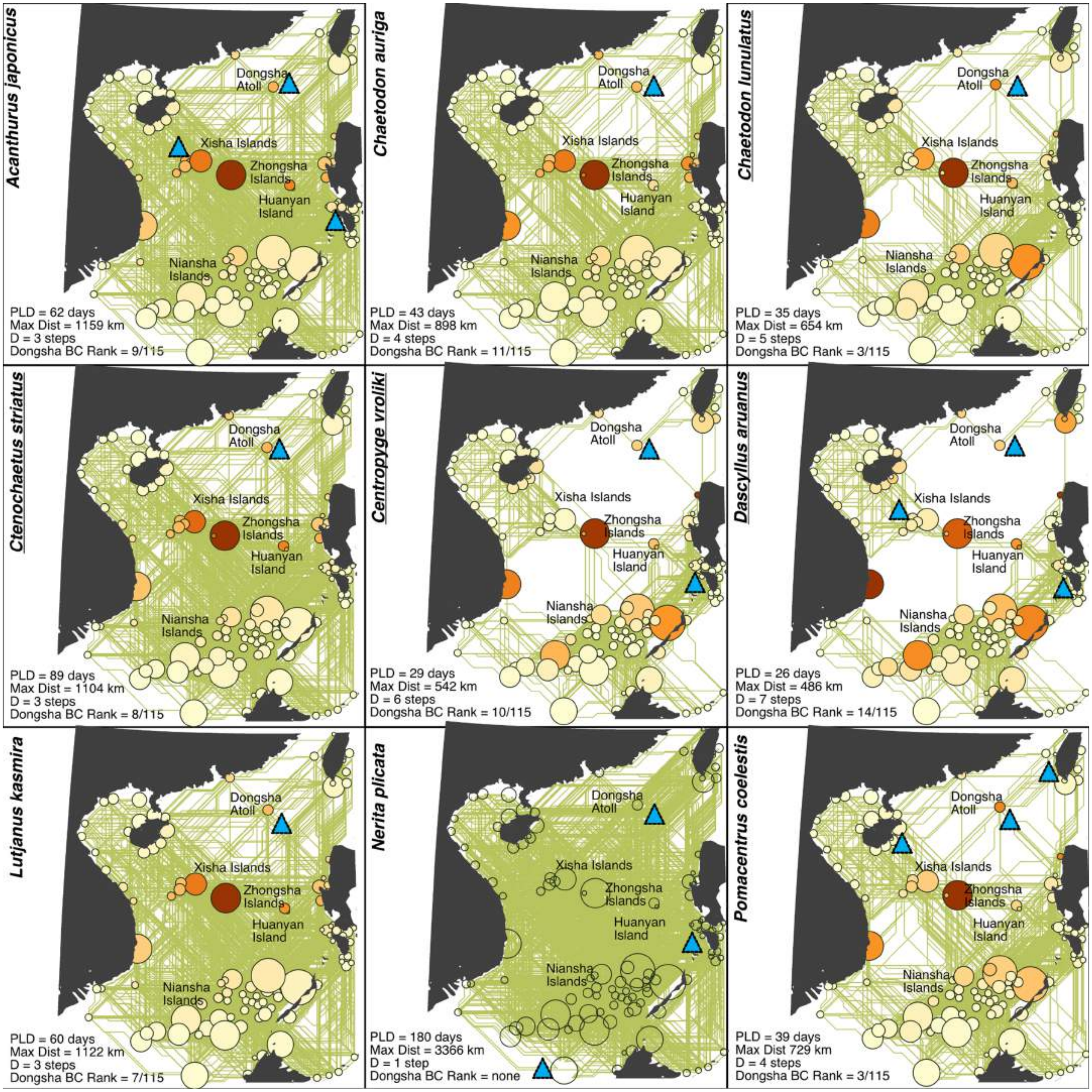

Figure 6 **Undirected binary simple graphs between 115 South China Sea reef patches with areas greater than 25 hectares.** Circle sizes are proportional to the approximate reef area of each patch, while darker colors indicate a higher relative betweenness centrality for a given patch. Blue triangles indicate a genetic sample for that species. Yellow lines show shortest overwater paths between reef patches that could potentially be connected by larval dispersal assuming a maximum distance given in the lower right corner. Additional statistics in the lower right corner include pelagic larval duration (PLD), graph diameter (D) as the shortest number of larval dispersal event required to cross the longest distance between reef patches for a given species and the ranking of betweenness centrality (BC) for Dongsha out of 115 reef patches. Genetic data for species with underlined names supported a stepping-stone model of dispersal. Full-size DOI: 10.7717/peerj.12063/fig-6

Genetic population structure between Dongsha Atoll and nearby populations, as measured by the sequence-based F_{ST} analog Φ_{ST}, was generally low and non-significant (Fig. S1). This finding is congruent with the results of connectivity studies targeting damselfishes between the SCS and Kuroshio regions which showed low and non-significant genetic structure among the Xisha (Paracel) Islands, Dongsha, and Taiwan (*Liu et al., 2011*, *2014*, *2019*). Failure to reject panmixia is generally common in marine species (*Waples, 1998*; *Kinlan & Gaines, 2003*), has been found consistently in the Indo-Pacific (*Keyse et al., 2014*; *Crandall et al., 2019a*), and is traditionally interpreted as evidence for relatively high levels of gene flow due to larval dispersal. However, these summary statistics can often be zero even when there has not been gene flow in thousands of generations (*Faurby & Barber, 2012*; *Crandall et al., 2019a*), and they do not provide any information about metapopulation structure.

Five of the nine species surveyed here demonstrate strong regional connectivity in the South China Sea such that their gene pools are well-mixed (effective panmixia; mean SCS graph diameter for these species = 3.0 intergenerational dispersal events, sd = 1.22). In contrast, the coalescent approach employed here clearly distinguishes these from the four species that have some regional metapopulation structure (stepping-stone; Table 3, Fig. 4). This latter group generally has shorter PLDs (mean PLD = 37 days, sd = 15 days) than the former group (mean PLD = 78 days, sd = 60 days), meaning that it will take more generations to cross the SCS (mean SCS graph diameter for these species = 5.25 intergenerational dispersal events, sd = 1.70). For these shorter PLD species, Dongsha Atoll provides an important intergenerational stepping-stone for maintaining gene flow across the SCS (highly ranked betweenness centrality for all species except *N. plicata*; Fig. 6). Furthermore, Fig. 5 demonstrates a significant relationship between PLD and metapopulation structure (albeit with wide confidence intervals) with a sharply increasing probability that a species will have a metapopulation structure that relies on Dongsha Atoll as PLD decreases to about 40 days or less. Below, we discuss the oceanographic context of the SCS as it relates to our findings.

Oceanographic circulation patterns in the SCS and larval dispersal

The seasonal circulation patterns in the SCS are mainly driven by monsoon winds and comprise several cyclonic/anticyclonic eddies. In contrast, northeastward monsoons and southwestward monsoons prevail during winter and summer, respectively (*Hu et al., 2000*, Fig. 1B). During winter, most currents are northeastward and turn east of Natuna Islands toward the west coast of Luzon in the Philippines. Meanwhile, the Kuroshio intrusion splits into two currents, with one branch moving toward Dongsha and another toward Xisha Islands (Paracel Islands), then turns northward to pass along the Taiwan coast. During summer, most of the currents flow southwestward, with a mean current velocity of 18.7 km/day, while the southwestward monsoon weakens the Kuroshio Intrusion.

Given this circulation pattern, Fig. 6 provides heuristic estimates of the maximum dispersal distances for larvae of each species during the summer, when most corals and fish are spawning (*Liu, 2011*; *Ho, 2017*). For example, even larvae from the species with the shortest PLD (*Dascyllus aruanus;* 26 days) should be able to drift to the nearest reefs 230 km away near Hong Kong, or to Taiwan, 433 km away (*D. aruanus;* Figs. 1B and 6). In contrast, species with the longest PLD (*Nerita plicata*; 180 days) should be able to reach anywhere in the SCS in a single larval dispersal event. These estimates are heuristic because the vast majority of larvae released at Dongsha or elsewhere will not be advected over the maximal distance due to diffusion and mortality (*Cowen et al., 2000*). On the other hand, it is possible that larvae may occasionally be advected beyond the depicted maximum distance by infrequent events such as typhoons or by the extension of their larval duration beyond what has been measured (*McCormick, 1999*). In the present study, Zongsha seems to act as an important hub for the connectivity in the area between Xisha, Zhongsha and Huangyang Island as revealed in Fig. 6. *Liu, Hsin & Cheng (2020)* suggested that the seasonal dynamic of eddies may facilitate the dispersal of marine organisms in this area which may support the role of Zongsha in term of population connectivity. Meanwhile, the heuristic estimates in Figs. 1B and 6 are useful in showing that, in general, the species for which a stepping-stone model of metapopulation structure was selected are only able to reach neighboring reefs, while those for which panmixia was selected have the capacity to disperse widely in the SCS and beyond.

Moreover, more sophisticated biophysical modeling of larval dispersal in the South China Sea indicates a clear regional structure for species with a PLD of 40 days or less (*Melbourne-Thomas et al., 2011*; *Dorman et al., 2016*; *Liu, Hsin & Cheng, 2020*). Although focused on the central and southern SCS, *Melbourne-Thomas et al. (2011)* modeled particles with 30 or 40 day PLD, active or passive dispersal with a rate of mortality of 0.1 to 0.2 per day, and showed that all particles released from the Nansha Islands (*i.e.*, Spratly or Kalayaan islands) settled either in the Nanshas or in western Palawan. Using more particles, slightly more realistic biological parameters, and tracking particles released from the Nanshas for 90 days or until settlement, *Dorman et al. (2016)* got similar results, with most particles staying in the Nanshas or moving eastward to Palawan, but they also showed limited connectivity from the Nanshas to the Xishas and Northern Luzon, especially during the Fall when currents shift to the northeast. Finally, *Liu, Hsin & Cheng (2020)* simulated benthic currents at 200-400 m depth over 60 days to show little connectivity between deep-sea coral (*Deltocyathus magnificus*) populations near Dongsha and the Xisha Islands, which was confirmed by clear genetic structure in microsatellites.

The significant relationship between PLD and the existence of metapopulation structure demonstrated here (Fig. 5) has wide confidence intervals due to two species. A metapopulation model of effective panmixia was selected for the neon damselfish, *Pomacentrus coelestis* despite having a maximum PLD of 39 days, while a stepping-stone model was most probable for *C. striatus*, even though it has a maximum PLD of 59 days (*Wilson & McCormick, 1999*). Although the best model for explaining metapopulation structure did not include sampling distance as a factor, we suggest that heterogeneous sampling may have played a role in the models that were selected for at least these two species. The nearest sampled population to Dongsha for the *P. coelestis* dataset was 411 km away in Taiwan, while the furthest was 1,304 km away in Okinawa. Furthermore, the fact that the Dongsha sample of *P. coelestis* deviated from average regional diversities suggests that our sample of this species may be non-representative. The low genetic diversities in Table 2 may be due to cohesive dispersal among related larvae (*Robitzch, Saenz-Agudelo & Berumen, 2020*) since the specimens that we collected were juveniles around the same size and collected at the same location. Therefore, the haplotypes identified from these samples may derive from a relatively small number of parents. For *C. striatus*, even the nearest sampled population was much further than Okinawa, 2,280 km away in Bunaken near Sulawesi, while the furthest sampled population was 3,217 km away near Krakatau in the Sunda Strait. Given these heterogeneous sampling distances and the possibly non-representative sample of *P. coelestis*, it is easier to understand how a stepping-stone model was inferred over large distances for *C. striatus* while a model of panmixia was selected over short distances for *P. coelestis*. Future efforts to comparatively model metapopulation structure should standardize sampling to the extent that it is possible.

CONCLUSIONS

For the relatively low cost of adding mitochondrial sequence data from nine coral reef species sampled within the national park at Dongsha Atoll to existing datasets we were able to successfully test metapopulation hypotheses of larval dispersal and gene flow for each of these reef species. While it is important to acknowledge that these results derive from only a single genetic locus, results from initial mitochondrial surveys are often borne out by multi-locus analyses (*Bowen et al., 2014*). Our results from both population genetic and graph theoretical analysis demonstrate that Dongsha is likely a key stepping-stone for promoting genetic and demographic connectivity among reefs in the northern South China Sea, especially for species with PLDs less than 40 days. Therefore, reinforcement of the management by Marine National Park Headquarters is crucial to reduce the fishing pressure (*i.e.*, illegal poaching) and maintain Dongsha populations. Meanwhile, research efforts need to be increased to better understand the role of Dongsha Atoll in connectivity partners across the region. Missing from these analyses are the habitat-building scleractinian corals and seagrasses that are essential to the long-term health of these threatened ecosystems. A comprehensive program to sample and sequence coral reef species throughout the South China Sea could provide a more detailed and empirical understanding of the valuable protections afforded by protected areas such as Dongsha Atoll.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

Robert J. Toonen is an Academic Editor for PeerJ.

Author Contributions

- Shang Yin Vanson Liu conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Jacob Green performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Dana Briggs performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Ruth Hastings performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Ylva Jondelius performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Skylar Kensinger performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Hannah Leever performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Sophia Santos performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Trevor Throne performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Chi Cheng performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Hawis Madduppa performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Robert J. Toonen conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

- Michelle R. Gaither conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Eric D. Crandall conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Animal Ethics

The following information was supplied relating to ethical approvals (*i.e.*, approving body and any reference numbers):

The species used in this study are non-regulated animals. Therefore, there is no relevant provision for the ethical review process in Taiwan.

Field Study Permissions

The following information was supplied relating to field study approvals (*i.e.*, approving body and any reference numbers):

Field experiments were approved by the Marine National Park Headquarters (Taiwan) under permit number 0000691.

Data Availability

The following information was supplied regarding data availability:

The combined data set used in this study has been shared with location and date metadata in GEOME (geome-db.org) within the "Reef Species of Dongsha Atoll" expedition of the Diversity of the Indo-Pacific Project, with GUID, available at: https://n2t.net/ark:/21547/Dos2. By clicking "Query All Reef Species of Dongsha Atoll Samples", the FASTA file can be downloaded through the download option next to "map" option.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.12063#supplemental-information.

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Guiding high seas conservation efforts by modelling coral and sponge habitat

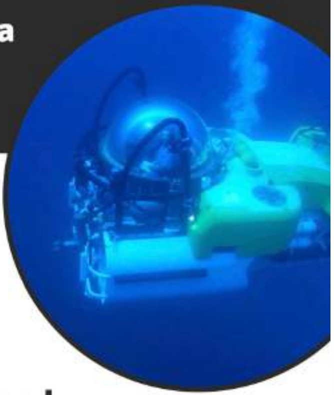
SEAMOUNT RIDGES WITH RICH AND DIVERSE MARINE LIFE

The **Salas y Gómez and Nazca ridges are two seamount chains** off the coast of South America. The ridges contain more than **110 seamounts**, with summit depths ranging between over 3,000 meters to just a few meters below the surface.

The ridges support an exceptionally rich diversity of marine life, inluding whales, corals and many other ecologically important species. The region also has the highest level of endemism found in any marine environment. For many groups of organisms, nearly half of the species that live there are not found anywhere else on Earth.

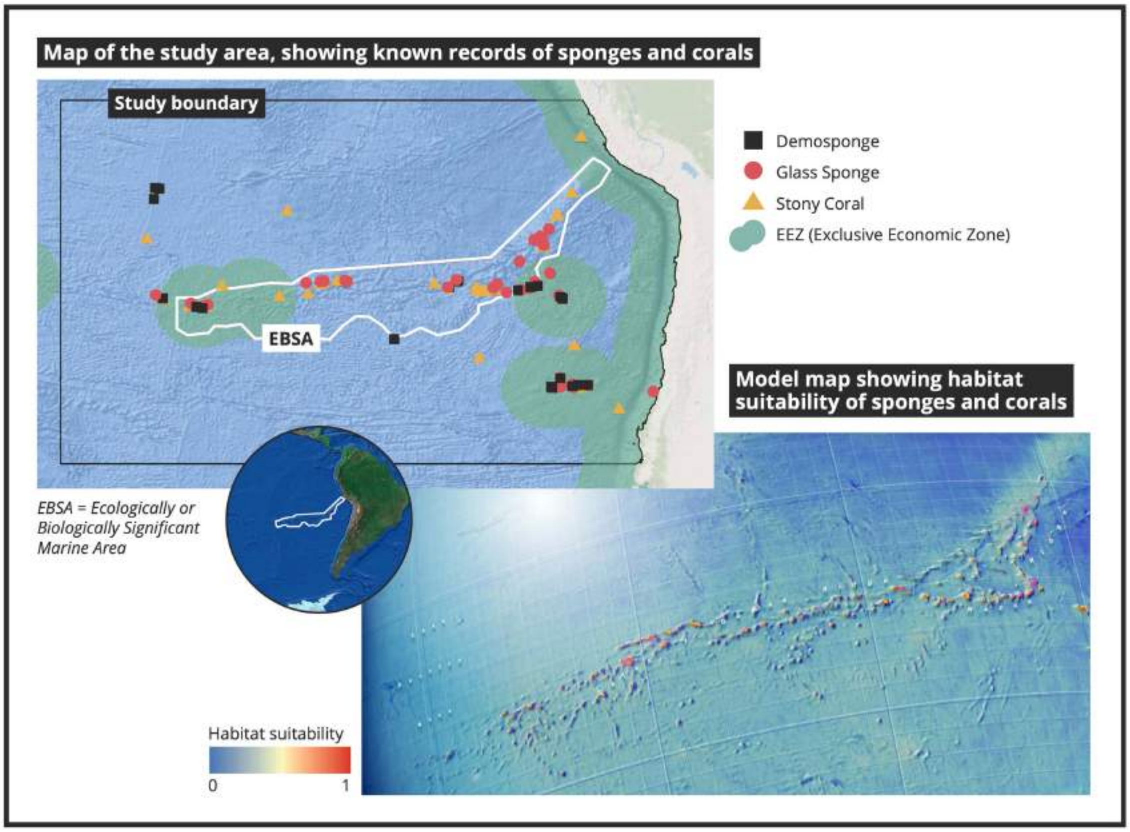
PROTECTING THE PRISTINE SEAMOUNTS

Despite some historical fishing in the region, the seamounts are relatively pristine. They are an excellent conservation opportunity to protect a global biodiversity hotspot before it is degraded. One **obstacle for effective protection is the scarcity of observational data from the region's deeper waters.**



MODELING DEEP-WATER CORAL AND SPONGE HABITAT

As a first step in mapping biodiversity along the ridges, we created **models that predict the distribution of sponges and corals**. These organisms create complex structures where diverse marine life is able to flourish.



Map of the study area, showing known records of sponges and corals

Model map showing habitat suitability of sponges and corals

EBSA = Ecologically or Biologically Significant Marine Area

Our models predict that the seamounts along both ridges contain highly suitable habitats for sponges and corals. This suggests that the ridges offer widespread suitable habitat for diverse marine life.

Our results strongly suggest that we must act quickly to protect these fragile habitats before they are damaged by human activities.

The modeled distribution of corals and sponges surrounding the Salas y Gómez and Nazca ridges with implications for high seas conservation

Samuel Georgian[1], Lance Morgan[1] and Daniel Wagner[2]

[1] Marine Conservation Institute, Seattle, Washington, United States
[2] Conservation International, Center for Oceans, Arlington, Virginia, United States of America

ABSTRACT

The Salas y Gómez and Nazca ridges are two adjacent seamount chains off the west coast of South America that collectively contain more than 110 seamounts. The ridges support an exceptionally rich diversity of benthic and pelagic communities, with the highest level of endemism found in any marine environment. Despite some historical fishing in the region, the seamounts are relatively pristine and represent an excellent conservation opportunity to protect a global biodiversity hotspot before it is degraded. One obstacle to effective spatial management of the ridges is the scarcity of direct observations in deeper waters throughout the region and an accompanying understanding of the distribution of key taxa. Species distribution models are increasingly used tools to quantify the distributions of species in data-poor environments. Here, we focused on modeling the distribution of demosponges, glass sponges, and stony corals, three foundation taxa that support large assemblages of associated fauna through the creation of complex habitat structures. Models were constructed at a 1 km^2 resolution using presence and pseudoabsence data, dissolved oxygen, nitrate, phosphate, silicate, aragonite saturation state, and several measures of seafloor topography. Highly suitable habitat for each taxa was predicted to occur throughout the Salas y Gómez and Nazca ridges, with the most suitable habitat occurring in small patches on large terrain features such as seamounts, guyots, ridges, and escarpments. Determining the spatial distribution of these three taxa is a critical first step towards supporting the improved spatial management of the region. While the total area of highly suitable habitat was small, our results showed that nearly all of the seamounts in this region provide suitable habitats for deep-water corals and sponges and should therefore be protected from exploitation using the best available conservation measures.

Subjects Conservation Biology, Ecology, Ecosystem Science, Marine Biology, Environmental Impacts
Keywords Cold-water corals, Sponge, Deep sea, Species distribution modeling, Habitat suitability, Conservation, Areas beyond national jurisdiction

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Corresponding author
Samuel Georgian, samuel.georgian@marine-conservation.org

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INTRODUCTION

The Salas y Gómez and Nazca ridges are two adjacent seamount chains stretching more than 2,900 km off the coasts of Peru and Chile (Fig. 1) (reviewed in *Wagner et al., 2021*).

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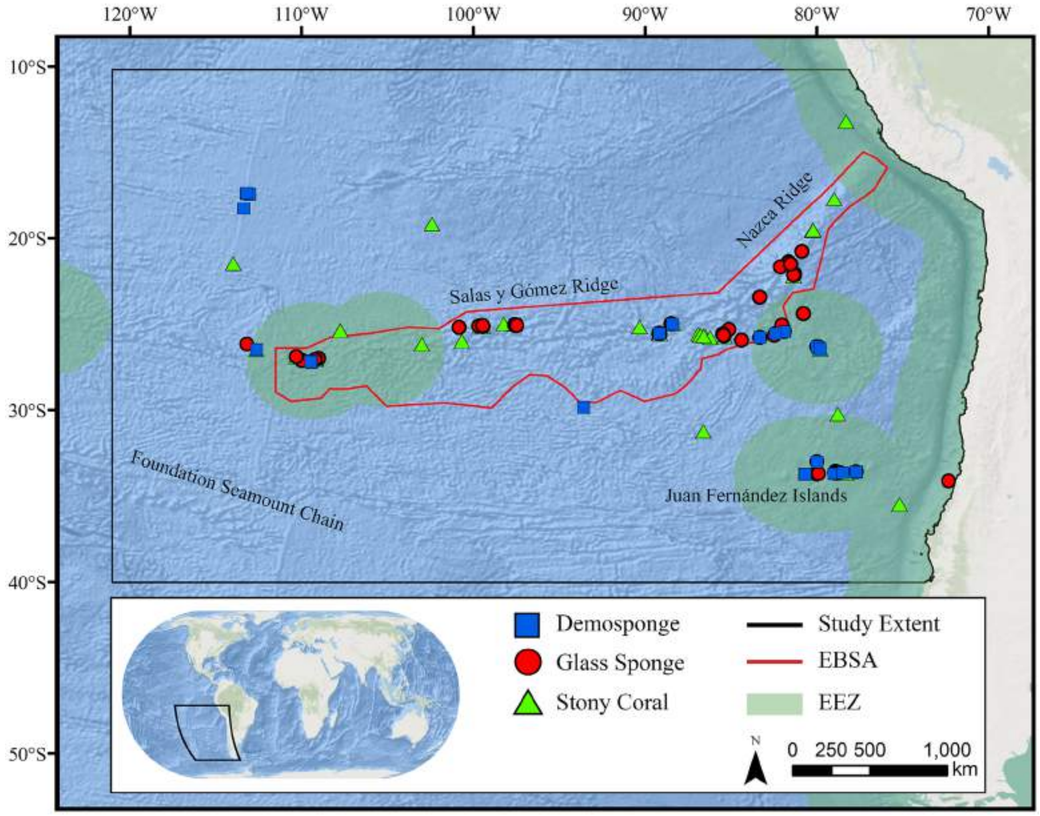

Figure 1 **Map of the study area.** The map shows the modeling extent, distribution of occurrence records for demosponges, glass sponges, and stony corals, national exclusive economic zones (EEZs), and Ecologically or Biologically Significant Marine Area (EBSA) designation.

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Combined, the ridges contain more than 110 seamounts that were created between 2–27 million years ago by a geological hotspot located on the western edge of the Salas y Gómez Ridge (*Parin, Mironov & Nesis, 1997*; *Steinberger, 2002*). The limited exploration that has been accomplished along the ridges has revealed exceptionally high biodiversity as well as unusually high endemism, due in part to its isolation from South America by the Humboldt Current System and the Atacama Trench (*Parin, 1991*; *Comité Oceanográfico Nacional de Chile, 2017*). More than 40% of known fish and invertebrate species are endemic to the region, the highest level of marine endemism in the world (*Parin, Mironov & Nesis, 1997*; *Friedlander et al., 2016*). New species have frequently and recently been discovered on the ridges (*e.g.*, *Andrade, Hormazábal & Correa-Ramírez, 2014*; *Sellanes et al., 2019*; *Shepherd et al., 2020*; *Diaz-Diaz et al., 2020*), indicating that many new species remain to be discovered. The waters surrounding the Salas y Gómez and Nazca ridges provide important feeding grounds and migratory pathways for an array of important species, including billfish, sharks, sea turtles, seabirds and marine mammals (*Weichler et al., 2004*; *Shillinger et al., 2008*; *Yanez et al., 2009*; *Hucke-Gaete et al., 2014*; *CBD, 2017*; *Serratosa et al., 2020*). On the seamounts and neighboring island habitats, diverse benthic communities form around shallow-water, mesophotic (*Easton et al., 2019*), and deep-water coral and sponge reefs (*Hubbard & Garcia, 2003*; *Easton et al., 2019*; *Friedlander et al., 2021*).

Deep-water corals and sponges are critical foundation species found in every ocean basin. The complex, three-dimensional habitat structures they produce support thousands of associated species including other invertebrates and commercially important fish (*Rogers, 1999*; *Costello et al., 2005*; *Cordes et al., 2008*; *Kenchington, Power & Koen-Alonso, 2013*). In addition to habitat creation, corals and sponges provide other critical ecosystem services including the alteration of local current regimes (*Dorschel et al., 2007*; *Mienis et al., 2009*), carbon cycling and long-term sequestration (*Oevelen et al., 2009*; *Kahn et al., 2015*), and nutrient cycling (*Wild et al., 2008*; *Tian et al., 2016*). Deep-water corals and sponges are also being increasingly used as avenues for research purposes ranging from biomedical research (*e.g.*, *Hill, 2003*; *Müller et al., 2004*) to reconstructing paleoclimate archives of climate change, pollution, and nutrients (*Smith et al., 2000*; *Williams et al., 2006*; *Cao et al., 2007*). The slow growth rates (*Prouty et al., 2011*), extreme longevity (*Roark et al., 2009*; *Fallon et al., 2010*), and life history strategies (*e.g.*, low recruitment; *Doughty, Quattrini & Cordes, 2014*) make these taxa extremely sensitive to anthropogenic disturbance, and the recovery of damaged communities may take many decades, centuries, or even longer (see *Ramirez-Llodra et al., 2011*; *Baco, Roark & Morgan, 2019*). Considering the extreme logistical difficulties and costs associated with restoration efforts in these remote habitats (*Van Dover et al., 2014*), improved conservation measures are urgently needed to protect these fragile ecosystems before long-term damage occurs.

Like most marine biodiversity hotspots, the Salas y Gómez and Nazca ridges are threatened by a variety of ongoing or imminent anthropogenic disturbances, including commercial fishing, marine debris and plastic pollution, seabed mining, and climate change (reviewed in *Wagner et al., 2021*). Despite these threats and the clear biological value of the ridges, protecting their sensitive benthic communities from anthropogenic disturbance is a complex challenge. Over 73% of the ridges are located in areas beyond national jurisdiction (ABNJ), commonly known as the high seas, where no one country has sole management responsibility and hence international cooperation is necessary. While the portions of the ridge located within the Chilean and Peruvian exclusive economic zones (EEZs) have several established marine protected areas (MPAs) (*MPAtlas, 2021*), the high seas portions of the ridges are more loosely regulated by intergovernmental agencies including the International Seabed Authority (ISA), the International Maritime Organization (IMO), the Inter-American Tropical Tuna Commission (IATTC), and the South Pacific Regional Fisheries Management Organisation (SPRFMO), which regulate seabed mining, shipping, and fishing, respectively. Despite ongoing United Nations negotiations to better protect vulnerable marine ecosystems (VMEs) on the high seas (*UNGA, 2007*; *Rogers & Gianni, 2010*), there is no legal mechanism to establish high seas MPAs that are applicable to all States or sectors. Industrial fishing occurs in an estimated 48% of ABNJ, with fisheries pushing into deeper waters each year as stocks deplete in shallower waters (*Visalli et al., 2020*). Commercial fishing in waters surrounding the Salas y Gómez and Nazca ridges has been relatively limited historically (*Wagner et al., 2021*), providing a unique opportunity to protect this diverse region before it is irrevocably damaged. However, effecting strong protection in ABNJ is difficult due to the lack of clear legal mechanisms, competing interests, and lack of sufficient data in lesser-explored regions (*Gjerde et al., 2021*).

Species distribution models, also referred to as habitat suitability models, are important tools that help characterize the distribution and niche of taxa in data-poor regions. These models can be particularly useful for deep-water taxa on the high seas, where extremely limited surveys have occurred relative to shallow-water coastal areas (*Fujioka & Halpin, 2014*; *Ortuño Crespo et al., 2019*), and data availability is a considerable obstacle to improved conservation management and scientific advancement (*Vierod, Guinotte & Davies, 2014*; *Wagner et al., 2020*). Species distribution models statistically couple the known distribution of species with relevant environmental parameters to predict niche and distribution in unsurveyed geographic regions or under varying environmental conditions (*Guisan & Zimmermann, 2000*; *Miller, 2010*). Quantifying the biogeographic distribution of ecologically important or threatened species is critical for designing and implementing management plans, shaping future research and exploration efforts, and assessing past, present, and future anthropogenic impacts. Increasingly, species distribution models are being developed specifically to inform marine conservation and management (*e.g.*, *Rowden et al., 2017*; *Georgian, Anderson & Rowden, 2019*) or to predict responses to recent anthropogenic disturbances (*e.g.*, *Georgian et al., 2020*). Models have been successfully developed for a large variety of benthic taxa, including global models for stony corals (*Davies & Guinotte, 2011*), black corals (*Yesson et al., 2017*), octocorals (*Yesson et al., 2012*), and gorgonian corals (*Tong et al., 2013*), as well as large-scale regional sponge models (*e.g.*, *Knudby, Kenchington & Murillo, 2013*; *Chu et al., 2019*). Given their status as foundation species, and the frequent classification of these taxa as indicators of VMEs, which SPRFMO and other fishery management organizations are mandated with identifying and protecting (*e.g.*, *Penney, Parker & Brown, 2009*), it is critical to quantify their distribution.

An improved understanding of the spatial distribution of key taxa throughout the Salas y Gómez and Nazca ridges is necessary for the evidence-based conservation of the region. The suitability modeling in this study will inform ongoing efforts to identify and prioritize key conservation targets along the ridges (see *Wagner et al., 2021*), reinforcing the increasingly clear need to protect sensitive benthic fauna in the region from further exploitation and disturbance from anthropogenic sources. In addition to conservation planning, these models will also support future expedition planning, and will improve our understanding of the niche of cold-water corals and sponges throughout the region.

MATERIALS & METHODS

Study area

The study area encompassed a large region (15,991,101 km^2) of the southeast Pacific Ocean centered on the Salas y Gómez and Nazca ridges off the coasts of Peru and Chile (Fig. 1). This area contains 755 seamounts and guyots covering a total area of 561,452 km^2 (3.5% of the total area; geomorphology data from *Harris et al., 2014*). The region includes an area that has been recognized as an Ecologically or Biologically Significant Marine Area (EBSA) by the Conference of the Parties to the Convention of Biological Diversity (*CBD, 2014*). The EBSA extends around the ridges (Fig. 1) and includes roughly 285 seamounts and guyots covering a total area of 294,225 km^2 (17.2% of the EBSA area). The region is bounded on the eastern side by the Atacama Trench, which along with the Humboldt Current System isolates the ridges from South America (*Von Dassow & Collado-Fabbri, 2014*). The Nazca Ridge is comprised primarily of a large plateau, while the Salas y Gómez Ridge is mostly comprised of a series of smaller seamounts, escarpments, and ridge features (Fig. S21). Seamounts and features farther east along the ridges are progressively older and deeper (*Rodrigo, Díaz & González-Fernández, 2014*). Closer to the South American coast, a series of deep-water canyons extends into the Atacama Trench, while farther offshore the terrain is dominated by a series of large spreading ridges as well as smaller seamounts, ridges, and escarpments. The study area is primarily categorized as abyssal, with the Atacama Trench extending into hadal environments and small areas along the coasts, islands, and shallower seamounts extending upwards onto the slope and shelf (Fig. S22).

Occurrence records

Geo-referenced coral and sponge records were obtained from the Ocean Biodiversity Information System (*OBIS, 2020*), the NOAA Deep-Sea Coral and Sponge Database (*NOAA, 2020*), and records from recent expeditions to the area (J. Sellanes and E. Easton, 2020, unpublished data). All records were obtained as presence-only records, with duplicate records removed prior to analysis. The bulk of records were focused on the Salas y Gómez and Nazca ridges, with another cluster of records in the neighboring Juan Fernández Islands region. We chose to focus on three higher taxonomic groupings that are often key foundation species on seamounts: stony corals (Order: Scleractinia, $n = 233$), demosponges (Class: Demospongiae, $n = 275$), and glass sponges (Class: Hexactinellida, $n = 134$) (Tables S3–S5).

Pseudoabsence records

Species distribution models are ideally constructed using either presence-absence or abundance datasets (*Winship et al., 2020*). However, obtaining high-quality, true absence data is often difficult or impossible in remote environments, and particularly for deeper-water species. Even when absences are recorded, they may reflect the lack of systematic observations throughout the entire study area rather than true absence (particularly given the narrow field of view of most submersibles or towed camera arrays and similar issues with other sampling techniques such as tows or dredges). Inferring suitable habitat from absence data may also be misleading due to dispersal limitation, biotic interactions, or historical disturbances (*e.g.*, *Hirzel et al., 2002*). Researchers are increasingly developing methods that account for the lack of true absence data by using sophisticated methods to produce better-than-random pseudoabsence or background data (*e.g.*, *Iturbide et al., 2015*).

One of the primary limitations with species distribution models, and especially with presence-only models, is sampling bias in the occurrence data (*Kramer-Schadt et al., 2013*; *Syfert, Smith & Coomes, 2013*). Although often unaccounted for, sampling bias can introduce significant errors into models, affecting both their performance and ecological interpretability (*e.g.*, *Syfert, Smith & Coomes, 2013*). We chose to reduce the effects of sampling bias by creating pseudoabsence data that has the same bias found in the presence data (*Elith, Kearney & Phillips, 2010*; *Huang, Brooke & Li, 2011*; *Fitzpatrick, Gotelli & Ellison, 2013*). To mirror the sampling bias that likely exists in our presence records, we created a two-dimensional kernel density estimate of sampling effort based on the presence locations for each taxon (Figs. S6–S8). Pseudoabsence records (n = 10,000) were sampled using this density estimate as a probability grid, resulting in a set of unique, sample-bias corrected pseudoabsences for each taxon.

Environmental data

Within the study area, a suite of 44 environmental variables known to influence the distribution of corals and sponges were constructed for use in models (Table 1). Bathymetry for the study area were obtained from the SRTM30+ dataset (*Becker et al., 2009*; *Sandwell et al., 2014*) at a resolution of 0.0083° (approximately 1 km) and used in the creation of several additional layers.

A number of terrain metrics were derived from this bathymetry layer to define the shape of the seafloor. Slope, roughness, aspect, general curvature, cross-sectional curvature, and longitudinal curvature were calculated using the ArcGIS (v10.8, ESRI) toolkit 'DEM Surface Tools' (v2; *Jenness, 2004*; *Jenness, 2013*). Slope was measured in degrees and calculated using the 4-cell method (*Jones, 1998*). Aspect represents the compass direction of the steepest slope and was converted to an index of eastness using a sine transformation and an index of northness using a cosine transformation. Curvature metrics assess the likely flow of water across a feature, with positive values generally indicating convex features that cause water to accelerate and diverge, in contrast to concave features where water would be expected to decelerate and converge. Roughness is a measure of topographical complexity, calculated here as the ratio of surface area to planimetric area, with more positive values indicating more complex terrain. The Topographic Position Index (TPI) was calculated using the toolkit Land Facet Corridor Designer (v1.2; *Jenness, Brost & Beier, 2013*). TPI assesses the relative height of features compared to the surrounding seafloor, with positive areas indicating locally elevated features and negative values indicating depressions. TPI is scale dependent, and was calculated at scales of 1,000, 5,000, 10,000, 20,000, 30,000, 40,000 and 50,000 m. Finally, the Vector Ruggedness Measure (*Hobson, 1972*; *Sappington, Longshore & Thompson, 2007*), which calculates terrain heterogeneity, was calculated with a neighborhood size of 3, 5, 7, 9, 15, 17 and 21 using the Benthic Terrain Modeler (v3.0; *Walbridge et al., 2018*).

To complement the suite of terrain metrics, large-scale geomorphological features expected to provide suitable habitat for corals and sponges were obtained from *Harris et al. (2014)*, including seamounts, guyots, canyons, ridges, spreading ridges, plateaus and escarpments. See Fig. S21 for a map of geomorphological features in the study area.

Table 1 **Environmental variables used in model creation.**

Variable name	Included in final models	Units	Native resolution	Reference
Bathymetry		meters	0.0083°	*Becker et al., 2009* *Sandwell et al., 2014*
Terrain Metrics				
Aspect–Eastness			0.0083°	*Jenness, 2013*
Aspect–Northness			0.0083°	*Jenness, 2013*
Curvature–General			0.0083°	*Jenness, 2013*
Curvature–Cross-Sectional			0.0083°	*Jenness, 2013*
Curvature–Longitudinal			0.0083°	*Jenness, 2013*
Roughness			0.0083°	*Jenness, 2013*
Slope	X	degrees	0.0083°	*Jenness, 2013*
Topographic Position Index (TPI)	X		0.0083°	*Jenness, Brost & Beier, 2013*
Vector Ruggedness Measure (VRM)	X			
Geomorphological Features				*Harris et al., 2014*
Seamount				*Harris et al., 2014*
Guyot				
Canyon				*Harris et al., 2014*
Ridge				*Harris et al., 2014*
Spreading Ridge				*Harris et al., 2014*
Plateaus				*Harris et al., 2014*
Escarpment				*Harris et al., 2014*
Benthic Conditions				
Total alkalinity		µmol l^{-1}	3.6 × 0.8–1.8°	*Steinacher et al. (2009)*
Dissolved inorganic carbon		µmol l^{-1}	3.6 × 0.8–1.8°	*Steinacher et al. (2009)*
Omega aragonite (Ω_A)	X		3.6 × 0.8–1.8°	*Steinacher et al. (2009)*
Omega calcite (Ω_C)			3.6 × 0.8–1.8°	*Steinacher et al. (2009)*
Dissolved oxygen	X	ml l^{-1}	1°	*Garcia et al. (2013a)*
Salinity		pss	0.25°	*Zweng et al., 2013*
Temperature		°C	0.25°	*Locarnini, 2013*
Phosphate	X	µmol l^{-1}	1°	*Garcia et al. (2013a)*
Silicate	X	µmol l^{-1}	1°	*Garcia et al. (2013b)*
Nitrate	X	µmol l^{-1}	1°	*Garcia et al. (2013b)*
Particulate organic carbon (POC)	X	g C m^{-2} year^{-1}	0.05°	*Lutz et al. (2007)*
Regional current velocity		m s^{-1}	0.5°	*Carton, Giese & Grodsky (2005)*
Vertical current velocity		m s^{-1}	0.5°	*Carton, Giese & Grodsky (2005)*
Surface Conditions				
Chlorophyll *a*		mg m^{-3}	4 km	Aqua Modis (NOAA)
Sea Surface Temperature		°C	4 km	Aqua Modis (NOAA)

Note:
Not all variables were retained in the final models produced. 'Reference' refers to either the tool used to create the variable (terrain metrics) or the original data source (other variables).

Data describing benthic conditions at the seafloor were obtained from the World Ocean Atlas (v2; 2013), including temperature, dissolved oxygen, salinity, nitrate, phosphate, and silicate. Carbonate data including dissolved inorganic carbon (DIC), total alkalinity, and the saturation states of calcite and aragonite, were obtained from *Steinacher et al. (2009)*. Current data describing regional horizontal and vertical current velocities were obtained from the Simple Ocean Data Assimilation model (SODA v3.4.1; *Carton & Giese, 2008*). Particulate organic carbon (POC) flux to the seafloor was obtained from *Lutz et al. (2007)*. Raw benthic data layers were transformed to match the extent and resolution of the other environmental variables using the upscaling approach developed by *Davies & Guinotte (2011)*. This upscaling technique incorporates bathymetry data to approximate conditions at the seafloor and has previously been demonstrated to work effectively on both global and regional scales for a variety of data (*Yesson et al., 2012*; *Georgian, Anderson & Rowden, 2019*). The upscaled WOA data (dissolved oxygen, nitrate, phosphate and silicate) were compared to quality-controlled bottom-water bottle data from the Global Ocean Data Analysis Project (GLODAP v2.2019) to assess how much error may have been present in the raw WOA datasets or introduced *via* our upscaling approach (see Fig. S23).

Surface conditions were assessed as chlorophyll *a* and mean sea surface temperature data obtained from the Aqua MODIS program (*Aqua MODIS, 2018*). Both layers were calculated as the mean value from 2002–2016 at a resolution of 4 km, and resampled to match the extent and resolution of the other environmental layers with no additional interpolation.

Modeling techniques

Models were constructed using four different techniques that have proven successful in modeling the distribution of cold-water corals and sponges: Boosted Regression Tree (BRT), Generalized Additive Models (GAM), Maximum Entropy (Maxent), and Random Forest (RF). For each modeling technique, the sampling-bias corrected set of pseudoabsences (n = 10,000) was used in place of either true absences or random pseudoabsences. Each model outputs a habitat suitability score between 0–1, with higher scores indicating more suitable habitat. While often erroneously referred to as the probability of occurrence, this score does not represent a true probability of occurrence in presence-only models due to the lack of true absences and nonsystematic observation of the study area. The refinement of model parameters, final model, model evaluations, and model outputs (*e.g.*, variable importance and response curves) were completed using 'biomod2' (*Thuiller et al., 2016*), 'gbm' (*Ridgeway, 2004*), 'dismo' (*Hijmans et al., 2017*), 'mgcv' (*Wood & Wood, 2015*), and 'randomForest' (*Liaw & Wiener, 2002*) in R (v3.6.1; *R Core Team, 2019*).

Boosted Regression Tree (BRT) models rely on binary splits in a regression-tree structure to define the response of species occurrence or abundance to environmental variables (*Elith, Leathwick & Hastie, 2008*), and have been successfully used to model the distribution of deep-sea fauna (*e.g.*, *Rowden et al., 2017*; *Georgian, Anderson & Rowden, 2019*). The minimum number of trees was set at 1,000, and a Bernoulli distribution of the presence-pseudoabsence data was assumed. Tree complexity was set to three to allow limited interactions between terms.

Maxent (*Phillips, Anderson & Schapire, 2006*) is a machine learning, presence-only modeling algorithm that has been shown to outperform other presence-only models

(*Elith et al., 2006*; *Tittensor et al., 2009*) and even presence-absence models (*Reiss et al., 2011*). Default model settings were used except the maximum number of iterations was increased to 500 to ensure that models converged. In addition, the regularization parameter (default of β = 1) was experimentally tested using values of β = 1–10. Regularization is a smoothing function that controls the complexity of models, with higher values resulting in simpler models with fewer parameters. An ultimate value of β = 5 was chosen for all taxa based on the performance of preliminary models. Previous Maxent modeling of cold-water corals has shown that increasing β improves model performance in areas or conditions outside of the training data, essentially by preventing the model from overfitting to its training data (*Georgian, Shedd & Cordes, 2014*).

A Generalized Additive Model (GAM) is a type of generalized linear model that employs smoothing functions for each explanatory variable (*Hastle & Tibshirani, 1986*). GAM has frequently been used to model the distribution and niche of a variety of marine species including corals and sponges (*e.g.*, *Rooper et al., 2014*). A binomial distribution of the presence-pseudoabsence data was assumed. Various types of smoothers and degrees of freedom allowed were explored in preliminary models, resulting in a thin plate regression spline smoothing function with 12 degrees of freedom used for all variables and modeling runs. Testing higher degrees of freedom (ranging from 4–15) resulted in small improvements in model performance but increased computational time, with no significant model improvements above 12 degrees of freedom (in general agreement with the findings of *Wood, 2017*).

Random Forest (RF) models (*Breiman, 2001*) are a classification or regression, tree-based algorithm that relies on a random selection of explanatory variables and an internal bootstrapping metric to produce and then combine a large number of trees. Default parameters were used except the number of trees was increased to 501 and tree depth was limited to a value of ten to prevent overfitting to the training data. Various tree depths (1–20) were investigated in preliminary models, and a tree depth of ten was ultimately selected as it appeared to improve model performance while preventing models from strongly overfitting to the training data. Tuning tree depth appropriately has been shown to improve model performance without significantly affecting computational time (*Duroux & Scornet, 2018*), with larger than default values often yielding the best results (*Segal, 2003*). It should be noted however that other studies have produced better results by limiting tree depth (*Nadi & Moradi, 2019*), suggesting that the correct tuning value may be dependent on the dataset used as well as how other model parameters are tuned in conjunction. The optimal value of 'mtry' was also experimentally altered in preliminary models, however, the default value (the square root of the number of explanatory variables) consistently performed well and was therefore used across all model runs.

Each modeling approach (BRT, Maxent, GAM and RF) is fundamentally distinct and depends on different structures and assumptions. Therefore, each will produce different habitat suitability maps that may reflect tradeoffs in various aspects of model performance, making it difficult to accurately determine which, if any, model type is superior (*Robert et al., 2016*). To create a more robust final model, we generated an ensemble model for each taxon based on a performance-weighted average of habitat suitability scores from each model type. The BRT, Maxent, GM, and RF model for each taxon were combined using a weighted average of habitat suitability, with weights based on model performance (AUC scores).

Model testing

Models were tested using a ten-fold cross-validation procedure that randomly partitioned occurrences into 20% test data and 80% training data. Metrics of model performance were calculated for each run and averaged across all ten runs, however, final models were trained using the entire dataset. Model performance was assessed through a combination of Area Under the Curve (AUC) and the true skill statistic (TSS). AUC is a threshold-independent performance measure that in presence-only models indicates the probability that the model correctly ranks occurrences over background locations. A random model has a theoretical AUC of 0.5, and while the maximum AUC is generally unknowable in presence-only models it is always less than 1 (*Wiley et al., 2003*; *Phillips, Anderson & Schapire, 2006*). The TSS metric is similar to the conventionally reported kappa, but is independent of species prevalence as well as the size of the validation dataset (*Allouche, Tsoar & Kadmon, 2006*). TSS ranges from −1 to +1 with negative values indicating more random performance and positive values indicating better performance. To fine-tune model parameters (see above), the Akaike Information Criterion (AIC) was also used to assess model performance. AIC helps assess the tradeoff between goodness of fit and simplicity of models, and is therefore commonly used for model selection. A similar ten-fold cross validation approach was used to estimate the spatial uncertainty of the models by randomly withholding 20% of occurrence and pseudoabsence data from model construction with replacement between runs. Uncertainty was then assessed as the standard deviation of habitat suitability scores across all ten model runs. This approach does not account for all possible sources of uncertainty, but provides a useful spatial measure of how sensitive the model is to the sampling of occurrence data and the construction of the pseudoabsence dataset.

Variable selection

The inclusion of highly correlated variables in species distribution models can reduce model performance and make the results more difficult to interpret ecologically (*Tittensor et al., 2009*; *Huang, Brooke & Li, 2011*). Therefore, we employed a variable selection process to refine our original list of 44 environmental layers to a more parsimonious list of less-correlated variables. Variable selection was based on (1) preliminary model testing including predicted variable importance and impact on overall model performance for BRT, Maxent, GAM, and RF models, (2) correlation and clustering among variables, and (3) known biological importance for each taxon. When variables were highly correlated (Pearson's correlation coefficients >0.7) and clustered together (see Figs. S1 and S2), preference was given to the variable that exhibited the best model performance, was less-correlated with other variables, clustered more independently, or was considered to be more biologically relevant.

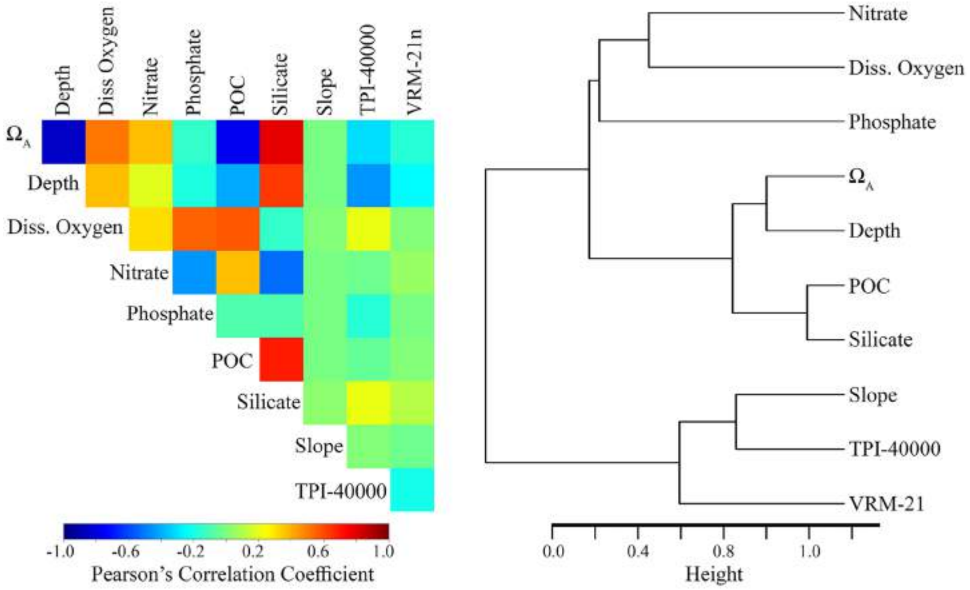

Figure 2 Relationship among the final set of environmental variables used to train the models. Depth was excluded from the final models but was included here for reference. Silicate was only included for demosponges and glass sponges. Ω_A was only included for stony corals. Left: Pearson's correlation coefficients among variables. Right: Cluster dendrogram showing the conceptual relationship among variables, with variables containing similar information clustering closer together. See Figs. S1 and S2 for the correlations and clustering of all environmental variables considered for modeling.

Full-size DOI: 10.7717/peerj.11972/fig-2

Depth was artificially removed despite high model performance due to its high correlation with several, more biologically-relevant variables. The saturation state of aragonite (Ω_A) was included for stony corals due to moderate to high performance in preliminary models and known importance for structuring cold-water coral distributions (*e.g.*, *Georgian, Shedd & Cordes, 2014*; *Georgian et al., 2016a*). Silicate concentration was included for both demosponges and glass sponges due to the inclusion of silicate in their skeletal structures and high performance in preliminary models. POC was retained despite relatively high correlations with both silicate (−0.684) and Ω_A (0.769) due to the known biological importance of all three variables and performance in preliminary models. However, it should be noted that ecological interpretations can be difficult when variables are highly correlated.

The final variable set included eight variables for each taxon, including dissolved oxygen, nitrates, phosphates, slope, TPI calculated at a scale of 40,000 m (TPI-40000), VRM calculated with a neighborhood size of 21 (VRM-21), POC, silicate (demosponge and glass sponges only), and Ω_A (stony corals only). Within the final variable set for each taxon, the highest correlation among variables was −0.684 (POC and silicate), and variables clustered relatively independently compared with the original set (Fig. 2 and Table S1).

RESULTS

Model performance

The models performed well across all taxa and modeling algorithms (Table 2). The 10-fold cross-validation procedure produced test AUC scores that were generally above 0.9, with a

Table 2 Model performance as evaluated by the AUC, and TSS metrics.

Taxa	Model	Test data		Training data	
		AUC	TSS	AUC	TSS
Demosponges	BRT	0.939 ± 0.02	0.783 ± 0.04	0.937	0.799
	GAM	0.976 ± 0.01	0.912 ± 0.03	0.974	0.799
	Maxent	0.975 ± 0.03	0.625 ± 0.06	0.817	0.524
	RF	0.837 ± 0.01	0.932 ± 0.03	0.998	0.959
	Ensemble	–	–	0.988	0.916
Glass sponges	BRT	0.868 ± 0.02	0.718 ± 0.04	0.872	0.739
	GAM	0.904 ± 0.04	0.770 ± 0.05	0.929	0.763
	Maxent	0.902 ± 0.04	0.738 ± 0.06	0.904	0.679
	RF	0.948 ± 0.04	0.862 ± 0.07	0.993	0.961
	Ensemble	–	–	0.968	0.770
Stony corals	BRT	0.915 ± 0.03	0.821 ± 0.07	0.924	0.842
	GAM	0.956 ± 0.03	0.827 ± 0.06	0.964	0.855
	Maxent	0.931 ± 0.03	0.820 ± 0.06	0.939	0.822
	RF	0.965 ± 0.02	0.901 ± 0.04	0.980	0.940
	Ensemble	–	–	0.973	0.845

Notes:
Higher values (closer to one) indicate better model performance in each metric. Each metric was calculated using test data during a ten-fold cross-validation procedure withholding 20% of records for testing, and also for the full model using all available training data. Test value are given as the mean ± standard deviation across 10 model runs.

lowest score of 0.837 (RF model for demosponges). Test TSS scores were similarly high, with an average TSS score of 0.809 across all model types and taxa. Test scores did not change considerably among different cross-validation runs, suggesting that ten runs were sufficient to capture the variation caused by withholding different testing data. Glass sponge models performed slightly worse across all modeling types (average test AUC of 0.905 and training AUC of 0.925), followed by demosponges (average test AUC of 0.932 and training AUC of 0.942). Stony corals performed the best by a small margin with an average test AUC of 0.942 and training AUC of 0.952.

Test data revealed that GAM and Maxent models consistently performed slightly better than BRT and RF models. When looking at the evaluation metrics for the final models built using all available training data, RF consistently outperformed the other approaches, consistently having the highest AUC and TSS scores. However, when looking at test scores during cross-validation, RF scores dropped considerably, suggesting that RF models were slightly overfitting to the training data despite optimization of model parameters.
In contrast, Maxent models, which generally performed slightly worse than RF models when using training data, had little to no decrease in scores when using testing data, in some cases even performing better against testing data. This suggests that the optimization of the Maxent regularization parameter ($\beta = 5$, default = 1) was successful in reducing model complexity to appropriate levels without a large effect on overall model performance. Testing and training scores were similar for BRT and GAM models, with a very slight decrease in most testing scores. BRT and RF models generally had the lowest

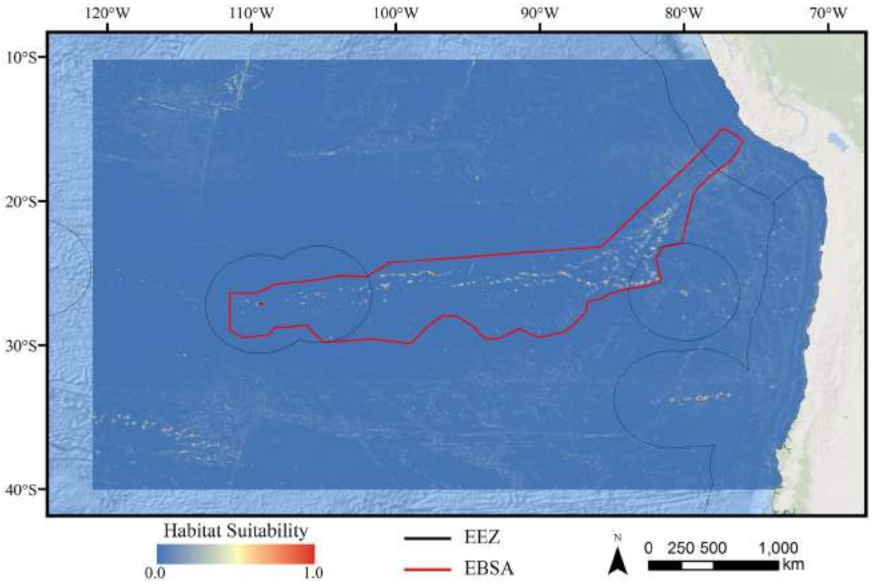

Figure 3 Predicted habitat suitability for the demosponge ensemble model. Warmer colors indicate more suitable habitat. Full-size DOI: 10.7717/peerj.11972/fig-3

uncertainty (Figs. S24–S35) compared to GAM and Maxent models, although GAM uncertainty was highly spatially restricted to very small areas of highly suitable habitat.

The full ensemble models performed well, with an AUC of 0.988 for demosponges, 0.968 for glass sponges, and 0.973 for stony corals. It is interesting that the demosponge ensemble model performed the best by a small margin, when the individual models performed slightly worse than the models for stony corals. This suggests that the ensemble modeling approach was successful in reducing potential structural inadequacies, lack of ideal model optimization, or bias in each model type that may affect the outputs (*Robert et al., 2016*). In general, the scores for the ensemble models suggest that they outperformed GAM, Maxent, and BRT models, but performed slightly worse than the RF model. However, this is likely because RF models were overfitting slightly, producing artificially elevated training scores. Collectively, the performance metrics suggest that the ensemble models were the best for each taxon.

Distributions

For all three taxa, areas with high predicted habitat suitability were largely restricted to small pockets clustered around the Salas y Gómez and Nazca ridges, the eastern portion of the Foundation Seamount Chain, and the waters around the Juan Fernández Islands (Figs. 3–5). Glass sponges and stony corals also had strips of low-moderate suitability along the South American coast and along the west flank of the Atacama Trench. Stony corals models also predicted low-moderate suitability on a large spreading ridge along the East Pacific Rise, although there were few highly suitable areas (see Fig. S21). Within the Salas y Gómez and Nazca ridges, suitability predictions were remarkably similar among the three taxa, with highly suitable habitat coinciding with the flanks and summits of most seamount, knoll, and ridge features (see Fig. 6). However, glass sponges appeared to have

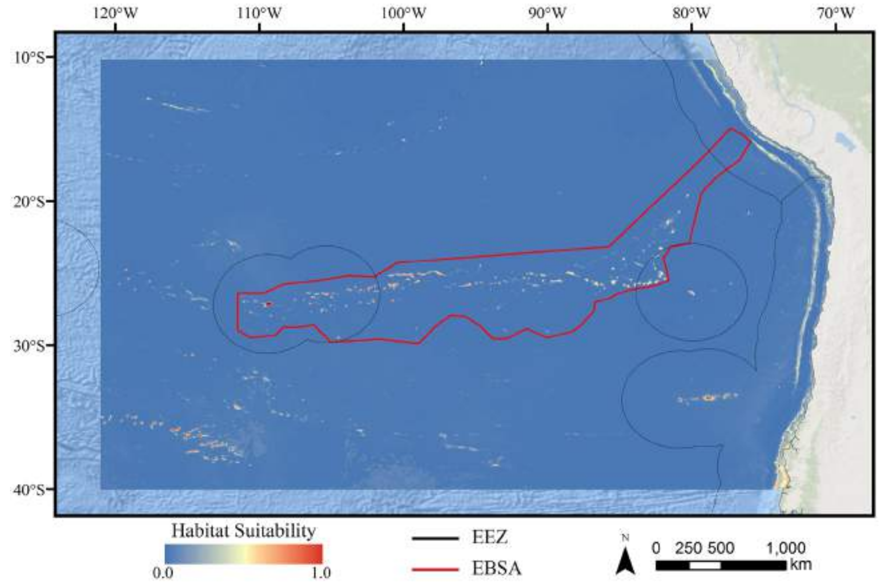

Figure 4 **Predicted habitat suitability for the glass sponge ensemble model.** Warmer colors indicate more suitable habitat. Full-size DOI: 10.7717/peerj.11972/fig-4

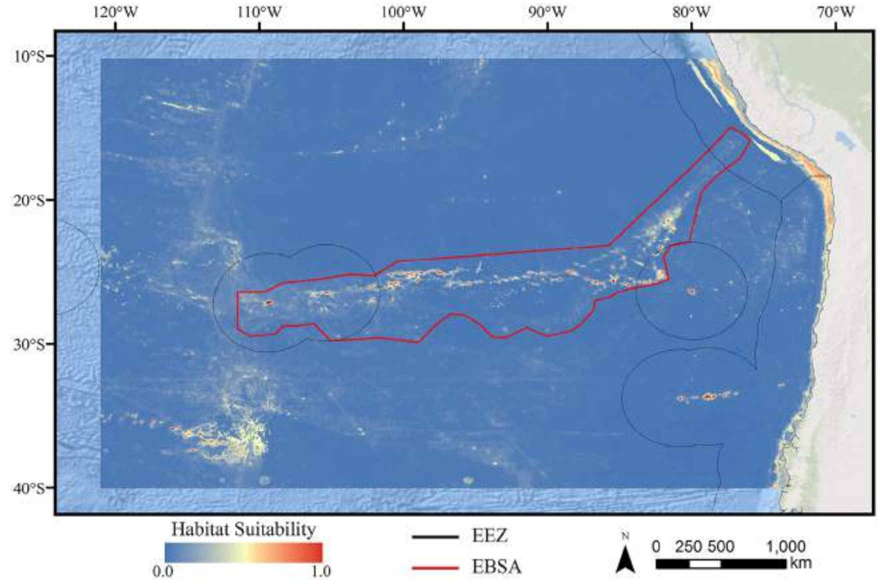

Figure 5 **Predicted habitat suitability for the stony coral ensemble model.** Warmer colors indicate more suitable habitat. Full-size DOI: 10.7717/peerj.11972/fig-5

higher suitability predicted on the steeper sides of large seafloor features, while demosponges and stony corals were predicted to occur on the flanks and especially on the summits of the same features.

When the predicted distribution of each taxon was assessed against the large-scale geomorphological classifications (*Harris et al., 2014*, see Fig. S21), a clear preference for escarpments, ridges, seamounts, guyots, and plateaus (primarily along the Nazca Ridge) emerged (Table S2). BRT and RF models typically predicted narrow distributions clustered

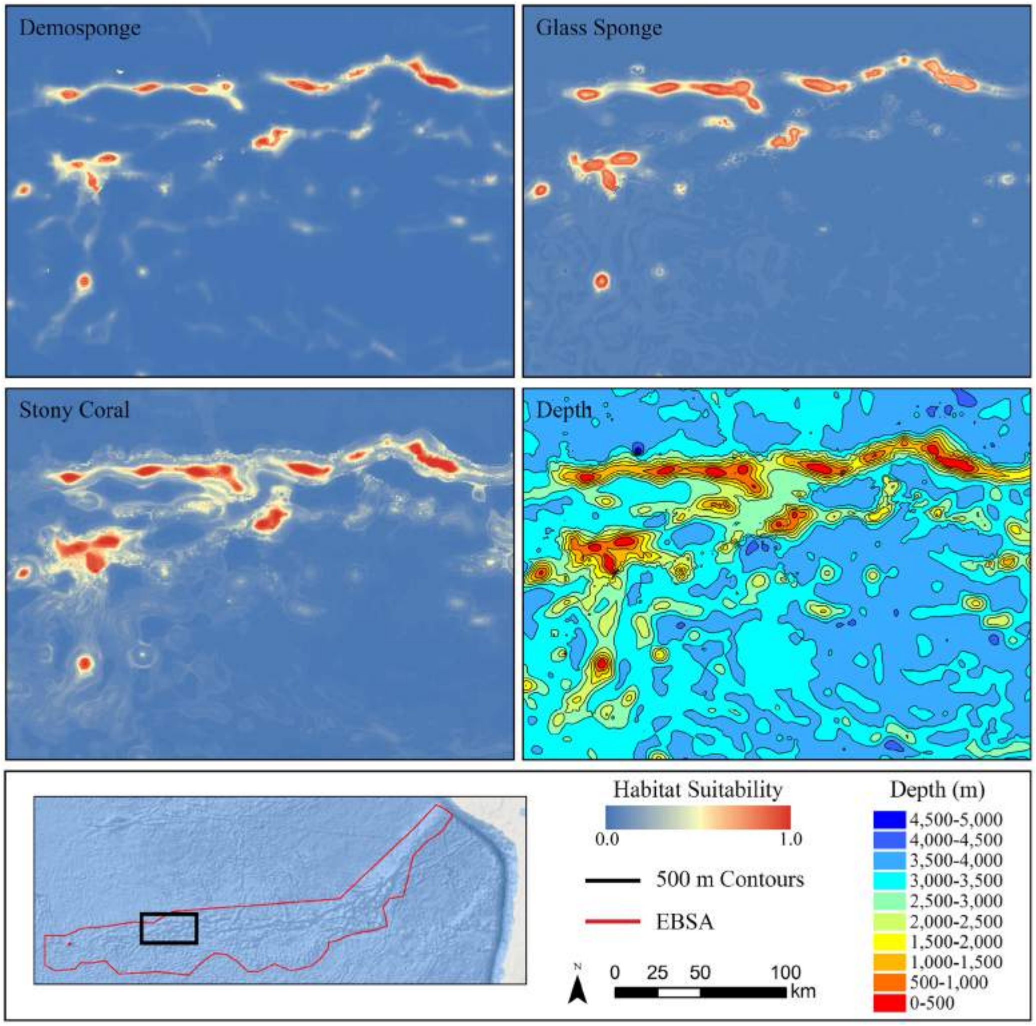

Figure 6 **Ensemble models for demosponges, glass sponges, and stony corals showing a subset of highly suitable seamounts on the western side of the Salas y Gómez Ridge.** Depth with 500 m contours is shown in the last panel for reference. Full-size DOI: 10.7717/peerj.11972/fig-6

almost exclusively on seamounts and other large terrain features, while Maxent and GAM also predicted areas of low-moderate suitability in bands along the coast, spreading ridges, and smaller-scale terrain features throughout the region (Figs. S9–S20). While the highly suitability regions were remarkably similar among modeling types, structural differences or assumptions in each model type did affect the overall suitability predictions, lending additional support for the creation and use of ensemble models rather than relying on a single model. It should be noted that model uncertainty was generally highest in areas with higher predicted habitat suitability (Figs. S24–S35), as well as in more coastal areas, suggesting that additional field surveys may improve models in these areas.

Niche

The niche of each taxa was assessed *via* a combination of variable contribution to the models (Table 3), response curves showing how predicted suitability changes over a range

Table 3 **Percent variable contributions to each model.**

Taxa	Model	Ω_A	Dissolved oxygen	Nitrate	Phosphate	POC	Silicate	Slope	TPI–40,000	VRM–21
Demosponges	BRT	–	0.0	0.4	0.3	**3.7**	**8.5**	0.1	**86.0**	1.0
	GAM	–	**19.0**	15.9	4.2	**16.7**	**27.4**	3.8	7.4	5.6
	Maxent	–	0.0	0.0	2.4	**19.3**	0.2	2.3	**50.4**	**25.4**
	RF	–	0.6	4.5	5.8	6.5	**35.5**	1.9	**37.4**	**7.7**
Glass sponges	BRT	–	0.1	0.3	0.1	**12.5**	**78.3**	**7.3**	0.6	0.9
	GAM	–	0.9	**8.5**	**25.7**	3.3	**52.5**	5.0	3.5	0.6
	Maxent	–	3.2	3.5	0.8	1.0	**62.8**	**11.8**	4.3	**12.7**
	RF	–	3.5	5.7	7.9	**26.8**	**31.1**	**13.6**	7.5	3.9
Stony corals	BRT	**80.3**	0.1	0.1	0.0	0.4	–	0.3	**18.1**	**0.6**
	GAM	**48.9**	1.0	1.6	**37.4**	**5.2**	–	0.5	2.4	2.9
	Maxent	**89.7**	0.1	0.0	0.0	**4.8**	–	0.3	0.0	**5.1**
	RF	**54.1**	2.2	**7.0**	3.2	1.6	–	1.1	**28.6**	2.2

Note:

Ω_A was only included in stony coral models. Silicate was only included in demosponge and glass sponge models. POC=particulate organic carbon. TPI–40,000 = topographic position index calculated at the 40,000 m scale. VRM–21 = vector ruggedness measure calculated with a neighborhood size of 21. The top three variables for each model are highlighted in bold.

of environmental conditions (Fig. 7), and bean plots showing the environmental conditions occurring in the known distribution of each taxa compared to background conditions (Figs. S3–S5).

Terrain metrics consistently contributed a considerable amount of information in each model. Across all model types for demosponges, slope contributed an average of 2% of information, TPI-40,000 contributed an average of 45.3%, and VRM-21 contributed an average of 9.9%. For glass sponges, slope contributed an average of 9.4%, TPI-40,000 contributed an average of 4.0%, and VRM-21 contributed an average of 4.5%. For stony corals, slope contributed an average of 0.6%, TPI-40,000 contributed an average of 12.3%, and VRM-21 contributed an average of 2.7%. Considered jointly, terrain comprised between 15.5–57.3% of information for each taxon, suggesting that the shape of the seafloor is an important component of their niche. Response curves and bean plots suggest that stony corals and demosponges have a clear preference for elevated TPI values (indicating large-scale elevated features). All three taxa show a preference for elevated VRM values (indicating more varied terrain). Interestingly, VRM-21 correlated and clustered with seamounts (Pearson's coefficient of 0.5; Figs. S1 and S2), indicating that at this scale, VRM-21 was a likely an indicator of features similar in topography to seamounts, guyots, and knolls. Bean plots showed that the known distribution of all three taxa coincides with higher slope values of approximately 5–20 degrees compared with background data, however, response curves indicated a more complex relationship. Demosponges exhibited a small preference for elevated slopes, while glass sponges had a large preference for slopes up to approximately 15 degrees, and then a lower preference for steeper slopes. Stony corals had a negative affinity for slopes steeper than 5°.

Silicate was the highest performing variable for glass sponge models (average contribution of 56.2 across model types), and the second highest for demosponges (average

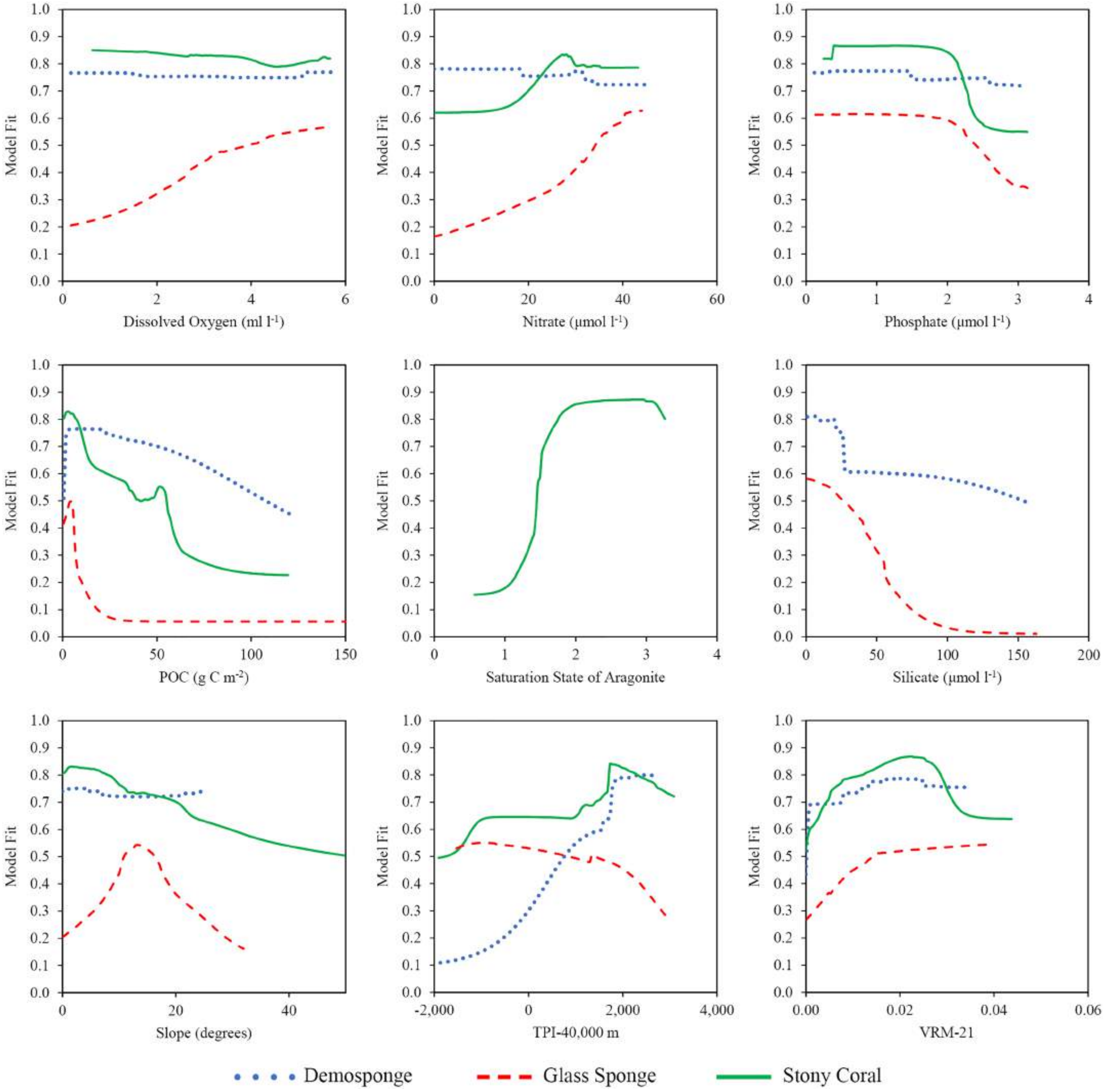

Figure 7 Response curves showing how the model fit changes over the range of each environmental variable. Values were calculated for the final variable set using the ensemble model for each taxa. Silicate was only included in demosponge and glass sponge models, and Ω_A was only included in the stony coral model.

Full-size DOI: 10.7717/peerj.11972/fig-7

contribution of 17.9% across model types). Response curves indicated that both sponge taxa have a large drop-off in predicted suitability once silicate values exceed approximately 30–40 µmol l^{-1}, and bean plots show that both taxa occur at lower than expected silicate values relative to the background environment. It should be noted that silicate had high correlations with other retained variables, including POC (Pearson's coefficient of −0.684) and nitrates (Pearson's coefficient of 0.538), which complicates the ecological interpretation of these results.

For stony corals, Ω_A contributed by far the most information in each model type with an average of 68.3% across all models. A clear preference in both response curves and bean plots for elevated Ω_A values above 1.5 indicated a need for a supersaturated environment. All three taxa were also moderately-highly influenced by POC, with response curves indicating a small spike in suitability between 0–10 g C m^{-2}, and then a rapid decrease in suitability at higher concentrations. However, an analysis of the bean plots indicates that POC values > 5 g C m^{-2} are rare in the study area, and that all three taxa occur at higher than expected concentrations compared with background values.

Dissolved oxygen, nitrate, and phosphate concentrations were only moderately important in the models for each taxon, generally only entering the top three variables in GAM models, which typically included more moderate contributions from all variables rather than receiving large contributions for a few variables. Response curves indicated that glass sponges preferred elevated dissolved oxygen concentrations, while demosponges and stony corals did not have a clear response. Both sponge taxa appeared to moderately prefer higher nitrate values, while stony corals indicated a small preference for lower values. All three taxa exhibited a moderate preference for lower phosphate concentrations.

DISCUSSION

Overview

In order to better inform the spatial management of fisheries and other human activities in the Salas y Gómez and Nazca ridges, we developed ensemble species distribution models for three taxa that are frequently classified as indicator taxa for VMEs (*e.g.*, *Penney, Parker & Brown, 2009*; *Parker, Penney & Clark, 2009*: demosponges, glass sponges, and stony corals). These taxa act as critical foundation species in deep waters due to their habitat creation and other critical ecosystem services (*Roberts et al., 2009*). These areas are VMEs due to their susceptibility to disturbance based on the fragility, rarity, functional significance, and life history traits of their members (*FAO, 2009*). The United Nations require that states and associated intergovernmental agencies identify and protect VMEs, including the closure of fisheries when necessary (*UNGA, 2007*). A better understanding of the spatial distribution and niche of key VME taxa is a critical step towards enacting protection for these fragile and diverse habitats.

The models show that only a small portion of the total study area contained moderately or highly suitable habitat, with the most suitable habitat clustered around topographic highs along the Salas y Gómez and Nazca ridges, the waters around the Juan Fernández Islands, and the Foundation Seamount Chain. The patchy nature of the predicted distribution of all three taxa highlights the difficulties in achieving optimal spatial management with limited observation data, and reinforces the need for species distribution modeling to fill in key knowledge gaps. While the total area of highly suitable seafloor was predicted to be small, these patches extend over large distances, necessitating a regional conservation approach. It is also important to note that most large-scale features (*e.g.*, seamounts, guyots, ridges, and escarpments) were predicted to be highly suitable for all three taxa, particularly within the Salas y Gómez and Nazca ridges. Surveys in the area have shown that seamounts along the ridges have unique assemblages, including species not found elsewhere along the ridges (*Comité Oceanográfico Nacional de Chile, 2017*), further supporting the argument that protecting all of these features should be a high priority for conservation.

Influence of environmental conditions

Elevated and more complex seafloor topography has long been known to exert a strong influence on the success of many benthic species including corals and sponges (*e.g.*, *Rowden et al., 2017*; *Chu et al., 2019*). As suspension and filter feeders, corals and sponges are heavily reliant on local and regional currents to increase food supply (*Purser et al., 2010*), transport larva (*Piepenburg & Müller, 2004*), and prevent sedimentation of both tissues and benthic surfaces required for recruitment (*Rogers, 1994*). Elevated and complex terrain affect current regimes in ways that can be favorable for the recruitment and success of cold-water corals and sponges (*Masson et al., 2003*; *Bryan & Metaxas, 2006*). Accordingly, all three taxa in our study appeared to have a strong affinity for seamounts, guyots, ridges, and escarpments, with a clear preference for high TPI and VRM values (indicating locally elevated and complex surfaces).

It was surprising that stony corals appeared to prefer flatter surfaces, while both sponge groups preferred steeper slopes. The response of stony corals to slope may be explained by the low variable contribution of slope to the stony coral model, and the larger contribution of other terrain features. However, a closer examination of the habitat suitability predictions around large seafloor features showed that stony corals appeared to prefer the summits of seamounts and flat-topped guyots to their steeper flanks, suggesting that this relationship may reflect a real preference for being on the tops, rather than the sides, of large terrain features. In contrast, highly suitable glass sponge habitats clustered preferentially on the steeper slopes of large features while also showing a preference for steeper slopes. The flanks and summits of seamounts can contain drastically different environmental conditions due to depth gradients, extreme hydrological forces, exposure to oxygen-minimum zones, and the topography and sediment type of the summit (*Clark et al., 2010*). Further observations on a finer scale than achieved here are necessary to confirm and explain this pattern.

The waters surrounding the Salsas y Gómez and Nazca ridges are generally oligotrophic (*Von Dassow & Collado-Fabbri, 2014*; *González et al., 2019*) and oxygen-poor (*Espinoza-Morriberón et al., 2019*), suggesting that these variables could play large roles in determining species distributions throughout the region. Nitrate and phosphate only contributed a low-moderate amount of information to the models for each taxon, although response curves did indicate that both sponge taxa had an apparent preference for higher nitrate and lower phosphate concentrations. However, research suggests that phosphate and nitrate uptake in sponges is negligible and unlikely to significantly limit distribution (*Yahel et al., 2007*; *Perea-Blazquez, Davy & Bell, 2012*).

Dissolved oxygen concentration is frequently suggested as being critically important for cold-water corals (*Dodds et al., 2007*; *Lunden et al., 2014*) and sponges (*Whitney et al., 2005*). However, it generally did not contribute considerable information to the models in this study, and only glass sponges demonstrated a notable increase in suitability in response to higher dissolved oxygen concentrations. For stony corals and demosponges, this may suggest that dissolved oxygen is not a limiting factor in the region, congruent with other work showing that cold-water coral communities can grow successfully even in very low oxygen conditions (*e.g.*, approximately 2.5 ml l^{-1} at deep-water reefs in the Gulf of Mexico; *Georgian et al., 2016a*). Similarly, research suggests that some sponges can tolerate periods of hypoxia, although they do so at the expense of other metabolic functioning (*Leys & Kahn, 2018*). In contrast, low dissolved oxygen concentrations have been suggested to be the primary limiting growth factor for glass sponge reefs in some regions (*Leys et al., 2004*), suggesting that dissolved oxygen may partially limit their distribution on the Salas y Gómez and Nazca ridges.

POC flux to the seafloor represents a proxy for food supply to benthic communities and is critically important for the success of deep-water corals and sponges (*Wagner et al., 2011*; *Kahn et al., 2015*). POC contributed significantly to the models for all taxa in this study, with suitability predicted to be highest at POC fluxes between approximately 5–50 g C m^{-2}. It was surprising that habitat suitability for each taxon actually decreased after POC fluxes of approximately 50 g C m^{-2}. However, correlations with other variables including depth, dissolved oxygen, temperature, Ω_A, and silicate may explain this trend. POC values greater than 50 g C m^{-2} were also spatially rare within the study region, with higher values almost exclusively occurring in shallower, coastal waters. In the offshore regions containing deep-water coral and sponge habitats, POC flux was extremely low (generally <10 g C m^{-2}), suggesting that these communities may be food limited by default. However, corals and sponges may also uptake dissolved organic carbon (DOC) (*Weisz, Lindquist & Martens, 2008*; *Gori et al., 2014*), or receive food from the lateral transport of POC (*e.g.*, *Rowe et al., 2008*), potentially decoupling the relationship between vertical POC flux to the seafloor and food supply.

Stony corals produce their hard skeletons using the aragonite form of calcium carbonate, with this mineral often serving as the foundation of entire deep-water ecosystems. The saturation state of aragonite (Ω_A) represents the tendency for aragonite to form or dissolve in seawater, with values >1 indicating supersaturated waters where formation is thermodynamically favored. In our study, Ω_A was the dominant contributing variable in each model type for stony corals, with response curves indicating a clear preference for supersaturated Ω_A values above approximately 1.5. This conforms with numerous field surveys (*Lunden et al., 2014*; *Georgian et al., 2016a*), experimental results (*Georgian et al., 2016b*; *Kurman et al., 2017*), and modeling studies (*e.g.*, *Guinotte et al., 2006*; *Davies & Guinotte, 2011*) suggesting that aragonite supersaturation is a primary requirement for the growth and success of deep-water stony corals. While survival is still possible in undersaturated waters (*Thresher et al., 2011*), there are large energetic costs associated with calcifying under these conditions (*McCulloch et al., 2012*; *Wall et al., 2015*), which generally require additional resources *via* increased feeding rates (*Georgian et al., 2016b*).

While silicate was important in both sponge models, it was surprising that demosponge and glass sponge suitability was lower in areas with higher silicate concentrations, as both taxa produce extensive silicate skeletal materials (as much as 80% of the dry weight of glass sponges can be made up of silicate; *Chu et al., 2011*). Previous work has found clear links between sponge distributions and silicate concentrations (*e.g.*, *Whitney et al., 2005*; *Howell et al., 2016*), with silicate uptake becoming more energetically costly when environmental concentrations are low (*Krasko et al., 2000*). However, extensive glass sponge reefs have been documented at similar silicate concentrations (approximately 50 µmol l^{-1}; *Chu et al., 2011*) that still coincided with predicted high suitability in our study, with response curves indicating a steep decline in suitability in concentrations starting only around 30 µmol l^{-1}. This suggests that it is possible that once a minimum concentration of silicate is reached, there is little additional biological benefit to growing in higher concentrations, allowing the relative importance of other variables to become more important. This finding aligns well with previous research suggesting that a lower silicate level of approximately 30–40 µmol l^{-1} may be the lower limit for optimal sponge growth (*Leys et al., 2004*).

It is also possible that the lower native resolutions of the nutrient, POC, aragonite saturation state, and dissolved oxygen datasets (see Table 1) precluded a more important role in the models, as well as potentially complicating their ecological interpretability. In addition, as comparisons of interpolated layers were not perfectly correlated with water-controlled bottle data from GLODAP (Fig. S23), it is likely that the environmental layers used in our study contain small errors, or that these data are temporally variable. These potential sources of error may complicate the ecological interpretation of these variables, especially when variables are already moderately to highly correlated with other variables (whether included or excluded in final models; see Table S1). However, bean plots and response curves generally demonstrated a strong habitat preference for most key variables, suggesting that these variables are more important on regional scales where the effects of small errors should be negligible. Future work should be completed to improve variable resolution and validate these data in order to more accurately assess how these environmental conditions affect the distribution and niche of these taxa throughout the region. Improved datasets would also considerably improve our ability to predict and map the potential shift in suitable habitat under future scenarios expected with ongoing warming, ocean acidification, shifts in primary productivity, and deoxygenation.

Threats

Anthropogenic impacts to deep-sea environments are increasing at an unprecedented rate and scale (reviewed in *Ramirez-Llodra et al., 2011*). Despite their remote offshore location, the Salas y Gómez and Nazca ridges are not immune to the risks posed by human activities, including commercial fishing, pollution, climate change, and potential seabed mining (reviewed by *Wagner et al., 2021*). Bottom fisheries are frequently cited as one of the most damaging activities for deep-water coral and sponge habitats (*Watling & Norse, 1998*; *Pusceddu et al., 2014*), given the indiscriminate and destructive nature of the trawls, lines, and other equipment used. Suitable habitat for corals and sponges often overlaps with bottom fisheries due to the strong association of many demersal fish species with seamounts and similar features, as well as with the habitat structures created by corals and sponges themselves (*Baillon et al., 2012*; *Kutti et al., 2014*). The Salas y Gómez and Nazca ridges have been sporadically but not heavily trawled in the past, with a bottom trawl closure for orange roughy enacted by SPRFMO in 2006 (reviewed in *Tingley & Dunn, 2018*). Long-lining and pelagic fisheries do target the ridges, but for most target species, fishing effort in the region has been historically low (*Wagner et al., 2021*). Therefore, this area presents a unique opportunity to implement strong protections before widespread and irrevocable damage occurs.

Like every major marine habitat studied, the Salas y Gómez and Nazca ridges are affected by marine debris pollution including abandoned fishing gear and plastics, with the bulk of materials stemming from high seas fisheries in the South Pacific (*Luna-Jorquera et al., 2019*) or coastal regions *via* the confluence of the Humboldt Current System and the South Pacific Subtropical Gyre (*Thiel et al., 2018*). Plastic pollution alone is estimated to affect more than 97 species in the region through entanglement and ingestion, including fish, sea turtles, seabirds, and marine mammals. While the harmful effects of marine debris are better documented in pelagic species, microplastics have been found to significantly reduce the growth and feeding of deep-water corals, and derelict fishing gear causes physical damage to deep-water reefs and harms mobile fauna *via* ghost fishing (*Chapron et al., 2018*; *La Beur et al., 2019*).

Seabed mining is a new but imminent threat to many deep-sea environments including the Salas y Gómez and Nazca ridges. Deposits of cobalt, manganese, and polymetallic massive sulfides are known to exist on or near the ridges (*Hein et al., 2013*; *Miller et al., 2018*; *García et al., 2020*), leaving this area susceptible to future mining interests. While seabed mineral extraction has not yet occurred, rising demand for minerals coupled with technological advances in mining equipment are rapidly increasing global interest in the mining industry. If allowed to occur, seabed mining will cause widespread and serious harm to sensitive benthic habitats *via* the physical disruption of the seafloor and sedimentation of neighboring habitats (*Van Dover et al., 2017*).

One of the largest threats to most marine habitats is anthropogenic emissions, which are driving unprecedented rates of warming, deoxygenation, acidification, and decreased productivity in deep-sea environments (*Mora et al., 2013*). For coral and sponge habitats along the Salas y Gómez and Nazca ridges that already experience average or seasonally low dissolved oxygen, low Ω_A, high temperatures, or low POC flux, climate change may rapidly render even highly suitable habitats unviable for the long-term survival of these taxa. If the rate of environmental change is faster than species can adapt or acclimate, the distribution of many fauna may be considerably reduced, potentially resulting in widespread ecosystem collapse (*e.g.*, *Ullah et al., 2018*). Climate change will also exacerbate local stressors including fishing and pollution, reducing both the resiliency of ecosystems as well as their ability to recover from disturbances. However, marine protected areas are increasingly viewed as a viable tool to mitigate the results of climate change (*Mumby & Harborne, 2010*; *Micheli et al., 2012*; *Roberts et al., 2017*).

Implications for high seas conservation and management

ABNJ, commonly known as the high seas, cover more than 61% of the global ocean surface and 73% of its volume. These remote ocean areas are not only vast, but also critical for sustaining life on Earth, as they contain nearly 90% of the total ocean biomass, produce nearly half of the oxygen, and capture over 1.5 billion tons of carbon dioxide each year (*Van den Hove & Moreau, 2007*; *Global Ocean Commission, 2014*; *Laffoley et al., 2014*). Yet only 1.3% of ABNJ are currently protected within marine protected areas (*MPAtlas, 2021*), despite widespread and rapidly increasing threats. The lack of high seas protections is in large part due to the makeshift legal framework that is currently in place to protect ABNJ (*Molenaar & Elferink, 2009*; *Gjerde et al., 2016*), as well as the lack of awareness that important ecosystems exist within these remote ocean areas. The results of this study indicate that deep-sea corals and sponges, which build the foundation for some of the most abundant and diverse communities in the deep sea (*Rogers, 1999*; *Costello et al., 2005*; *Kenchington, Power & Koen-Alonso, 2013*), are widespread on seamounts and ridges located in high seas waters of the South Pacific. Given the ecological importance of deep-sea corals and sponges, and their high vulnerability to human impacts, areas that host these communities should be protected from exploitation using the best available conservation measures. Regional fishery management organizations that manage fisheries in this region, namely SPRFMO and IATTC, as well as the ISA which manages seabed mining in international waters globally, already have established mechanisms to protect sensitive marine habitats. Commercial fishing in this region has been very limited in recent years, and deep-sea mineral exploration has not occurred (*Wagner et al., 2021*), providing a time-sensitive opportunity to protect this region without significantly impacting those industries. We thus urge member States of SPRFMO, IATTC, and ISA to close this region to fishing and mining activities before it is too late.

CONCLUSIONS

The scarcity of data concerning the distribution of key habitat-forming fauna represents an obstacle to conservation efforts. We found that highly suitable habitat for demosponges, glass sponges, and stony corals likely occurs throughout the study area, particularly on large terrain features including seamounts, guyots, ridges, and escarpments of the Salas y Gómez and Nazca ridges. When previously visited during the limited expeditions to the area, these taxa were found to support abundant and diverse ecosystems housing a wide array of associated species (*e.g.*, *Comité Oceanográfico Nacional de Chile, 2017*). It is our hope that these models will inform expedition planning and future research, improve our understanding of the niche and distribution of key taxa, and be considered in a science-based spatial management plan for the region. Anthropogenic disturbance in the deep sea is increasing at an alarming rate, making it imperative to enact strong, permanent protection before these communities are irrevocably damaged.

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Samuel Georgian conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Lance Morgan conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Daniel Wagner conceived and designed the experiments, authored or reviewed drafts of the paper, secured project funding, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

Data are available at Dryad: Georgian, Samuel (2021), The modeled distribution of corals and sponges surrounding the Salas y Gómez and Nazca ridges with implications for high seas conservation, Dryad, Dataset, DOI 10.5061/dryad.vdncjsxtc.

Supplemental Information

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Navigating paths through science as early career researchers:

A WCMB panel discussion

Navigating the winding, complicated, uncertain path through science can be stressful even for seasoned scientists, and often completely overwhelming for early career researchers. A useful method to provide a roadmap for this path is to learn from those who have walked it before you. With this in mind, we hosted a panel at the 5th World Conference on Marine Biodiversity with Maria Dornelas, Graham Edgar, Madeleine van Oppen, and Moriaki Yasuhara to discuss their paths through marine science and offer advice to early career researchers. Here, we share the stories, recommendations, and advice they conveyed to the audience during the panel.

Trevyn Toone, Elin Thomas, Georgia Sarafidou, and Ariadna Nocera

Members of the WCMB Early Career Committee

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Prof Madeleine van Oppen

Dr Maria Dornelas

Dr Moriaki Yasuhara

Prof Graham Edgar

The adage that one's journey through life is never straight was exemplified by our panellists' routes from their doctorates to their current positions. Dr. Edgar was quick to volunteer that he has never had a permanent job, rather bouncing between fellowships and contract positions. This path was not without its downsides including a lack of job security; however, he enjoys the freedom it allows to shift between different interesting ideas. Dr. Dornelas's career has also followed a winding path including a series of postdocs, a child, and multiple moves before her position at the University of St. Andrews. Dr. Yasuhara moved to the U.S. from Japan as a postdoc before moving back to East Asia to take up his current position in Hong Kong. This multi-national journey was shared by Dr. van Oppen who moved between the Netherlands, England, and Australia for various opportunities before ultimately negotiating her current Australian position.

All four panellists agreed that the most successful students were not necessarily the ones with the highest grades, but rather the ones who were curious about the world around them.

Along these paths each of our panellists identified key turning points in their career as largely being acts of serendipity that led them to discover their talents and passions. For Dr. van Oppen this was learning RNA sequencing in her masters which would be vital to future research, while for Dr. Edgar it was a trip to the Galapagos as a postdoc that broadened his perspectives. For Dr. Dornelas her career turning point was largely defined by discovering what she enjoyed (field work and modelling) and what she did not (lab work) and then building her career along those lines. Dr. Yasuhara, on the other hand, uncovered his skill and passion for deep-sea biology later in his career as a postdoc, a discovery which he credits as shaping the rest of his career.

Looking back on their careers, our panellists were largely in agreement about which skills were most useful to them. While hard skills were important, they unanimously identified soft skills - primarily creativity and drive - as the most useful to develop as an early career researcher. Dr. van Oppen specifically mentioned not being afraid to push the boundaries of science while Dr. Dornelas commented on the importance of building a space that allows for creativity to flourish. All four panellists agreed that the most successful students were not necessarily the ones with the highest grades, but rather the ones who were curious about the world around them.

Opening the door for others when you receive fortuitous opportunities, then, becomes not just a matter of kindness but of fairness.

When it came to the role of serendipity on their path through science our panellists were quick to point out the importance of luck, but also noted that taking advantage of opportunities is a skill itself. Being in the right place at the right time is important, but it takes skill to recognize which opportunities are the good ones, and how best to harness these. Dr. Dornelas also noted the role privilege plays in these discussions and the importance of considering who is even allowed into the right room. Opening the door for others when you receive fortuitous opportunities, then, becomes not just a matter of kindness but of fairness.

For many young scientists, particularly new Ph.D. students, starting a path in research can seem like one long stream of criticism and rejections. On this front our panellists were unanimous - science is a marathon not a sprint, and it is vital to focus on your successes and future rather than drowning in negative feedback. Dr. Dornelas connected this perceived ‘cycle of failure’ with imposter syndrome and noted that sometimes ideas that initially get rejected blossom into successful projects years or even decades later. She also emphasized the importance of effectively filtering feedback.

The impact of a good mentor is impossible to overstate and many, if not most, researchers can point to mentors in their past who shaped their career in science. Our panellists were quick to note the wide range of relationships and interactions that can constitute mentorship, from fully supervisory positions to short conversations between colleagues at conferences. Dr. Dornelas suggested viewing mentors not as those opening doors for someone but rather as any flow of advice, meaning mentors can be anyone who is more familiar with certain systems, not just established researchers or older individuals. Dr. van Oppen suggested prioritizing mentors outside of your own field to avoid bias in perspectives, as well as noting the importance of peer-to-peer mentorship.

Science is a marathon not a sprint, and it is vital to focus on your successes and future rather than drowning in negative feedback.

For early career researchers just starting on their path through science, our panellists emphasized the importance of learning skills outside your comfort zone. For example, seeking colleagues within your lab who can help teach new techniques or connecting with someone outside the lab who can bring in new ideas.

Looking to the future, we asked our panellists how they stay positive in a field like conservation and marine biodiversity where trends can often be negative. The responses ranged from the metaphysical (“the Great Barrier Reef did not exist 2 million years ago and will not exist in 2 million years”) to the eminently practical (“go for a walk”). Overall, however, the panellists agreed that passion for the environment and the world around us can motivate any researcher to look past the negatives and embrace the future.

Finally, we offered each of our panellists the opportunity to provide one final piece of advice to early career researchers. Dr. van Oppen recommended studying statistics and developing the quantitative skills that are necessary for wrangling the large data sets that have come to define conservation science, while Dr. Moriaki advised having a strong skin and not worrying about rejection. Dr. Edgar recommended broadening horizons and generalizing results to larger audiences. Dr. Dornelas, on the other hand, was succinct: “be curious, and be stubborn”.

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Our paths through life and through science are circuitous, but hopefully the thoughts and words of our panellists will be inspiring and helpful to early career researchers. We want to offer our sincerest thanks to WCMB for organizing and allowing us to host this event and, of course, to the four wonderful panellists for sharing their time and thoughts.

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Dr Maria Dornelas is the Deputy Director of the Centre of Biological Diversity at the University of St Andrews in the UK.

Professor Madeleine van Oppen is an Australian Research Council Laureate Fellow at the University of Melbourne and the Australian Institute of Marine Science.

Professor Graham Edgar is a Senior Research Fellow at the Institute for Marine and Antarctic Studies at the University of Tasmania.

Dr Moriaki Yasuhara is an Associate Professor of Environmental Science at the School of Biological Sciences and the Swire Institute of Marine Science at the University of Hong Kong.

Navigating Early Careers as Women in Marine Science:

A WCMB panel discussion

Every scientist transitions through the initial phases of their career as an early career researcher. It is a challenging career phase, marked by numerous transitions, short term contracts and a lot of uncertainty. In addition, navigating this phase as women in marine science can bring extra challenges of its own. To provide guidance and advice, the brilliant Dr. Suchana Apple Chavanich, Dr. Lisa Levin, Dr. Patricia Miloslavich, and Dr. Amanda Bates accepted our invitation to be panellists in a forum specifically for female early career researchers at the 5th World Conference of Marine Biodiversity. During an online panel discussion with over seventy participants, they answered moderator and audience questions relating to women's early careers in science. The four accomplished panellists shared their own experiences and thoughts on the early career process.

Emilee D. Benjamin, Erin Satterthwaite, Priscila M. Salloum, Jasmin M. Schuster

Members of the WCMB Early Career Committee

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Dr. Suchana Apple Chavanich

Dr. Lisa Levin

Dr. Patricia Miloslavich

Dr. Amanda Bates

What was your path from early career researcher to the permanent academic position you now hold?

The panellists shared their journey from their PhDs to their current position, which included overcoming challenges like moving to different places and failed job applications. Dr. Bates said she wanted to travel the world, so had some breaks from academia, but she always ended up returning to science. Dr. Miloslavich did not have such gaps, but moved to a number of different countries for postdocs and research, while raising her three children with her husband. Dr. Levin changed to a slightly different field, from zoology to oceanography, after working as a consultant and realizing she was much happier in science. From their answers, it was clear that it can be hard to make decisions such as coming in and out of academia, moving places and changing fields, but the answers of all panellists echoed the essence of what has really driven them through their journeys: a passion for science.

How have you balanced life with your career?

Women in particular face a lot of pressure to balance life and career, and women scientists are no exception. The panellists agreed that it is hard to balance having enough time for your kids, spouse, students, and research, but Dr. Levin emphasized that it is important to not be hard on yourself and to understand that you are doing the best you can. Dr. Miloslavich added that having a supportive partner is important, but that Moms are priceless when it comes to childcare. She acknowledged that when your children are young it can be difficult to balance your life and your career, but she also said that, "It isn't going to be easy, but it can be done." Dr. Bates added that it is important to know yourself and to put energy into what is important for you, so you can enjoy those things.

What would be important on a CV for getting a postdoc?

A central piece of advice from panellists was to be open to opportunities and work in a collaborative way. The panellists suggested that building relationships, being open to opportunities, and making sure to work in a connected, networked way is essential. Dr. Bates also suggested that you often can't predict what someone is looking for by the job description. She encouraged recent grads to explore many career options in different sectors.

Do you have any advice for people that are trying to move from the postdoc loop to a permanent position?

The panellists highlighted the importance of multidimensionality in this context. Dr. Levin advised accepting opportunities that give you new skills, especially if you have multiple choices available to you; choose the ones that add something new to your skillset. She added that, "After all, a range of skills could lead to your dream job."

In times where you felt it was hard to be a woman in academia what kept you going?

It can be hard being a woman working among male colleagues, and Dr. Chavanich agrees with that. But she said that she was inspired by Sylvia Earle, and that having role models, as well as using whatever support from resources available in your institution can help. Dr. Levin said that there was not much institutional support when she was an early career researcher, and that women used to sacrifice everything, including family, for their careers. However, she had a close group of female friends that supported each other. Thus, regardless of where support is coming from, it is key to face those hard moments, and reach out for support - nobody should feel alone.

The audience brought to the discussion a recently retracted article that suggested female mentorship can negatively affect career paths, both for mentors and mentees.

Dr. Bates responded by emphasizing that people can have a great mentorship relationship regardless of gender. She went on to say that we often look for people we want to emulate and, as women, we sometimes look to other women. She mentioned she has had both male and female mentors that have helped her in different ways.

How can we be more inclusive and diversify science in general?

A conscious effort to include underrepresented groups was highlighted as essential across the panellists. Diversity is something that we should consciously include in everything that we do since it is such an important, cross-cutting theme. The panellists emphasized the importance of enhancing the participation of underrepresented groups in all facets of our work as scientists, such as in guest lectures, working groups, publications, who we cite etc.

How do you deal with patronizing comments from male colleagues?

Early career researchers and especially women and minorities, often have to deal with patronizing comments. Whilst the panellists say there is no single answer for how to respond to being patronized, they highlight that responses need to be tailored to the situation, such as if you are being patronized by a professor, a colleague, or your advisor. Yet, regardless of the source, being honest and making your boundaries and standpoint clear, whilst remaining respectful was advised.

What can we do to be more inclusive of non-native English speakers?

As a non-native English speaker, Dr. Chavanich recognised how important it is to allow ourselves to be exposed to foreign scientists, and to eventually get in tune with different accents. She highlighted that collaboration with other countries is important, so we have to network and break the language barrier to move our research and career forward. She said that, in her experience, exposing herself to work more often with foreigners made communication become easier than expected. On the other side of the spectrum, Dr. Levin advised native English speakers to be conscious of the speed that they normally talk at, and give space for foreign speakers to talk as well.

Did you have to sacrifice anything throughout your career?

This question was answered first by Dr. Bates by advising attendees to decide what is most important to them. She shared that she was one of the first people in Canada to be given maternity leave and she was extremely grateful for that. She also shared that she spaced her kids out by 6 years which helped with her career. Dr. Levin shared that she luckily did not have to sacrifice anything for her family but that she regrets that she has not been to Antarctica.

If you had one piece of advice to early career researchers, what would it be?

When asked about one piece of advice for early career researchers, panellists agreed that being passionate, positive, and confident is critical. The panellists mentioned that it is important to be confident in your work, know your own worth and sustain a positive attitude. Dr. Chavanich added that having the skills to take great photos of your work is very important for scientists right now. To round the question off, Dr. Levin advised to be compassionate and take time to help others, which in some way, will have a big impact on yourself and others.

Any last-minute words of advice, specifically for women in science?

The session closed with some final words by Dr. Miloslavich who said: “Your body is strong now and you have the ability to do things that you won't be able to do in 20 years; enjoy your life, do sports, dance, read, go hiking, take time for yourself and keep your body young in spirit as long as you can.”

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Dr. Suchana Apple Chavanich is an Associate Professor at the Centre of Excellence for Marine Biology at Chulalongkorn University in Thailand.

Dr. Lisa Levin is a Distinguished Professor at the Centre for Marine Biodiversity and Conservation at the Scripps Institution of Oceanography in San Diego (USA), and a founding member of the Deep-Ocean Stewardship Initiative.

Dr. Patricia Miloslavich is the Executive Director of the Scientific Committee on Oceanic Research (SCOR), based at the College of Earth, Ocean and Atmosphere at the University of Delaware, USA.

Dr. Amanda Bates is an Associate Professor and Canada Research Chair in Marine Physiological Ecology at Memorial University of Newfoundland, Canada.

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PeerJ Awards Winners at the 5th World Conference on Marine Biodiversity

The PeerJ Awards program aims to support students and early career researchers by highlighting their work, as well as bringing continued awareness to the benefits that open access has in keeping science open and available to all.

PeerJ sponsored four Early Career Researchers awards at the 5th WCMB – two for presentations and two for posters – the winners of each receiving a free publication in any PeerJ journal (subject to peer review).

Yi-Yang (Alex) Chen PhD candidate at the Australian National University, Australia

Can you tell us a bit about yourself and your research interests?

I'm originally from Taiwan, now doing my PhD with Dr. Rebecca Fox and Dr. Michael Jennions at the Australian National University. I'm interested in the feeding preferences of reef fishes, and how much production they can access from epifaunal invertebrates in tropical seascapes.

Can you briefly explain the research you presented at the WCMB conference?

I've presented one chapter of my PhD thesis which was about the secondary production from macroalgae-associated epifaunal invertebrates. I've found that epifaunal production was positively correlated to macroalgal canopy size, and can be affected by predatory fish biomass and sea temperature. I've also found that epifaunal production was sensitive to environmental disturbances. Understanding how epifaunal production response to changing habitats can help us model the consequences of marine warming events.

What first interested you in this field of research?

I was born and raised in Taiwan, a beautiful island surrounded by seas which is famous for its amazing marine biodiversity. I've been obsessed with marine animals since I was a child.

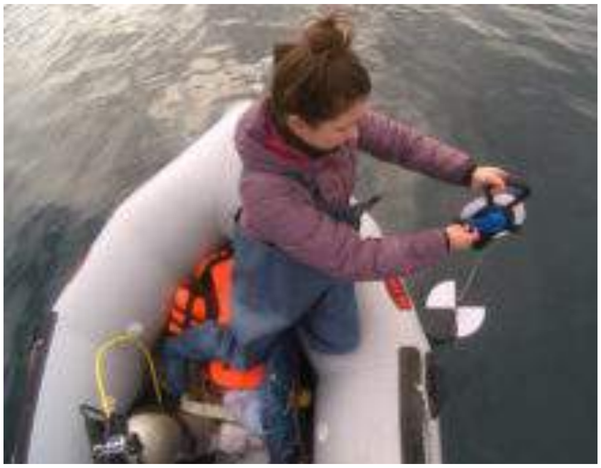
How did you find the virtual conference experience?

I'm still trying to get used to this new trend. Missing the chance of attending the conference and meeting outstanding people in person was quite frustrating. But I did find that this time I was able to watch all the talks I was interested in. I was also motivated by everybody's passion for marine research that can not be stopped by COVID-19.

What are your next steps? How will you continue to build on this research?

My next step is to estimate how much epifaunal production can be consumed by carnivorous fishes, by conducting underwater caging experiments. Since most carnivorous fishes in tropical seascapes are fishery targets or recreational species, results of my study can be used to help marine habitat management and conservation.

Ariadna Nocera PhD candidate at the National University of Patagonia San Juan Bosco - CONICET, Argentina



Can you tell us a bit about yourself and your research interests?

I'm a marine biologist from Argentina who later specialized in biological oceanography in Canada. In 2018 I started my PhD focused on zooplankton dynamics in coastal marine ecosystems in northern Patagonia. I'm interested in how these organisms that are fundamental for marine food webs can change under future possible scenarios, but first it is important to update the baseline studies.

Can you briefly explain the research you presented at the WCMB conference?

I presented the most recent data from the Valdés Biosphere Reserve, corresponding to the composition and abundance of zooplankton in relation to environmental variables. This involved sampling at sea and the identification of hundreds of organisms under a stereo microscope.

What first interested you in this field of research?

I think I was always curious about how small organisms can have such a big influence on other larger organisms, and even on an entire marine ecosystem. I started the study through modeling and now looking more closely at their characteristics, morphologies and behavioral differences allow me to pose new questions that motivate even more my interest in these incredible organisms.

How did you find the virtual conference experience?

Even if there is still less interaction between researchers when compared to an in-person one, the virtual conference gave me the opportunity to participate at WCMB that otherwise would have been more difficult due to the distance and travel costs. It also allowed me to be part of the Early Career Researcher Committee, which organized two different panels during the conference, while interacting with young researchers from different countries. It was definitely a very positive experience and I recommend it!

What are your next steps? How will you continue to build on this research?

The next steps in my research are to continue gathering more data about plankton community composition and distribution over the coming year to strengthen and complete my thesis. In addition, I have planned to carry out experiments to evaluate the effect of atmospheric dust on zooplankton and, finally, to carry out a numerical model for the area with all the information gathered from the fieldwork and experiments.

Trevyn Toone Ph.D. Candidate at the University of Auckland, New Zealand

Can you tell us a bit about yourself and your research interests?

I'm a marine ecologist interested in how we can merge ecology, conservation, and restoration to improve coastal environments. I grew up in coastal North Carolina near salt marshes, shellfish reefs, and seagrass beds, inspiring a career in conserving these ecologically and culturally vital ecosystems. My current work focuses on mussel beds and how we can most successfully restore lost shellfish reefs via scientifically supported methods including harnessing positive species interactions, improving early life stage retention, and minimizing stressors.

Can you briefly explain the research you presented at the WCMB conference?

I presented the first stage of my work in Kenepuru Sound, an area at the top of New Zealand's South Island. The Kenepuru was historically an area with dense and healthy mussel reefs along much of the shoreline, but those populations have been decimated in the last fifty years leading to calls for restoration. My project sought to find the exact extent of this loss, as well as potential causes. We pinpointed the cause of the depletion to commercial handpicking, which began in the late 1960's. Our results also suggest a number of factors that may be responsible for a continued lack of recovery since the end of handpicking, including loss of settlement surfaces, predation, and sedimentation.

What first interested you in this field of research?

Growing up on the coast I've always been interested in the ocean and the fascinating ecosystems it creates. In my undergrad I was introduced to the world of ecology and how species interactions and connections build the world around us. From there I was hooked on research and finding out ways to use ecological principles to conserve and restore the ecosystems I first fell in love with growing up.

How did you find the virtual conference experience?

The virtual conference experience was never going to perfectly replicate an in-person event, but if 2020 has taught us anything it's that adaptability and change are sometimes necessary. I particularly liked being able to go back and rewatch talks after they initially aired as it opened the door to seeing talks in sessions I wasn't able to attend the first time. While the networking aspect of a virtual conference will never be the same as an in-person experience, I still enjoyed WCMB and wouldn't have been able to create the presentation I did without the virtual environment.

What are your next steps? How will you continue to build on this research?

My next steps are building on the results of this project. Shoreline resurveys and interviews with residents have confirmed the need for successful restoration and provided valuable information on where to start these efforts. Specifically my next project will focus on improving recruitment success for mussels which was one of the most commonly identified problems during my interviews. After that I plan on trialing restoration methods for intertidal mussels and looking beyond shellfish to other coastal ecosystems.

If you want to watch Trevyn's presentation, it has been uploaded to YouTube.

Ohad Peleg PhD candidate at the University of Auckland, New Zealand

Can you tell us a bit about yourself and your research interests?

I am a marine ecologist studying shallow temperate reef ecosystems. My study focuses on how human stressors, such as overfishing and sedimentation, affect kelp forest ecosystem health and stability.

Can you briefly explain the research you presented at the WCMB conference?

Phase shifts from kelp forests to unforested ecosystem states due to anthropogenic activities are widely considered a catastrophic decline in ecosystem health on temperate reefs. Using 20 years of monitoring data from inside and outside New Zealand's oldest marine reserve, I demonstrated that by protecting sea urchin predators, long-term marine reserve protection can promote more stable and healthier kelp forest ecosystems. In contrast, unprotected sites lacked stability and fluctuated between less healthy urchin barren and algal turf states. Remediation, however, can take decades, and it is unclear whether this will be possible under future climatic scenarios. Therefore, prompt protection of larger reef areas is strongly advised.

How did you find the virtual conference experience?

Given the current world pandemic, being able to meet and have an excellent conference cannot be taken for granted. With such an outstanding line-up of speakers and presenters communicating excellent top-notch science, I did not have any expectation to win a prize, and I am stoked and humbled to have won the award for the Best ECR presentation (speed-talk). I am also delighted to have won the best 'story' photograph for my photo titled 'the battlefront' showing sea urchins grazing on kelp. I wish to thank the participants, organisers, and sponsors for an outstanding conference, and for these awards and prizes.

What are your next steps? How will you continue to build on this research?

I hope my study can promote marine protection and kelp forest ecosystem restoration and thereby its health. Communicating this work is, therefore, extremely important. Currently, I am looking for a postdoctoral opportunity on kelp forest ecosystem ecology and human impacts.

Dr. Shang Yin Vanson Liu discusses the role Dongsha Atoll plays in connecting the coral reefs of the South China Sea

Can you tell us a bit about yourself?

Hi, I am Dr. Shang Yin Vanson Liu, currently an associate professor at the Department of Marine Biotechnology and Resources, National Sun Yat-sen University. I am a molecular ecologist and have an interest in marine biodiversity and the evolutionary processes of reef organisms.

Can you briefly explain the research you published in PeerJ?

Well, this study is an international collaboration of marine biologists and students from Taiwan, the United States, Sweden and Indonesia funded by NSC (National Science Council, US) and MOST (Ministry of Science and Technology, Taiwan) who were interested in understanding the role that Dongsha Atoll plays in connecting the coral reefs of the South China Sea (SCS). Dongsha Atoll, located 340 km southeast of Hong Kong and 850 km southwest of Taipei, with an area of about 600 km^2, is the largest and oldest atoll in the South China Sea.

In this study, by comparing DNA sequences obtained from 9 reef species collected at Dongsha atoll with sequences from nearby populations in a database compiled by DIPnet, we found that species with larvae that spend a relatively short duration in the plankton (< 40 days) tend to rely on Dongsha as a critical stepping-stone that connects SCS reefs which indicate its' importance in term of marine connectivity in the SCS.

Do you have any anecdotes about this research?

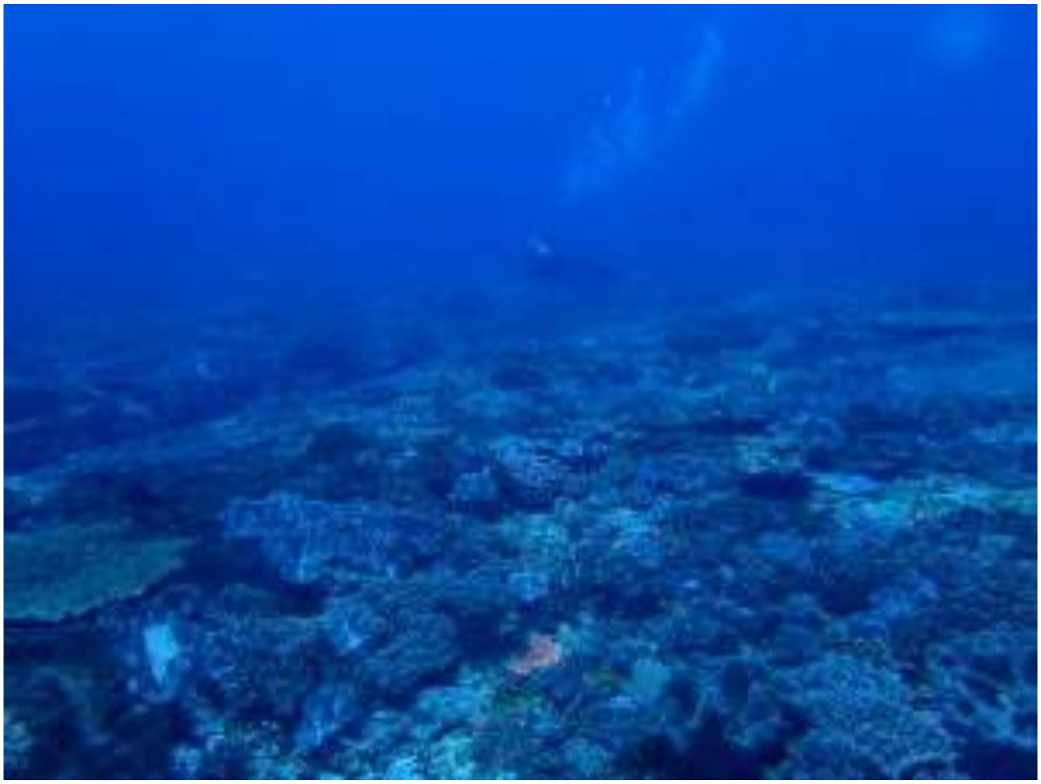
The data collecting of this study was done by a group of students from California State University, Monterey Bay and National Sun Yat-sen University under the supervision of Dr. Eric Crandall and I. It was fun to see how this joint project impacts their career and with interesting findings and fruitful results. The field trip led by scientists from three nations in 2017 to the Dongsha atoll was also amazing, Dongsha Atoll Research Station (DARS) is equipped with well-established facilities and equipment that we need for sampling with SCUBA (https://dongsha-mr.nsysu.edu.tw/) around the atoll and the diversity and coral coverage was stunning.

What kinds of lessons do you hope your readers take away from the research?

This multispecies study provides the most comprehensive examination of the role of Dongsha Atoll in marine connectivity in the South China Sea to date. Combining new and existing population genetic data for nine coral reef species in the region with a graph theoretical analysis, this study provides evidence that Dongsha Atoll is an important hub for sustaining connectivity for the majority of coral-reef species in the region.

Do you have any comments about your overall experience with us?

I have 4 papers published in PeerJ including this study, and definitely will submit again since the review process is transparent and fair under the handling editors in the field of aquatic biology.



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