

Okinawa Institute of Science and Technology
Graduate University

PhD Thesis

**The Role of Connectivity in Structuring
Community Composition and Diversity at
Hydrothermal Vents Across the Northwest
Pacific**

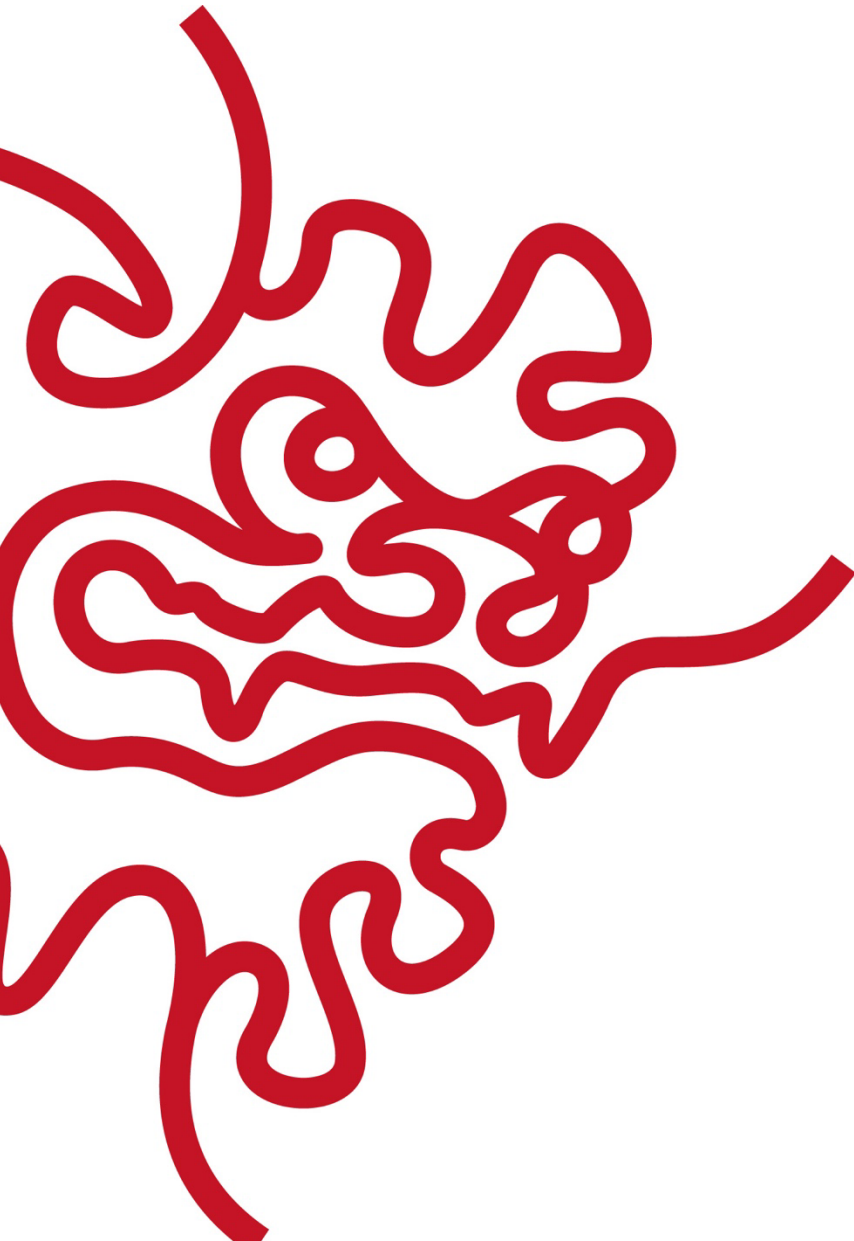
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June 2023



Declaration of Original and Sole Authorship

I, Otis Brunner, declare that this thesis entitled “The role of Connectivity in Structuring Community Composition and Diversity at Hydrothermal Vents Across the Northwest Pacific” and the data presented in it are original and my own work.

I confirm that:

- No part of this work has previously been submitted for a degree at this or any other university.
- References to the work of others have been clearly acknowledged. Quotations from the work of others have been clearly indicated, and attributed to them.
- In cases where others have contributed to part of this work, such contribution has been clearly acknowledged and distinguished from my own work.
- None of this work has been previously published elsewhere, with the exception of the following:
 - **Brunner, O.**, Chen, C., Giguère, T., Kawagucci, S., Tunnicliffe, V., Watanabe, H.K. and Mitarai, S., 2022. Species assemblage networks identify regional connectivity pathways among hydrothermal vents in the Northwest Pacific. *Ecology and Evolution*, 12(12), p.e9612.

Date: June 21st, 2023

Signature:

A handwritten signature in cursive script that reads "Obrunner". The signature is written in black ink on a white background.

Abstract

Connectivity, or the movement of individuals among isolated habitat patches, promotes local and regional biodiversity, and its resilience to disturbances both natural and anthropogenic. Species associated with seafloor hydrothermal vent habitats are distinctly reliant on connectivity due to their spatial restriction to the point source of chemical energy from vent chimneys that fuels their chemosynthetic food web. Measuring connectivity among hydrothermal vents is particularly urgent in regions where mining of these ecosystems is imminent. Our understanding of connectivity is limited by the scarcity of observational data from these inaccessible deep-sea ecosystems. Modelling is a viable alternative to the study of connectivity, as the dispersal that facilitates connectivity is mostly dictated by predictable ocean currents, which can be reliably simulated. This thesis combines empirical observations of species' distributions and environmental conditions at hydrothermal vents with simulations of dispersal, to model connectivity among vent sites in the Northwest Pacific. First, I curate a regional dataset of hydrothermal vent species distributions to infer connectivity in the form of a species assemblage network (Chapter 1). I then simulate how the planktonic larvae of vent species disperse among the vent sites in this region using Lagrangian particle tracking methods within an Ocean General Circulation Model (Chapter 2). Finally, I combine the among-site dispersal estimates with observations of local environmental parameters to create a simulated species assemblage network using a metacommunity model (Chapter 3). This metacommunity model accurately recreated the empirical observations from chapter 1 and gives crucial insight into the interacting effects of dispersal barriers and environmental niche on driving diversity and community composition patterns at hydrothermal vents. Furthermore, I used the combination of observed and simulated connectivity results to quantitatively evaluate the relative role each individual hydrothermal vent plays in maintaining connectivity and biodiversity in the region. Such an evaluation has critical and timely implications for proposed mining and the spatial management of hydrothermal vents in this region. Lastly, we demonstrate that hydrothermal vents are natural laboratories for the advancement of metacommunity theory and conservation ecology due to their characteristic isolation and discrete nature.

Acknowledgements

I would firstly like to thank my supervisor Satoshi Mitarai for his support and guidance from the moment I arrived in Okinawa through to my decision to carry out the PhD all the way to this point, and likely beyond. I am extremely grateful to the Okinawa Institute of Science and Technology for their high-trust financial support of my research. I also acknowledge that as a publicly funded university, the money for my research comes from Japanese taxpayers via the ‘budget for the promotion of Okinawa’. My research would not have been possible or enjoyable without the friendly and inspiring individuals that have made up the Marine Biophysics Unit over the past six and a half years. Within OIST I have received invaluable support from Scientific Computing & Data Analysis Section (SCDA). Without the access they provide to the High-Performance Computing (HPC) service, I would not have been able to accomplish the dispersal simulations that represented the most challenging part of my research. Additionally, I would like to make a special mention of Meria Miller from the graduate school, who sparked my passion for teaching and science communication. We have gone on many adventures together over the years to bring marine science to the children of Okinawa and beyond. I would like to give a special thanks to my co-authors, in particular Chong Chen, Hiromi Watanabe, and Verena Tunnicliffe. These collaborators have gone beyond expectations to the point that I consider them secondary supervisors and academic mentors.

Finally, I would like to thank those friends and family who have encouraged me and kept me (reasonably) sane. Those friends that I live and work with have opened my eyes to new fields of research and new perspectives in general. I recognise the valuable support and advice I have received from my close friend Sam ‘Uncle-Sam’ Ross. My parents are responsible for my academic curiosity as well as my field of interest. My wife Kimberlie Ward deserves the highest level of recognition for all the ways she has enabled me to succeed, from bringing me to Okinawa in the first place to proofreading my work. All the ways she has directly supported me through the years pale in significance compared to the ways she indirectly supports me by making me feel at home wherever we are and bringing our son in to the world, reminding me of what is truly important.

List of Abbreviations

- dbMEM – Distance-based Moran’s Eigenvector Map
- IBMa – Izu-Bonin-Mariana Arc
- MANOVA – Multivariate Analysis of Variance
- MT – Mariana Trough
- OT – Okinawa Trough
- PARCELS – Probably a Really Computationally Efficient Lagrangian Simulation
- P_i – Participation Coefficient
- PLD – Planktonic Larval Duration
- SIMPROF - similarity profile routine
- z_i – Within-module degree

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Introduction

Hydrothermal Vents

Hydrothermal vents are geothermally active structures at the seafloor, which are characterized by the venting of high temperature seawater enriched with minerals from the earth's crust. These hot venting fluids, when interacting with the cold ambient seawater, precipitate metal sulfides which form the characteristic chimney structures (Haymon, 1983). Hydrothermal vents exist where the layer of crust between the upper mantle and the seafloor are at the thinnest, such as spreading centres on mid-ocean ridges and areas associated with volcanic activity such as back-arc basins and subduction zones between plate boundaries. The animal communities found at hydrothermal vents, first observed by Corliss et al. (1979), were found to exist almost entirely independent from sunlight due to their reliance on chemosynthetic rather than photosynthetic primary production. The synthesis of biomass from venting fluid by the microbial primary producers of the community (both symbiotic and free-living) makes the community distinct from most others on earth. Although there are other seafloor chemosynthetic ecosystems such as whale falls (Deming et al., 1997), wood falls (Maddocks and Steineck, 1987), and cold seeps (Sibuet and Olu, 1998), they generally contain communities distinct from those at deep-sea hydrothermal vents (Tunnicliffe et al., 1998). The connection between these chemosynthetic ecosystems over evolutionary and ecological scales however is contentious (Tunnicliffe and Fowler, 1996; Van Dover et al., 2002; Kiel, 2018). Hydrothermal vent communities do experience some external energy input, in the form of surface derived phyto-detritus (Colaco et al., 2009), and output, in the form of chemosynthetically derived organic carbon (Levin et al., 2020). External influences on vent-associated communities are however negligible in comparison to their self-contained trophic interactions (Levin et al., 2020). The chemosynthetic base of the food web comes in various forms within a vent community. Bacterial mats that cover large areas of the sediment can be harvested by mobile epibenthic invertebrates such as copepods (Humes, 1987). Chemosynthetic symbionts inhabit specially adapted organs called trophosomes (Cavanaugh et al., 1981) within various worm species, and molluscs generally cultivate these symbionts within other tissues. Other chemosynthetic symbionts are farmed as epibionts on the tissue of crustacea (Van Dover et al., 1988). The reliance on the proximity of venting chemicals for these trophic interactions results in extremely discrete habitat patches 10s – 100s of meters (Van Dover et al., 2018) in area, outside of which adult vent-associated species are generally unable to survive.

By cataloguing the fossilized, as well as living, species that inhabit vents across the globe, distribution patterns are emerging that give clues as to the evolution of this ecosystem and how it is sustained. Extensive observations at the East Pacific Rise, where vent fauna were first discovered (Corliss et al., 1979), suggests that species inhabiting vents came from a shared local species pool (Van Dover and Hessler 1990). As researchers expanded the scale of their biogeographical studies, they found that species assemblage dissimilarities across the Pacific Ocean could be explained by the large geographic isolation of these vents from one another. Isolation by distance, through the moving of tectonic plates, is considered an important barrier between once connected vent regions. The similarities between the assemblages across the Pacific was linked to the palaeotectonic history. Hessler and

Lonsdale (1991) explained the faunal similarities between the West Pacific back-arc basins and the East Pacific Rise by demonstrating the existence of an extinct mid-ocean ridge (the Kula Ridge) which may have been relevant for migration between now distinct regions 32 – 15 million years ago. The existence of such tectonic pathways of vent activity demonstrates that, although modern vents are separated by distances large enough to represent dispersal barriers, they may have been connected over evolutionary timescales. The relative faunal dissimilarities between basins at a global scale was first investigated by Tunnicliffe and Fowler (1996), who found predictable patterns of higher similarity within basins than between. The dissimilarity resulting from geographical isolation was found to outweigh the dissimilarity that result from differences in the tectonic settings of vents. The location and characteristics of regions of tectonic activity across the globe controls the scale and spacing of venting, resulting in fundamental biogeographic patterns between regions (biogeographic regions) (Van Dover, 1995; Juniper and Tunnecliffe, 1997). Certain patterns of community composition may however come from the differing dispersal potential caused by variations in plume production (Rudnicki and Elderfield, 1993) and topography (Smith and Cann, 1993) between regions. Hydrothermal vents are often referred to as ‘island-like’ systems due to their discrete nature and unique faunal composition compared to the surrounding habitat (Dawson & Santos, 2016; Kiel, 2016; Mullineaux et al., 2018). In some ways, hydrothermal vents are the architype island system as they support unique, isolated communities that are partially maintained through immigration and phylogenesis. The theory of island biogeography (MacArthur and Wilson, 1976) emphasized the key role of isolation in driving diversity and community composition in island systems. The number of endemics found at individual vent sites (Tunnecliffe et al., 1998) suggests that many vents are within a ‘radiation zone’ (Wilson and MacArthur, 1976) where the level of isolation resembles that of an isolated oceanic Island. Due to their arrangement along tectonic plate boundaries, hydrothermal vents perhaps more closely resemble isolated archipelagos (Kiel, 2016). The movement of vent-associated species among island-like habitat patches is therefore a key process in maintaining local and regional diversity.

Although most vent-associated species have a sessile or low motility adult stage (Chapman et al., 2019), they can travel between hydrothermal vent habitat patches during their juvenile, planktonic larval stage by dispersing on ocean currents (Adams et al., 2011, 2012). This larval dispersal is the process which facilitates connectivity, or sharing of individuals, among distant habitat patches. The process of connectivity maintains both the local and regional biodiversity of hydrothermal vent fauna as well as facilitating local recovery and regional resilience following disturbance events (Mullineaux et al., 2018). Anthropogenic disturbances, in the form of mining the seafloor massive sulfides that comprise vent chimneys, now threatens hydrothermal vent communities (Van Dover et al., 2018). The world’s first large-scale test mining of vents began in Japan in 2017 (Okamoto et al., 2019), with little to no publicly available information on the outcome or impacts. To minimize the impacts from deep-sea mining, it is vital to understand how connectivity maintains biodiversity and ecosystem resilience so that keystone communities (Mouquet et al., 2013) can be protected as ‘Ecologically and Biologically Significant Areas’ (Convention on Biological Diversity, 2008). Climate change also poses a risk to hydrothermal vent biodiversity by reducing dispersal in some regions through the interacting effects of increasing temperature and changes to regional currents (Levin et al., 2020).

Connectivity

To understand and quantify ongoing population connectivity among hydrothermal vents, we cannot solely rely on direct observations because it is practically impossible to observe the entire process from birth to successful settlement of an individual. There are two approaches to understanding connectivity of any marine system. The first is a process-based approach that focusses on gaining insight into the biological and hydrodynamical processes that drive dispersal. The second is evidence-based and involves the collection of data that indicates ongoing or historical connectivity in the form of species, genetic, and/or geochemical indicators (Cowen et al., 2002). The remote nature and associated costs of collecting evidence of connectivity at hydrothermal vents means that there is a remit to focusing on the process-based approach. However, due to the considerable geographic extent of sampling efforts at hydrothermal vents around the world (Thaler and Amon, 2019), much of the evidence for connectivity over long-distances (hundreds of kilometres) comes from observations of genetic differentiation (reviewed by Vrijenhoek, 2010).

Dispersal ability could be considered a species trait, as species-specific biological and behavioural characteristics contribute to dispersal ability. Although hydrothermal vents support many species with specialized forms and functions, their reproductive biology is phylogenetically conserved and therefore not dissimilar from more well-studied shallow-water species of the same phyla (Tyler and Young, 1999). For instance, most vent species are invertebrates with a planktonic larval/juvenile stage in which dispersal generally occurs (Dixon et al., 1995). The development of invertebrate larvae in the ocean are split into three categories; direct, planktotrophic, and lecithotrophic, each of which has been recorded from vent-associated species (McHugh, 1989; Lutz et al., 1986; Zal et al., 1995). Direct development is defined by its lack of a dispersal stage. While it is often assumed that planktotrophic larvae can survive the longest periods of dispersal due to their active feeding within the planktonic food web (Herring and Dixon, 1998; Beedessee et al., 2013). Lecithotrophic larvae rely on a limited food supply but have been observed to exhibit planktonic larval durations of over 1 year (Watanabe et al., 2006). By itself, these categories are insufficient to make predictions of larval dispersal distances as shown by Lutz et al. (1986) who demonstrated differing dispersal potential between co-distributed, lecithotrophic limpet species.

For planktonic larvae of vent species, direct observations of biology and behaviour are rare due to the inherent difficulties in culturing deep-sea organisms (Arellano et al., 2014; Matabos et al., 2015; Yahagi et al., 2017). A key determinant of a species' dispersal ability is its Planktonic Larval Duration (PLD). A general estimation of PLD can be made by simply extending the duration of their more well-studied counterpart, to account for the decreased rate of metabolism in the colder, deep-waters they likely inhabit (O'Connor et al., 2007; Hilário et al., 2015; Mitarai et al., 2016; Breusing et al., 2021). Other dispersal behaviours found to be crucial in determining the distance and distribution of dispersal in marine ecosystems are the timing of larval release and the depth at which the larvae disperse (Carson et al., 2010; Young et al., 2012; Kough and Paris 2015; Mitarai et al., 2016; McVeigh et al., 2017; Romero-Torres et al., 2017; Breusing et al., 2021). Most species of planktonic larvae are physiologically capable of controlling their vertical position in the water column, either by buoyancy or swimming against relatively weak vertical currents (Sponaugle et al., 2002). For multiple species from hydrothermal vents, ex-situ observations of larval vertical migration behaviour have led to the conclusion that they have an optimal dispersal depth, which they likely maintain through at least part of their planktonic larval development

(Yahagi et al., 2017). There are various hypothesized reasons for planktonic larvae to modify their depth, including the availability of food for planktotrophic larvae (Dittel et al., 2008), the ability to modify their dispersal distribution (James et al., 2019), and to extend their PLD (Beedessee et al., 2013). Both the depth and timing of dispersal affect the PLD of larvae via temperature and its variability with depth and season, resulting in a complex interaction between these behaviours and species-specific dispersal ability. Unlike in shallow-water marine environments, the production of gametes (gametogenesis) in hydrothermal vent species was considered to lack seasonal cues (Van Dover, 1994) and so is often referred to as continuous or aperiodic. As ecosystems independent from both sunlight and the associated photosynthetically derived energy sources, it is unsurprising that seasonality has rarely been observed at hydrothermal vents. However, an increasingly diverse array of taxa have been shown to reproduce periodically in response to seasonal signals such as tidally driven temperature fluctuations (McHughe, 1989; Zal et al., 1995) or peak arrival of photosynthetically derived materials (Perovich et al., 2003; Dixon et al., 2006; Tyler et al., 2007). Other species have been found to reproduce periodically but independent from any seasonal cue (Methou et al., 2022). Why species at hydrothermal vents would adapt periodic reproduction at hydrothermal vents independent from seasonal signals is unknown. However, it has been suggested that surface generated mesoscale eddies could act as both a seasonal cue and source of variability for the dispersal of planktonic larvae from hydrothermal vents (Adams et al., 2011).

Large-scale ocean currents are well resolved in accessible Ocean General Circulation Models and are suitable for simulating the long-distance dispersal among hydrothermal vents over yearly to decadal timescales (Mitarai et al., 2016; Mullineaux et al., 2018). However, the role of mesoscale eddies and intra-annual stochasticity on dispersal (e.g. Siegel et al. (2008)) is poorly understood for non-coastal ecosystems (Adams et al., 2011). Additionally, it has been proposed that immediately after release, larvae are entrained into the advective plumes from hydrothermal vents (Mullineaux and France, 1995). With the occurrence of ‘megaplumes’ caused by volcanic eruption, it has been proposed that these can lead to very large-scale dispersal events (Mullineaux and France, 1995). However, this mode of transport is thought to be less important than tidal-driven flows (Kim and Mullineaux, 1998). As well as large-scale dispersal events, these plumes have also been used as a potential mechanism to aggregate larvae at vents (Mullineaux and France, 1995). Mesoscale vortices at hydrothermal vents could cause larvae to circulate within a vent field for ~45 days before being transported away (Lupton et al., 1998), giving them time to settle if favourable conditions are detected (Rittschof et al., 1998; Shank et al., 1989).

There are various biological and physical processes in the form of species-specific behaviours and fine-scale oceanography that are difficult to incorporate into simulations of dispersal from hydrothermal vents due to a lack of in-situ observations (Hilario et al., 2015). However, even if these biophysical parameters were accurately resolved, the resulting rates of dispersal among hydrothermal vents would still be a poor proxy for connectivity. Connectivity of a population between habitat patches begins with the successful dispersal between them but is not complete unless the dispersing individuals are able to successfully colonize the new habitat (reviewed by Kritzer and Sale (2004)). Connectivity is therefore influenced by the local biotic and abiotic conditions as well as the regional controls of dispersal, for all of which there is a distinct lack of data and understanding at hydrothermal vents (Mullineaux et al., 2018).

Metacommunity Ecology

In this thesis I define connectivity as the movement of individuals among isolated hydrothermal vent habitat patches via planktonic larval dispersal to a degree that the demographics of one population is affected by the other. The influence of regional dispersal on local demographics is conceptualized within the topics of metapopulation and metacommunity ecology (Levins, 1969; Leibold et al., 2004). In a simplified metapopulation model, a species' abundance or occupancy of a habitat patch is dictated by the local abiotic conditions (environmental filtering) and regional immigration (dispersal) from other patches in the metapopulation network (Levins, 1970). In a comparable metacommunity model, multiple species' abundances or occupancy is dictated by the same dispersal and environmental filtering, as well as the interactions with other species (Wilson, 1992; Thompson et al., 2020). Metacommunity theory represents an ideal perspective with which to study hydrothermal vents. Estimates of regional-scale dispersal can augment the limited local-scale biological and environmental data available in order to model diversity patterns (Mullineaux et al., 2018). Furthermore, the metacommunity perspective is particularly well-suited to the application of spatial management strategies designed to conserve biodiversity at patchy ecosystems under threat from anthropogenic disturbances (Chase et al., 2020). Current threats from deep-sea mining (Van Dover et al., 2018) and climate change (Levin et al., 2020) have led to calls for the implementation of such spatial management strategies for hydrothermal vents, which may mitigate the impact of disturbances from deep-sea mining (Amon et al., 2020).

Empirical evidence of connectivity among hydrothermal vents can come in the form of direct observations of juvenile dispersal or settlement (Van Dover et al., 1988), genetic connectivity (Vrijenhoek, 2010), and perhaps even geochemical signatures (Thorrold et al., 2007; Mouchi et al., 2023). Studies of such connectivity and the resultant effects on community composition have been mostly limited to the East Pacific, specifically the East Pacific Rise (Mullineaux et al., 2018). At the East Pacific Rise, frequent disturbance events, in the form of volcanic eruptions, result in a mosaic of local communities at various states of recovery (Mullineaux et al., 2014). Additionally, the ridge topography at spreading centres in the Northeast Pacific can act to constrain dispersal along the ridge (McGillicuddy et al., 2010). In contrast, the influence of topography on dispersal from hydrothermal vents in the Northwest Pacific is poorly understood (Mitarai et al., 2016). Furthermore, natural disturbances, in the form of volcanic eruptions, are relatively infrequent in the Northwest Pacific as this is dictated by tectonic spreading rates (Perfit et al., 1988). Such natural disturbances likely occur on the order of once within thousands of years, compared to the decadal frequency at the East Pacific Rise (reviewed by Mullineaux et al. (2018)). The low disturbance rates at vent sites in the Northwest Pacific most likely result in a central role of connectivity in local community composition, and simultaneously makes these vents a target for mining industries due to the undisturbed accumulation of sulfide deposits (Van Dover et al., 2018). In-situ observations from anthropogenic disturbances have been made at vent sites in the Northwest Pacific (Nakajima et al., 2015), as well as observations of recovery potential using settlement plates (Nakamura et al., 2018). However, such observations made at the scale of individual vent-sites are unable to extrapolate their findings to communities at other sites, let alone multi-site metacommunities because of the high variability of local biotic, abiotic and oceanographic conditions. Local abiotic conditions that are important to community composition are strongly associated with vent depth and vent fluid chemistry (Watanabe et al., 2019; Giguère and Tunnicliffe, 2021). Both of which can differ greatly even between adjacent vents on volcanic arcs and back-arc spreading centres in the West

Pacific (Giguère and Tunnicliffe, 2021). Additionally, within volcanic arcs, fluid chemistry has been found to differ greatly at the scale of tens of kilometres (German and Von Damm, 2006). Because of the imminent nature of hydrothermal vent mining, Suzuki et al. (2018) simulated the impacts of localized disturbances and recovery rates of hydrothermal vents in the Northwest Pacific, based on estimates of dispersal rates from a biophysical model (Mitarai et al., 2016) and a model of population dynamics. The estimates of recovery rates from Suzuki et al. (2018) are based on a single hypothetical species' local population, so has little relevance to conservation objectives that focus on community-scale biodiversity (Balbar and Metaxes, 2019). Additionally, their simulation does not consider the variability in local conditions among vent sites and assumes that they all represent a suitable habitat for this species. Metacommunity models represent an appropriate methodology to incorporate both regional dispersal estimates and local conditions into a simulation of connectivity among hydrothermal vents (Mullineaux et al., 2018).

Metacommunity models are often formatted as a network of interconnected patches, with features of the edges in the network representing the regional dispersal parameter and features of the nodes representing local biotic and/or abiotic conditions (Economo and Keitt., 2010; Borthagaray et al., 2015). However, many of the foundational metacommunity models are spatially implicit, in that they do not acknowledge the spatial arrangement and varying degrees of dispersal among habitat patches in the network (Urban and Keitt, 2001). A foundational spatially explicit metacommunity model by Economo and Keitt (2010) found a relationship between diversity and a habitat patch's isolation in terms of dispersal, even in the absence of local habitat differences. More recent metacommunity models have incorporated local biotic and abiotic habitat differences into spatially explicit habitat networks, to simulate connectivity and the resultant diversity patterns in hypothetical ecosystems (Thompson et al., 2020; Suzuki and Economo, 2021). The focus of these studies has been primarily an investigation into metacommunity processes and the interacting effects of regional and local drivers on community composition, rather than the application of metacommunity models to simulate real world ecosystems based on empirical data. The discrete nature of hydrothermal vent habitats, dictated by the point source of chemosynthetic resources, and their predictable mode of dispersal, make them an ideal system for the application of metacommunity models (Mullineaux et al., 2018).

Thesis Outline

In this thesis I combine empirical observations of community composition with simulations of local and regional parameters to describe patterns of connectivity among hydrothermal vents in the Northwest Pacific. Using these connectivity patterns, I investigate how this dispersal and environmental filtering interact to influence biodiversity and detect those sites central to maintaining this biodiversity.

Hydrothermal vents are small natural features - the total area of this habitat around the world is estimated to be around 50km² (Van Dover et al., 2018) – with ecological importance disproportionate to their size, making them particularly vulnerable to anthropogenic disturbances (Hunter et al., 2017; Levin et al., 2020; Van Dover et al., 2018). Revealing connectivity pathways among hydrothermal vents and the underlying local and regional processes that facilitate this connectivity is crucial to conserve the biodiversity of this ecosystem (Turner et al., 2019). This natural laboratory also provides an opportunity to extrapolate our findings on metacommunity dynamics to other patchy/island-like ecosystems (Mullineaux et al., 2018). I use community composition, more specifically the

shared species between vent sites, to infer connectivity. Shared species should be considered more an inference of connectivity rather than a direct observation, as shared species can be attributed to historical connectivity (Kiel, 2017) and does not necessarily indicate contemporary connectivity. In order to determine the likely scale of contemporary connectivity I simulate the process of dispersal on ocean currents to determine the likely scale of connectivity and detect possible dispersal barriers. As well as regional dispersal barriers, local environmental conditions can act as a barrier to connectivity. I incorporate empirical observations of environmental conditions to explain patterns of shared species between hydrothermal vents within a reasonable dispersal distance to one another. I hypothesize that the prevailing oceanography that drives dispersal will have an interacting effect with the spatial autocorrelation of local environmental filters to determine connectivity patterns across the Northwest Pacific. These connectivity patterns will highlight keystone habitats; sites that have a disproportionate role in regional connectivity and value for the conservation of regional biodiversity.

The first chapter of this thesis characterizes the diversity of species at hydrothermal vents in the Northwest Pacific in order to infer connectivity based on shared species. I formatted this shared species connectivity as a network in order to employ methods from graph theory and describe the structure of regional connectivity. In the second chapter I simulate the dispersal process under various hypothesized behaviours (namely vertical position and release timing) to investigate the impact species-specific behavioural traits may have on dispersal ability. In chapter 3 I take the output of a single dispersal simulation, in the form of a dispersal probability network among vent sites and incorporate it into a model of metacommunity dynamics. The focal result of this metacommunity model, that also incorporates local environmental conditions, is a simulated community composition at the hydrothermal vents of the Northwest Pacific. I am therefore able to directly compare the observations of connectivity from the first chapter to the connectivity that I simulate based on oceanographic dispersal, local environmental features and metacommunity theory. The use of graph theory throughout this thesis allows me to analyse empirical data and simulated data in the same framework. Networks are well suited for interpreting and presenting connectivity data in an intuitive way for dissemination to the public and policy makers, and to inform the conservation of this uniquely vulnerable and threatened ecosystem.

Chapter 1

Species Assemblage Networks Identify Regional Connectivity Pathways Among Hydrothermal Vents in the Northwest Pacific

Introduction

This chapter is published in the *Journal of Ecology and Evolution* and represents a description and exploration of species diversity at hydrothermal vents. Additionally, inferences on conservation using a novel combination of techniques from graph theory make this study potentially valuable beyond a simple description of biodiversity. The species occurrence data used in this chapter was compiled with the help of the co-authors and represents a valuable resource as the world's most comprehensive regional database of hydrothermal vent species. This dataset is foundational to the entire thesis, it guided the design of chapter 2 and is heavily utilized in chapter 3. The contributions of the co-authors were primarily the provision of species occurrence data, as well as guidance and contribution to the final manuscript. The design, analysis and interpretation of results was carried out by me.

Published article

Brunner, O., Chen, C., Giguère, T., Kawagucci, S., Tunnicliffe, V., Watanabe, H.K. and Mitarai, S., 2022. Species assemblage networks identify regional connectivity pathways among hydrothermal vents in the Northwest Pacific. *Ecology and Evolution*, 12(12), p.e9612.

Conclusion

In this first chapter, I characterised the distribution of species among hydrothermal vent ecosystems in the study region of the Northwest Pacific. As species diversity is an important factor in regional conservation objectives, the results of how species diversity is structured via overlapping distributions has important implications for conservation. The occurrence of shared species indicates contemporary or historical connectivity over unknown timeframes. The role of dispersal in determining the proportion of shared species is indirectly explored by quantifying the relationship between distance (straight-line) and difference (community composition). However, the question remains, how does the dispersal among hydrothermal vents on ocean currents dictate connectivity? In the next chapter we expand upon a distance-based inference of dispersal and build a dispersal simulation.

Chapter 2

The Role of Reproductive Periodicity in Dispersal Among Hydrothermal Vents and its Implications for Regional Connectivity and Conservation

Introduction

This chapter has been submitted to a special edition in the journal of Scientific Reports titled: ‘Deep sea biodiversity and conservation’. It has also been submitted to the pre-print journal ‘bioRxiv’.

Connectivity is the process by which populations and communities at distant habitat patches interact through the sharing of individuals, to the extent that these isolated populations/communities influence each other’s demographic processes (Crooks and Sanjayan 2006; Correa Ayram *et al.* 2016). Connectivity at this scale supports the local and regional diversity of the habitat in question as well as providing resilience to disturbance events. For these reasons, connectivity and its maintenance are considered central to conservation objectives (IUCN, 2017). With a high sensitivity to natural disturbance, due to their ephemeral nature and high degree of isolation, connectivity in hydrothermal vents, is an essential aspect of a species’ survival over successive generations (Mullineaux *et al.*, 2018). Added to that, are the growing anthropogenic pressures at these ecosystems, with the prospect of deep-sea mining in the foreseeable future (Van Dover 2014; Turner *et al.*, 2019).

Connectivity among hydrothermal vents is difficult to quantify or predict because it requires knowledge on several sequential steps in a species’ life history, from reproduction at the source site to successful colonization at the target site, all of which are influenced by a complex interaction of biotic and abiotic factors (Kritzer and Sale 2004; Pineda *et al.* 2007; Thompson *et al.*, 2020). Genetic models using multiple markers are often used as evidence for direct or indirect connectivity among distant hydrothermal vent sites based on the ongoing or historical transfer of genetic material (reviewed by Vrijenhoek, 2010). However, the process of dispersal, which facilitates genetic connectivity, is inherently difficult to observe directly. Thus, larval transport among hydrothermal vents has often been predicted using hindcast velocity fields within models of ocean circulation (Mitarai *et al.*, 2016; Breusing *et al.*, 2016; Breusing *et al.*, 2021). To simulate dispersal within these ocean circulation models, it is necessary to incorporate the biological and behavioural traits of larvae, such as the planktonic larval duration (PLD), vertical position, spawning behaviour etc. (Swearer *et al.*, 2019; Jahnke and Johnson, 2021). There is considerable uncertainty surrounding dispersal behaviour of deep-sea species (reviewed by Hilario *et al.* (2015)), but generalizations of dispersal behaviour have been used to answer important questions using a range of dispersal abilities supported by the best available biological and oceanographic data (Young *et al.*, 2012; Mitarai *et al.*, 2016; McVeigh *et al.*, 2017; Breusing *et al.*, 2021). As in other marine ecosystems (Cowen and Sponaugle, 2009; Treml *et al.*, 2015), these studies have highlighted the importance of the PLD and vertical position at hydrothermal vent ecosystems, by testing a range of different dispersal depths and larval duration. Although it is common for simulations of dispersal to ignore temperature dependent growth rates and use a fixed PLD (Swearer *et al.*, 2019), previous works have contradicted these assumptions for vent ecosystems and shown that ocean currents and temperature have an

interacting effect on dispersal at different depths (Mitarai et al., 2016; Breusing et al., 2021). In addition, Yahagi *et al.* (2017) also demonstrated the importance of temperature dependent growth in *Shinkailepas myojinensis* larvae dispersing from hydrothermal vents in the Northwest Pacific. Conversely, the influence on dispersal of other life-history traits, such as those related to reproductive strategies, have been poorly investigated in hydrothermal vent species. Yet, both timing and frequency of spawning have been shown to drastically impact connectivity of species from coral reefs and coastal ecosystems (Carson et al. 2010, Kough & Paris 2015, Romero-Torres et al. 2017); (reviewed by Swearer *et al.*, 2019)). Moreover, surface generated mesoscale eddies potentially result in the seasonal and interannual variability of larval transport from hydrothermal vents (Adams et al., 2011), which could be exacerbated by variations in spawning behaviour. For example, species that reproduce synchronously at a certain time in the year (periodically) may be more strongly influenced by annual and inter-annual variability than those that reproduce throughout the year (aperiodically).

Endemic fauna from hydrothermal vents exhibit a wide range of reproductive strategies and spawning behaviours, similarly to species from other marine ecosystems. Although most have aperiodic reproductive patterns — sometimes defined as continuous — (Jollivet et al., 2000; Faure et al., 2007; Tyler et al., 2008; Hilário et al., 2009; Matabos and Thiebaut, 2010; Nakamura et al., 2014; Marticorena et al., 2020), cases of periodic reproduction have also been observed in some families despite the absence of sunlight at these depths (Perovich et al., 2003; Dixon et al., 2006; Methou et al., 2022). In *Bathymodiolus* mussels from the Atlantic and some bythograeids crabs from the East Pacific, reproductive periodicity correlates with seasonal variations of the photosynthetic primary production sinking from the surface, with a spawning or hatching period preceding the peak of photosynthetic production (Perovich et al., 2003; Dixon et al., 2006; Tyler et al., 2007). Unlike all these previous works, the intriguing case of *Rimicaris exoculata* and its sister species *R. kairei* revealed a brooding phase restricted to the period between January and early April, regardless of the hemisphere and therefore without any apparent relationship with a known seasonality pattern (Methou et al., 2022). This contrasts with reproductive rhythms in other shrimps from the same family, with brooding phases that match seasonal variations from the surface (Copley and Young, 2006) or are simply aperiodic (Methou et al. in review). Thus, periodic and aperiodic reproduction sometimes coexist in species of the same family (Perovich et al., 2003; Copley and Young, 2006; Hilário et al., 2009; Methou et al., 2022), resulting in different timings of larval release among conspecifics.

In this paper we investigate the role of reproductive periodicity on dispersal by comparing simulations of year-round spawning to those where spawning is restricted to a single month. Although it has been found that the stochasticity of surface currents means that periodicity will have little effect on connectivity in coastal ecosystems on the annual scale (Siegel *et al.*, 2008) this has not been tested for deep-sea ecosystems. It is not unreasonable to assume that dispersal in deeper waters should result in less stochasticity and therefore a more consistent inter-annual signal of reproductive periodicity.

The geographical extent of these simulations is limited to an area of the Northwest Pacific which represents a distinct bioregion (Bachraty et al. 2009) with little influence from external sites in terms of dispersal (Mitarai *et al.*, 2016). Local and regional diversity is particularly high in the Northwest Pacific compared to other hydrothermal vent regions (Thaler and Amon, 2019) and species distributions are somewhat spatially structured (Brunner *et al.*, 2022) within the region. This region is also home to the world's first full-scale test mining of a hydrothermal vent ecosystem, which was carried out in the central

Okinawa Trough in 2017 (Okamoto *et al.*, 2019). The regional impacts of localized disturbances have been poorly studied in the Western Pacific (Mullineaux *et al.*, 2018) and the only such study to attempt this so far (Suzuki *et al.*, 2018) utilized dispersal estimates that assumed aperiodic dispersal (Mitarai *et al.*, 2016) and do not account for any variability associated with larval release timing. Currently, periodic reproduction has not yet been clearly reported in vent species from the Northwest Pacific, however this region hosts several vent species – including bathymodiolin mussels, alvinocaridid shrimps or bythograeid crabs –, with known cases of seasonality in congeners from other bioregions (Perovich *et al.*, 2003; Dixon *et al.*, 2006; Methou *et al.*, 2022). Aside from release timing, we kept the important parameters of dispersal depth and PLD in our simulations mostly consistent with those used in previous studies (Young *et al.*, 2012; Mitarai *et al.*, 2016; Breusing *et al.*, 2021). In this study we test whether or not reproductive periodicity influences the dispersal ability of species from hydrothermal vents and how this interacts with other dispersal parameters such as depth of dispersal. Furthermore, we investigate how periodicity and depth affect the applicability of certain metrics used to assess regional connectivity and inform conservation.

Methods

Study Sites

The hydrothermal vent sites that are the focus of this study are mostly distributed within the Okinawa Trough, Izu-Bonin Arc, Mariana Arc, and Mariana Trough (Figure 1). We considered sites listed in InterRidge version 3.4 (Beaulieu and Szafranski, 2020) as active and confirmed, viable ‘source sites’ for the dispersal of larvae. We added several hydrothermal vent sites that are not included in InterRidge version 3.4 but have been recently confirmed (Methou *et al.* in review) as well as a number of cold-seep ecosystems that have been found to share species with hydrothermal vents in the region (Tokuda *et al.*, 2006; Feng *et al.*, 2018; Xu *et al.*, 2018). A list of the sites with associated metadata can be found in Supplemental Table 1 and a map of their locations in Supplemental Figure 1. The dominant oceanographic features within the extent of this study are the Kuroshio western boundary current and the North Equatorial Current (NEC) (Figure 1).

Dispersal Simulations

All simulations of larval dispersal, as well as the analyses and plotting of outputs, were carried out using Python version 3.10.2 (<http://www.python.org>) and PARCELS version 2.3.1 (Delandmeter and Sebillie, 2019). PARCELS is a set of methods for Lagrangian particle tracking, which use oceanographic velocity data as an input, and track the advection of simulated particles based on this velocity data and subgrid-scale diffusion (Smagorinsky, 1963). The velocity data was obtained from the ‘MOI GLORYS12_FREE’ Ocean General Circulation Model via MERCATOR. Temperature data was also obtained from the same source. The resolution of the velocity and temperature field data used was 1/12th of a degree horizontally with daily timesteps across 50 depth bands from 0.5m to 5728 m depth. The temporal extent of the data was five years from 1997 to 2003 in order to minimize the affect of Kuroshio ‘large meandering events’ (Qui and Chen, 2021) on inter-annual

variability. The spatial extent of the data covered the entire North Pacific Ocean to eliminate the boundary effects of larvae dispersing to the edge of this extent.

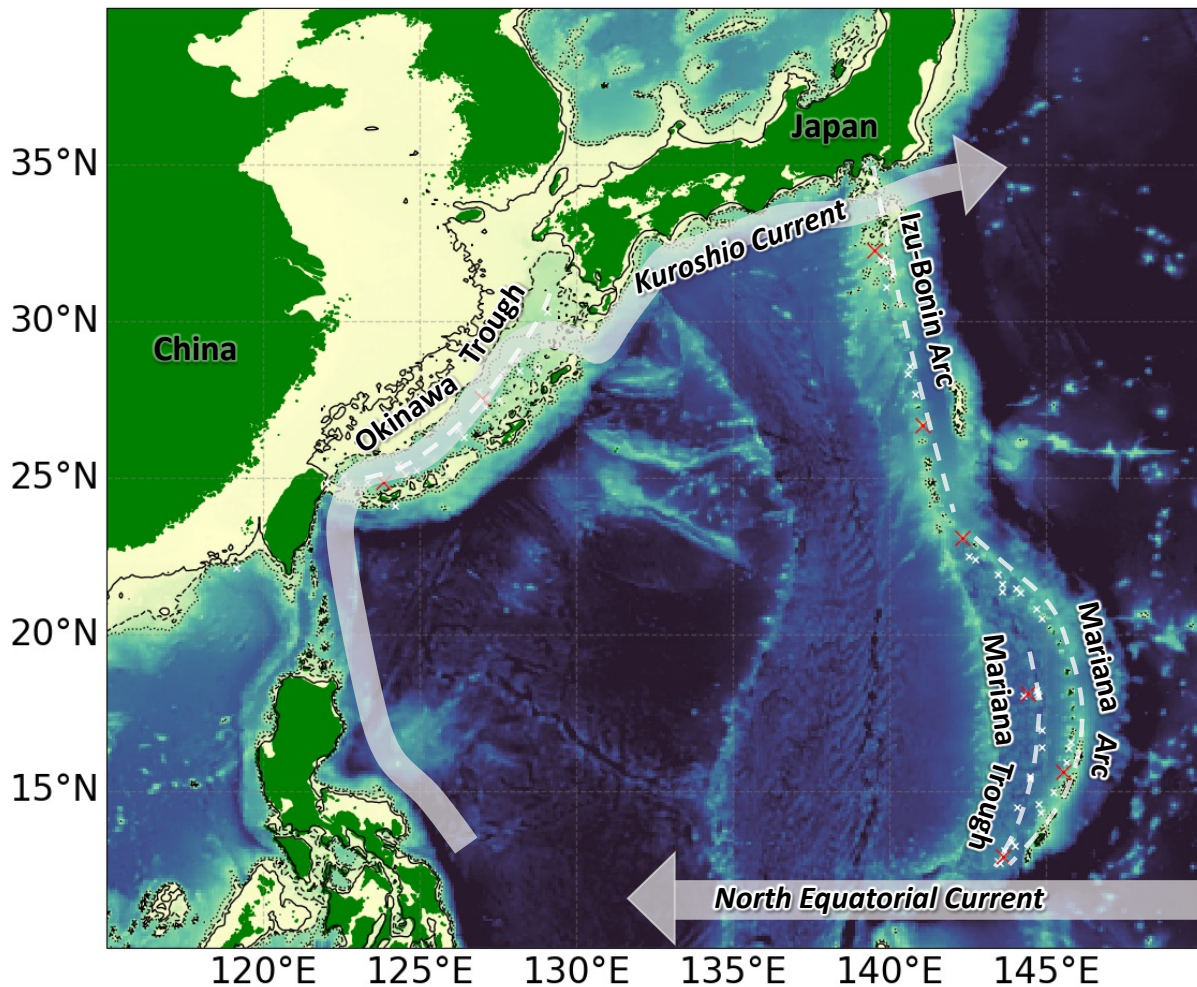


Figure 1: Study site in the Northwest Pacific showing the distribution of vent sites (red 'x' for focal sites and white for the rest) on their respective tectonic features (dashed white lines) and the approximate location of the two most dominant currents in the region (grey arrows). The colourmap is based on bathymetry data from 'MOI GLORYS12_FREE' 1/12th Ocean General Circulation Model with the contours plotted as black lines at 100m (solid line), 500m (dashed line), and 1000m (dotted line).

Using the same oceanographic field data, we ran simulations under three hypothesized dispersal depths; 100m, 500m, and, 1000m. In each simulation, Lagrangian particles (with behaviours that approximate planktonic larvae) were released simultaneously from the same 69 source sites around the Northwest Pacific. In cases where the maximum depth of the oceanographic data at a source site exceeded the depth of dispersal, the output from that source site was not included in analyses. This resulted in a total of 69 sites for 100m, 66 sites for 500m, and 63 sites for 1000m scenario (Supplemental Table 1). 20 Lagrangian particles were simultaneously released from each source site every six hours during the release window dictated by the periodicity of larval release. The total number of particles released from each site was 146,000 across the five years and roughly 2433 (146,000/60) for each month release within the five years. The number of days from release to termination/settlement (PLD) for each larva was individually calculated based on the seawater temperature they encountered at hourly time intervals. The equation to calculate

PLD from temperature was adapted from O'Connor *et al.* (2007) following the methods of Mitarai *et al.* (2016) and Breusing *et al.* (2021). Based on O'Connor *et al.* (2007) finding that the magnitude of the PLD-temperature relationship varied for each of the 69 species they tested, we used the highest magnitude which they found to suitably fit this relationship. We therefore assume that deep-sea hydrothermal vent species have a relatively long PLD compared to the shallow-water species tested by O'Connor *et al.*, (2007). For reproducibility and consistency with other studies, we followed the methods recommended by the creators of PARCELS as closely as possible. The details of the simulation parameters along with links to scripts and tutorials can be found in Supplemental material.

Analysis

In the simulations we recorded each Lagrangian particles' age, average temperature experienced, and coordinate position at the end of its PLD. We analysed the variability of these outputs in response to the addition of more Lagrangian particles and years of data as a form of sensitivity analysis, following the recommendations of Brickman and Smith (2002). We determined that the results were representative by calculating the coefficient of variance with the cumulative addition of five years of results, where it fell below 5% in all treatments. We then compared the mean and confidence interval of each output to determine the effects of periodicity and depth. We conducted a 2D Kolmogorov-Smirnov (K-S) test (Peacock, 1983; Fasano and Franceschini, 1987) to compare the latitude and longitude distribution of particles released periodically each month and aperiodically. Following the technique outlined by Press *et al.* (1992), we calculated a K-S statistic 'D' that measured the difference between periodic and aperiodic treatments. The statistic is a normalized value between 0 and 1 and was comparable across release, location, depth, and timing. We separately calculated D for each of the 60 monthly release windows over the five years and repeated it at each of the three depths resulting in 180 D values for every site. To detect the presence of an annual signal in D, a discrete Fourier Transform method (Cooley and Tukey, 1965) was applied to the 60 sequential months of D-values for each site and depth using the numpy package (Harris *et al.*, 2020) in Python. From all the sites, we selected several that represent the different geographic areas in the region, for a further comparison of dispersal characteristics and distributions between periodic and aperiodic scenarios.

Results

The distributional difference between particles released periodically and those released aperiodically (D) was highly variable depending on the month of periodic release for all sites (Figure 2). There was no consistent pattern of variation in D across years based on the month of release. In most cases there was little to no effect of the dispersal depth on the inter-/intra-annual variability of D on each site. However, those sites contained within the Okinawa Trough had a lower mean D and smaller within-site variability of D at 500m, as did several sites in the Northern Izu-Bonin area (Figure 2 b). The most distinct geographical trend in the D values was the on average lower D values in the Okinawa Trough when compared to other regions (Figure 2).

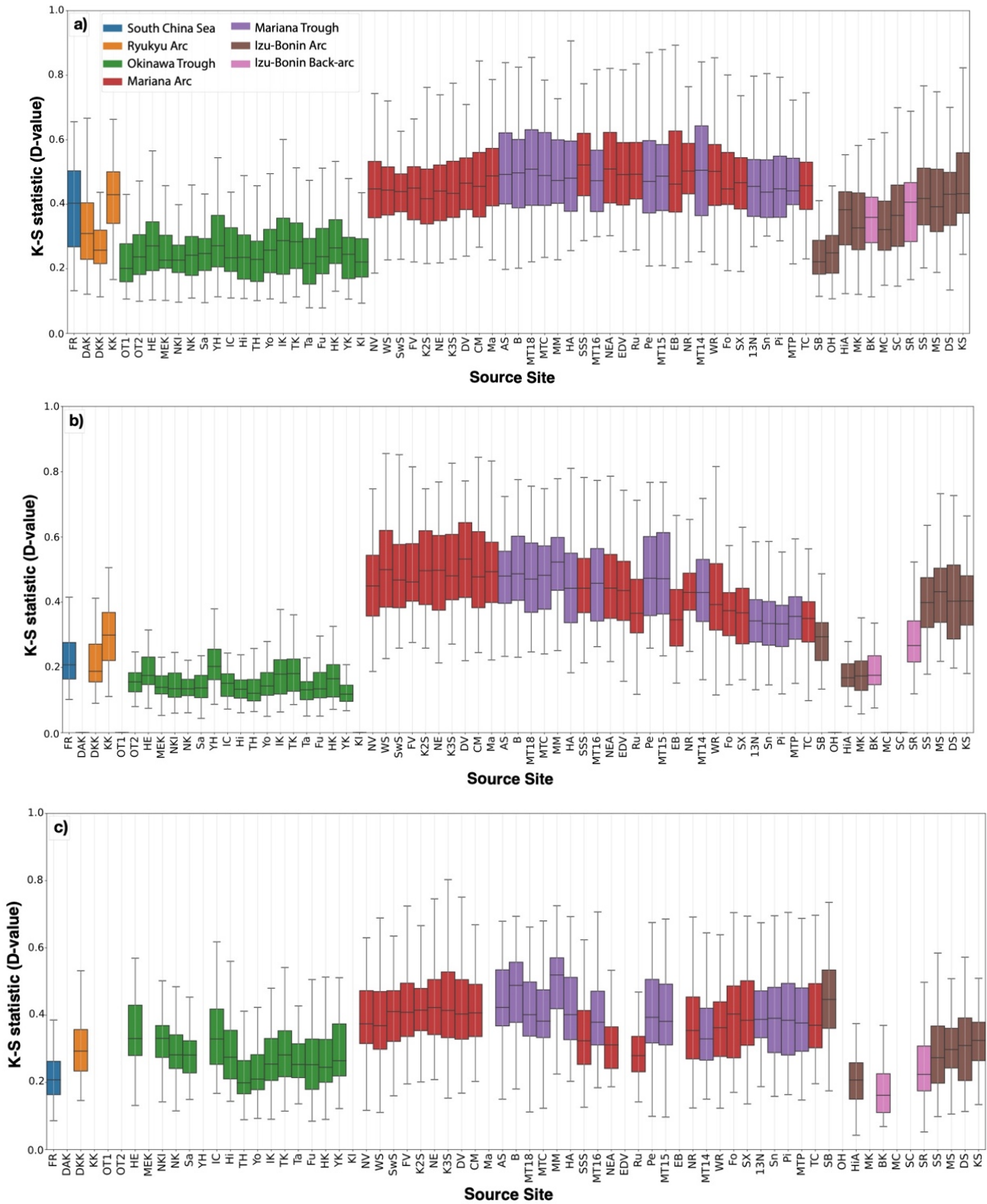


Figure 2. The distribution of the Kolmogorov-Smirnov statistic (D) across all 60 months (5-years) of release for each site. The sites are arranged by their tectonic region and then by latitude (North – South) to demonstrate the geographical consistency that occurs among depth scenario (a – c). Full names and other metadata for each Source Site in Supplemental material

At all depths, there is a trend of increasing D values from north to south among the Izu-Bonin sites, while the Mariana sites exhibit a decrease in D values from north to south at a depth of 500m. The distribution of particles aperiodically from each site is consistent with those in close proximity (Figure 3 and 4).

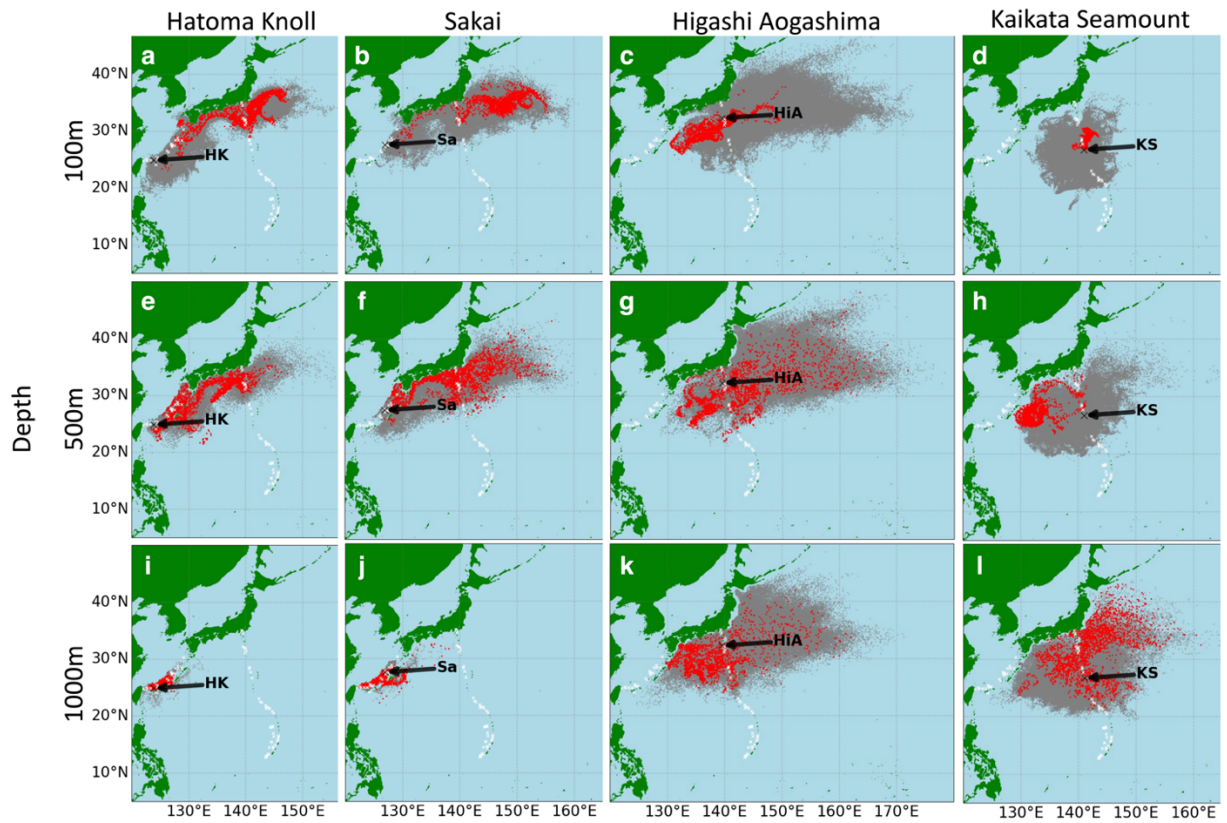


Figure 3: The distribution of Lagrangian particles dispersed aperiodically (grey) and during the single month that resulted in the greatest D-value (red) from the Okinawa Trough or Izu-Bonin area. The source sites (black 'x') of the Lagrangian particles were selected as representative of the other sites (white 'x') within their vicinity.

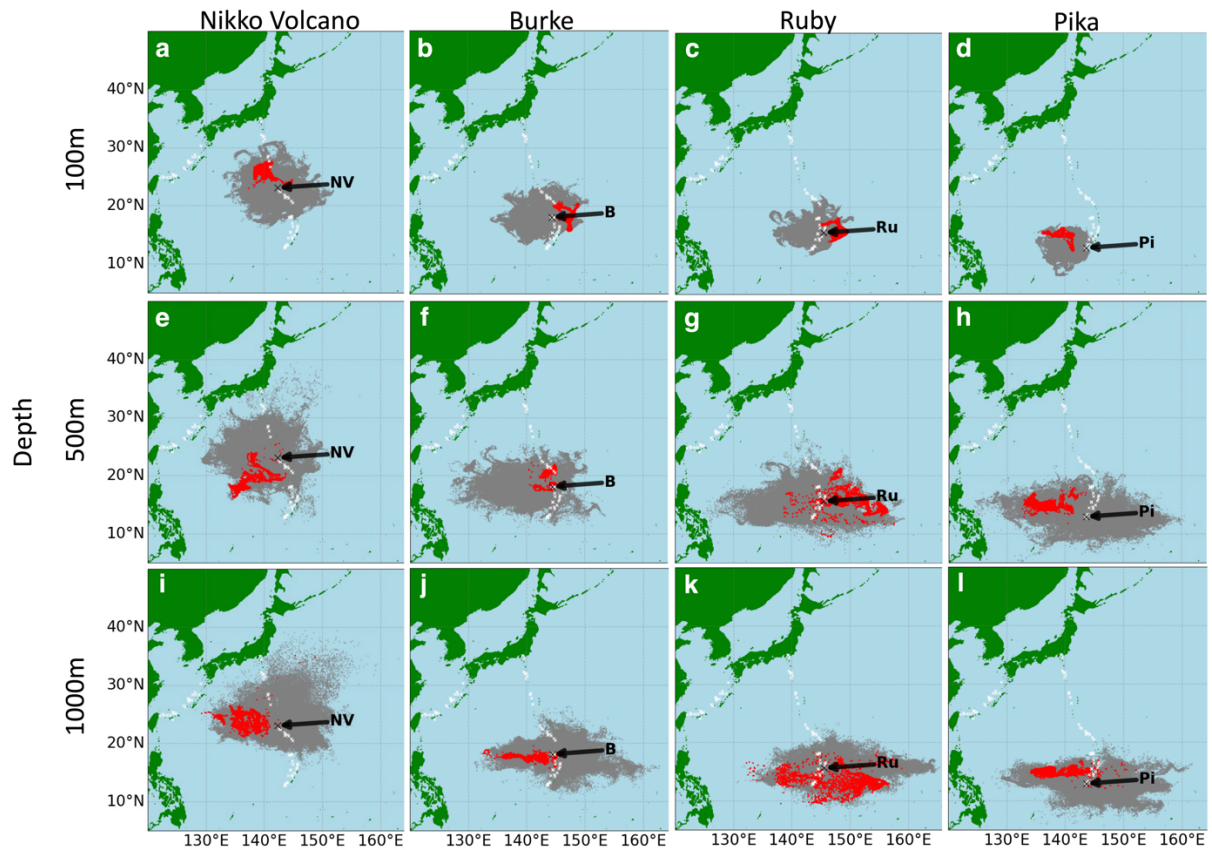


Figure 4: The distribution of Lagrangian particles dispersed aperiodically (grey) and during the single month that resulted in the greatest D-value (red) from the Mariana area. The source sites (black 'x') of the Lagrangian particles were selected as representative of the other sites (white 'x') within their vicinity.

For example, those particles released from sites in the Southern Mariana area show an East-West distribution while those in the Northern Mariana area have a more typical circular distribution around the source site (Figure 4). Across the Mariana area, constraint of particles within the vicinity of the source site decreases with depth (Figure 4) while the opposite is true for sites in the Okinawa Trough (Figure 3). The Fourier Transformation detected the presence of an annual frequency in D-values at several sites across all geographic areas. However, the strength of these signals did not stand apart from other non-annual frequencies in all cases apart from Nikko Volcano at 100m, Daiichi-Amami knoll at 500m, and South Sarigan Seamount at 1000m. There was no discernable pattern in this annual signal across dispersal depths or source site locations.

The dispersal characteristics (PLD, average temperature experienced and total distance travelled) of particles released during the month that resulted in the highest D-value, showed no clear or consistent difference with those particles released aperiodically (Figure 5). The monthly variability of PLD, temperature and distance of Lagrangian particles was highly dependent on the location of the source site with more adjacent sites showing a similar range (Figure 5). The average temperature experienced, and therefore PLD, of particles was strongly affected by the dispersal depth, much more so than the distance traveled. Lagrangian particles dispersing from all sites aperiodically had an average PLD of 38 at 100 m, 163 days at 500m, and 304 days at 1000m depth. The average temperature experienced decreased with depth as did the variability between sites. The mean total distance travelled

by particles increased with depth for most source sites apart from Hatoma Knoll and Sakai (Figure 5).

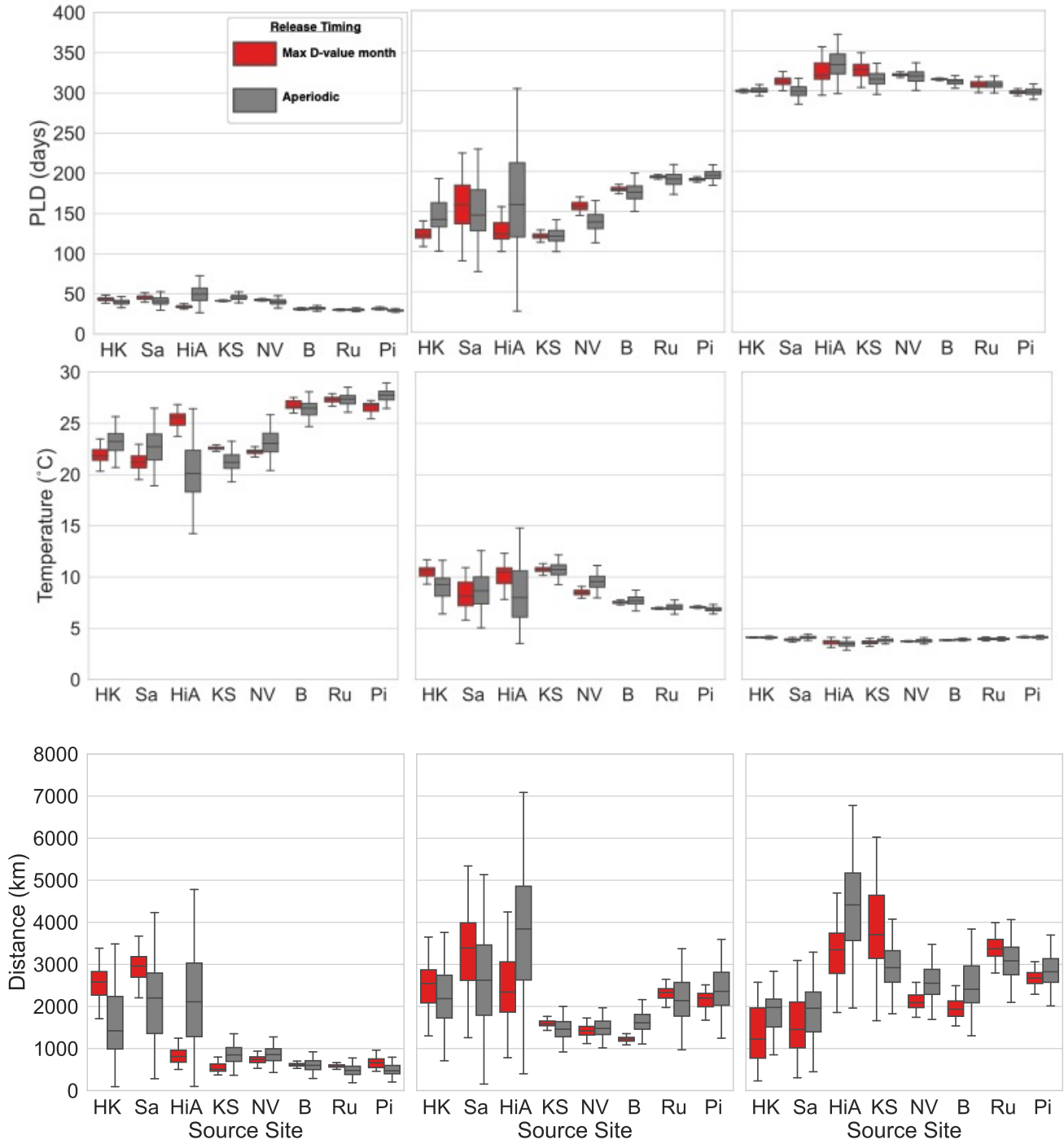


Figure 5: Dispersal characteristics of Lagrangian particles from the example sites shown in figures 3 and 4. There is no consistent difference between the characteristics of particles dispersed from the maximum D-value month (red) and those dispersed aperiodically (grey).

Discussion

Dispersal Characteristics

The variability of oceanographic conditions across the region may explain the varying effects of periodicity on dispersal distributions and characteristics among source sites (Figure 2 and 5). A dominant oceanographic feature of this region is the ‘Kuroshio’ western boundary current that travels North within the Okinawa Trough and then Northeast along the Eastern coast of Kyushu, Japan. Most particles released from sites in the Okinawa Trough at 100 or 500 meters are entrained into the Kuroshio, this is likely the reason for the generally low periodic-aperiodic distributional differences (Figure 2.a and 2.b) as the strong and consistent current constrains their distribution. In the 100 and 500 meter scenarios in the Okinawa Trough those months with the highest D values generally show more particles being carried away by the Kuroshio than in the aperiodic scenario, resulting in fewer particles remaining in the Okinawa Trough (Figure 3. a, b, e, f). In the 1000 meter scenarios however, high D-values are caused by a larger than usual proportion of particles leaving the Okinawa Trough through the Kerama Gap (Figure 3. i, j). Particles released from Hatoma Knoll, in the south the Okinawa Trough, are susceptible to being strongly retained in the south at depths of 1000m in certain months (Figure 3. i). The retention of particles in the southern region at 1000m is consistent with the observed distribution of NEMO floats deployed from Hatoma Knoll at the same depth by Mitarai *et al.* (2016). This retention can even occur at 100m where particles are more often entrained into the Kuroshio and exhibit long-distance dispersal (Figure 3. a). The influence of the Kuroshio can also be seen in the Northern Izu-Bonin sites (Figure 3. c, g, k), and in general has a tendency to decrease the difference in dispersal between periodically and aperiodically released particles at 100 and 500 meters. It is unexpected that particles dispersing from vent sites within the path of the Kuroshio experience less variation in dispersal distributions as it has been demonstrated that the Kuroshio exhibits both annual and intra-annual variation in its pathway (Yin *et al.*, 2014; Wang *et al.*, 2022). The absence of large meandering events from 1990 to 2004 (Qui and Chen, 2021) may result in particularly low or inconsistent inter-annual variation, but this variability is beyond the scope of this study on the effect of intra-annual variability in dispersal based on release periodicity. Our findings suggest that the role of the Kuroshio in driving long-distance transport of Lagrangian particles from Okinawa Trough to the Izu-Bonin Arc is consistent regardless of reproductive periodicity at least outside of large meandering years.

Much like the Kuroshio Current, the North Equatorial Current (NEC) appears to have an impact on the effect of periodicity on dispersal distributions. The southernmost sites in the Mariana region, which are most directly affected by the NEC, exhibit a relatively low degree of variability in larval dispersal distribution depending on the timing of release. This trend is observed across all depths tested, but is particularly pronounced in the 500m scenario, where there is a clear increase in the average D-value further North in the Mariana area, beyond the influence of the NEC (Figure 2. b). In the 100m scenario, the distribution of particles released aperiodically from southern Mariana sites is primarily to the west of the release site (Figure 4. c, d), in contrast to the larger easterly and westerly distribution observed at greater depths (Figure 4. g, h, k, i). Kendall and Poti (2014) previously demonstrated that the seasonality of the NEC contributes to the self-recruitment potential of surface drifters. This seasonality is driven by wind-stress (Qui and Lukas, 1996; Kim *et al.*,

2004), which may explain the greater degree of constraint observed for particles dispersing at shallower depths. The greater spatial distribution of particles travelling at 500 or 1000 meters depth in the Southern Mariana region is likely the result of less frequently reversing current regimes at that depth in combination with the extended planktonic larval duration at the low temperatures experienced. The relative lack of directionality for particles released from the southern Izu-Bonin and northern Mariana sites, as well as the lowed D-values in many cases, is indicative of the absence of prevailing currents in this area. However, the large range in D-values across release months indicates the importance of intra-annual variability on dispersal, even beyond the reach of seasonally fluctuating current systems. The variability beyond the Kuroshio and NEC, and indeed the large variability at all depths, supports the assertions of Adams *et al.* (2011) that surface seasonality can impact the transport of larvae from hydrothermal vents even at great depths.

Based on our results, it is unlikely that temperature variation is the main driver of variations in dispersal distributions, as the temperature range recorded across the extent of this study was very minimal at 1000m (Figure 5). However, it is difficult to separate the role of temperature and ocean currents on dispersal distances because of temperatures influence on PLD in this study. A fixed PLD approach would likely lead to a starker difference in dispersal distance and distribution with depth (Mitarai *et al.*, 2016) and effect the significance of periodicity by not incorporating seasonal temperature variations. Although the resultant PLD of individuals has a large range within this study, all the PLDs of deep-sea species (bar one outlier) collected by Hilario *et al.* (2015) fall within this range.

Implications for Connectivity

The stochasticity of ocean circulation at depths as great as 1000m, as observed in this study and by drifting NEMO floats at this depth (Mitarai *et al.*, 2016), results in no annual consistency of dispersal over multi-year scales, as is also the case in surface waters (Siegel *et al.*, 2008). It is unlikely that the addition of more years or even decades of simulations will result in lower inter-annual variability due to the effects of Kuroshio large meandering events or ENSO (Enfield, 2001). We therefore conclude that at time-scales pertinent to conservation objectives for hydrothermal vents (years – decades), it is not possible to predict the probability of dispersal among hydrothermal vents without sufficient information on species-specific reproductive timing or synchrony. Population genetics studies of vent-associated species in the region, when combined with the results of this study, may provide insights into the role of larval release timing in observed connectivity. For example, Xu *et al.* (2018) investigated the genetic connectivity of *Bathymodiolus platifrons* and inferred that the South Okinawa Trough sites of Yonaguni Knoll (YK) and Hatoma Knoll (HK) were source populations for the Mid-Okinawa Trough. Dispersal from the South to the mid Okinawa Trough is consistent across depths but is less likely during months that result in higher entrainment into the Kuroshio at 100m and 500m or in cases where southern retention is strong at 1000m depth. It is certainly possible that this species exhibits periodic spawning as there is evidence for it in species of the same genus (Dixon *et al.*, 2006) as well as other chemosymbiotic mussels (reviewed by Laming *et al.* (2018)) which carry out dispersal in the upper layers of the water column (Arellano *et al.*, 2014). If this species has adapted a periodic reproduction strategy, our findings suggest that this would have minimal impact on its dispersal success as their larvae would consistently be transported north by the Kuroshio if dispersing in the upper layers of the water column, with relatively low intra-annual differences (Figure 2) and no inter-annual consistency. Even in the month that results in the

highest deviation from this northern dispersal (low entrainment into the Kuroshio) the particles are mostly lost to the south beyond the vicinity of other suitable habitats or self-recruitment (Figure 3 a). Similarly, the absence of periodicity in the brooding phase of *A. longirostris* from the Okinawa through (Methou et al. in review), in contrast to observations of periodicity in congeneric species from the Atlantic (Copley and Young, 2006; Methou et al., 2022), could be related to the relatively minimal effect of periodicity on dispersal characteristics in this area. It should be noted that no dispersal scenarios tested were able to explain the observations of genetic connectivity from Sagami Bay and the South Okinawa trough to the South China Sea for *B. platifrons* (Xu et al., 2018) or *A. longirostris* (Li, 2015; Yahagi et al., 2015). However, certain release months showed a strong and consistent (within the month) Westward directionality in dispersal from the Northern Izu-Bonin area (Figure 3 c and k) and supports the possibility of dispersal in this direction as evidenced from genetic observations of *Gandalfus yunohana* populations (Watanabe et al., 2020). In this way, observations of intra-annual variability may reveal dispersal processes that can resolve inconsistencies between the directionality of connectivity among hydrothermal vent populations as observed from genetic data and simulations of aperiodic dispersal (e.g. Breusing et al. (2021)).

Conservation

Our results have revealed the effects of release timing on dispersal from hydrothermal vents, which are annually inconsistent and principally constrained by prevailing oceanographic currents or topographic features. Although informed by in-situ and ex-situ observations of vent-associated species, our simulations do not represent a single species or taxonomic group. To accurately represent the dispersal of any hydrothermal vent species through simulations, more research is required into the life history and dispersal behaviour of species, particularly their reproductive periodicity and temperature dependent PLD. Any consequences of periodic reproduction in terms of dispersal potential would be highly dependent on the distribution of the species in question as well as the distribution of suitable habitat. For species that compete for the same local niche space and exhibit similar larval behaviour, having differing dispersal periodicity may reduce the chance of regional exclusion through competition and allow them to coexist in the larger metacommunity (Leibold et al., 2004; Mullineaux et al., 2018; Chase et al., 2020). In the Southern Mariana Trough/Arc, larvae are entrained by currents that are highly variable but predominantly disperse them away from other vent sites (Figure 4). In such areas, periodically dispersing species may be particularly vulnerable to low recruitment and more strongly impacted by the effects global climate change has on the seasonality of ocean currents and temperatures in the Pacific (Fukasawa et al., 2004). Due to stochastic dispersal on multi-year timescales, predictions of regional impacts from proposed hydrothermal vent mining in the region (Okamoto et al., 2019) may not be generalizable across species with different or unknown reproductive periodicity. Therefore, it is recommended to apply the Precautionary Principle (Principle 15, Declaration 1992) and assume the worst-case scenario regarding mining's disruption of regional dispersal and resultant connectivity.

Conclusion

The stochasticity of dispersal at intra-annual scales and the importance of local current regimes highlights the value of high-resolution dispersal simulations to the study of connectivity at scales of relevance to conservation. The periodicity of reproduction does not represent a clear or consistent advantage to vent-associated species in terms of self-recruitment or large-scale connectivity. To resolve species-specific population connectivity, it is therefore vital to determine the species reproductive timing on top of larval behavioural characteristics such as dispersal depth. The methods and behavioural parameters used in these dispersal simulations are replicated in chapter 3 and expanded upon to create a dispersal network. This dispersal network forms the foundation of the final chapter's exploration of metacommunity dynamics and their role in structuring diversity and patterns of connectivity.

Chapter 3

Simulated Metacommunities Reveal the Interacting Role of Dispersal and Environmental Filtering on Hydrothermal Vent Diversity

Introduction

This final chapter combines the results of chapters 1 and 2 into a model of metacommunity dynamics. This chapter is not currently submitted to and peer-reviewed or pre-print journals. This chapter is an extended summary of the relationship between community composition (chapter 1) and dispersal processes (chapter 2).

Connectivity in the form of inter- and intra-specific interactions among distant habitat patches is a crucial driver of biodiversity and community stability at regional scales (Crooks and Sanjayan, 2006). Genetic data can be used as a measure of a species' ability to move among habitat patches, defined as 'functional connectivity' (Hilty *et al.*, 2020). With sufficient genetic data, functional connectivity among isolated populations can be identified along with its strength and directionality (reviewed by Lowe and Allendorf (2010)). However, in marine systems such data is rarely available at the regional or community scale upon which conservation objectives should be based (Balbar and Metaxes, 2019). To infer connectivity at such a scale, it is important to understand and model the processes underlying connectivity, namely, the movement of individuals among habitat patches (Hilty *et al.*, 2019). In the marine environment, biophysical models can simulate how ocean currents influence the dispersal of individuals (reviewed by Swearer *et al.*, 2019). Biophysical models, and alternative methods to predict the movement of individuals among habitat patches, can be considered models of 'structural connectivity' (*censu* Hilty *et al.*, 2020). Simulating 'structural connectivity' is of particular value in remote marine ecosystems such as hydrothermal vents, where observations of dispersal and evidence of functional connectivity are severely limited by practical factors (Mullineaux *et al.*, 2018). Such dispersal simulations were carried out for hydrothermal vents in the Northwest Pacific in previous studies (Mitarai *et al.*, 2016; Chapter 2/Brunner *et al.*, *in review*) but these previous studies did not explore dispersal's role in shaping functional connectivity. Breusing *et al.* (2021) combined simulations of dispersal and genetic connectivity data among hydrothermal vents and found discrepancies through qualitative comparisons. Across ecosystems, previous studies have either compared structural and functional connectivity results qualitatively or correlatively, neither of which are necessarily appropriate if the temporal and spatial scales used to generate the structural and functional connectivity estimates are not comparable (Bode *et al.*, 2019). However, previous studies have used simulations of genetic connectivity informed by biophysical models. Comparing such simulated connectivity with equivalent observational data can confront assumptions of scale and quantitatively test dispersal's role in structuring connectivity (White *et al.*, 2010; Foster *et al.*, 2012; Legrand *et al.*, 2022).

Simulations of dispersal alone are not able to confirm connectivity among habitat patches because the ability of individuals to move between habitat patches is only one of the multiple sequential steps required for species to persist a given location (Kritzer and Sale, 2004). Dispersal to a habitat patch is considered a 'regional process' which is required for connectivity, but for an individual to persist they must also overcome the 'local processes' including biotic and abiotic interactions that may inhibit or facilitate colonization and persistence (reviewed by Pineda *et al.* (2007)). Here, the habitat patches in question are the hydrothermal vent sites of the Northwest Pacific, a system with evidence of species persistence, in the form of distribution data (Chapter 1/Brunner *et al.*, 2022). To infer connectivity patterns, by combining simulations of dispersal (Chapter 2) with observations of shared species (community composition) (Chapter 1), we need to parameterise the other processes that determine community composition.

The study of community composition across multiple habitat patches is an integral part of the metacommunity concept (Leibold *et al.*, 2004) and island biogeography (MacArthur and Wilson (1967)). In these overlapping fields of study, the response variable of focus is most often the abundance or presence of species across a landscape (*i.e.* their distribution). Local processes related to abiotic conditions (environmental filtering) and biotic interactions (trophic, competitive, facilitative, *etc.*), as well as regional processes (dispersal) play key roles in the study of biogeographic, metacommunity, and connectivity patterns (Ricklefs, 2009; Vellend 2010; Pineda *et al.* 2007). The defining difference between these fields of study is the role that time plays as a driving process. In biogeography, time affects patterns in abundance through vicariance, which refers to the role of historical events - often over evolutionary or geological timescales - in disconnecting communities (Cunningham and Collins, 1998). In metacommunity ecology, the temporal process of interest is most often ecological drift, which refers to stochastic processes that result in changes to community composition over generational timescales (Vellend, 2010; Chase *et al.*, 2020). Connectivity, specifically population connectivity, does not explicitly consider time as a driving process in terms of vicariance or ecological drift because connectivity can occur within a single generation (Pineda *et al.*, 2007).

In this study we apply the metacommunity perspective to observations of species distributions (Chapter 1/Brunner *et al.*, 2022) and simulations of dispersal (Chapter 2/ Brunner *et al. in review*) among hydrothermal vents in the Northwest Pacific. These vent sites are considered part of a distinct 'bioregion' (Bachraty *et al.*, 2009) that receives little or no contemporary input from other vent sites via dispersal (Mitarai *et al.*, 2016). The modular spatial arrangement and large range of local environmental parameters of these vent sites, compared to those of other bioregions, make them a natural laboratory to investigate the roles that dispersal and local environmental filtering play in structuring the metacommunity (Mullineaux *et al.*, 2018). The relative importance of local and regional drivers in metacommunity composition can be categorised into one of the non-mutually exclusive metacommunity archetypes (Leibold *et al.*, 2004). For example, the relative importance of dispersal and local environmental filtering can shift metacommunity dynamics from a 'species-sorting' archetype, where species are mostly found in habitat patches to which they are optimally adapted, to 'mass-effect' archetype where strong dispersal allows species to inhabit habitat patches to which they are sub-optimally adapted (Mouquet and Loreau 2002; 2003; Thompson and Gonzalez, 2016; Leibold *et al.*, 2017). Understanding the processes that drive diversity from such a metacommunity perspective allows for a holistic approach to answering questions pertinent to conservation (Chase *et al.*, 2020). The recent expansion of deep-sea mining as an industry means that regional,

metacommunity-scale studies of hydrothermal vents are of increasing importance (Mullineaux *et al.*, 2018). Nowhere is such a study more urgent than within the Northwest Pacific, where the commercial-scale mining of hydrothermal vents has happened for the first time in the world (Okamoto *et al.*, 2019).

Using this natural laboratory system, we build upon spatially implicit (Mouquet and Loreau, 2002; 2003) and explicit (Suzuki and Economo, 2021) metacommunity models by creating an empirical metacommunity model. We refer to this metacommunity model as empirical because it uses estimates of dispersal distance and local environmental conditions among habitat patches based on empirical observations. Our application of this empirical metacommunity model has three objectives:

1. To combine and compare the first two chapters of this thesis to investigate the relationship between structural connectivity (dispersal) and functional connectivity (species distributions).
2. To determine the interacting effects of metacommunity processes (model parameters) that best replicate the observed diversity structures of the Northwest Pacific and explore remaining discrepancies.
3. To examine the applicability of a spatially explicit metacommunity model to the hydrothermal vents of the Northwest Pacific by comparing the results to those of Suzuki and Economo (2021).

Methods

Study Sites

The hydrothermal vents sites used in this study are those within the Okinawa, Mariana and Izu-Bonin areas of tectonic activity, contained within the Northwest Pacific. The location and associated metadata of each site was obtained from InterRidge ver. 3. 4 (Beaulieu and Szafranski, 2020) and supplemented with additional sites and metadata from several sources (Tokuda *et al.*, 2006; Feng *et al.*, 2018; Xu *et al.*, 2018). The full list of sites can be found in the appendices (A1). A subset of 36 sites were the primary focus of this Chapter, since species assemblage data are available for these sites (Chapter 1/Brunner *et al.*, 2022).

Spatially Explicit Metacommunity Model

We generated simulated communities, using the metacommunity model of Suzuki and Economo (2021) coded in Julia (Bezanson *et al.* 2017), which we refer to as the ‘Suzuki Simulation’ hereafter. The Suzuki simulation is based on that of Mouquet and Loreau (2002; 2003), which was originally designed to focus upon marine sessile species that disperse passively, such species at hydrothermal vents are the focus of this thesis. This lottery model (Chesson, 1985; Muko and Iwasa, 2000) includes discrete timesteps where simulated species can disperse between connected habitat patches in a spatially explicit network. In this model, a species’ relative abundance (relative to other species at the same site) is a response to the distance from adjacent occupied sites as well as the suitability of the site’s environment. Dispersal ability is constant across species, but the suitability of a site’s environment is defined by their ‘fitness’. The fitness of each species in the simulation is defined as a Gaussian function of environmental condition and species trait. When the variability of abundance between sequential timesteps reduces below a threshold (*i.e.*, a “stationary condition”), the simulation stops. Suzuki and Economo (2021) expanded on the Mouquet

and Loreau (2002; 2003) model to include structurally complex and spatially explicit networks. Here, we further extend this model to incorporate a ‘real-world’ empirical network. In this empirical network, hydrothermal vent sites of the Northwest Pacific represent habitat patches with explicit local environmental conditions and pairwise distances. In our simulation, the ‘distance’ among vent sites is determined by the probability of dispersal between them. Each of the 100 species we simulated has the same dispersal ability but a different fitness relative to local environmental conditions.

Empirical/Dispersal Network Formation

We calculated the pairwise dispersal probability between all vent sites using a generalised simulation of planktonic larval dispersal within an ocean general circulation model using PARCELS version 2.3.1 (Delandmeter and Sebillie, 2019) in Python version 3.10.2 (<http://www.python.org>) following the methods outlined in Chapter 2 (Brunner *et al.*, *in review*) and appendix (A4). To ensure the inclusion of all 36 vent sites within the empirical metacommunity, we set dispersal depth to 400m, a reasonable dispersal depth for deep-sea species (Young *et al.*, 2012; Mitarai *et al.*, 2016; Breusing *et al.*, 2021; McVeigh *et al.*, 2017). The pairwise probability of dispersal was based on the number of individuals from a source site that ended their dispersal within the same ~8km grid cell as a target site. The number of individuals dispersing from each source to each target site was divided by the total number of particles released from the source (146,000) to give a probability value. We then formatted these pairwise dispersal probabilities into a network using ‘NetworkX’ package (Hagberg *et al.*, 2008) in Python and applied a threshold that removed all incoming edges that represented less than 1% of the node’s total in-degree (Myers *et al.*, 1991; Cecino and Trembl, 2021). The primary focus of this study is on the dispersal among the same 36 vent sites from chapter 1/ Brunner *et al.* (2022). However, we created a second dispersal network using the same methods but including an additional 31 vent sites to see if the number of habitat patches influenced the outputs of the Suzuki Simulation. We compared the structure of the 36-site and 67-site networks using two structural statistics: diameter and characteristic path length. To calculate these structural statistics, we first identified the ‘most reliable path’ among all pairs of nodes as the series of edges between the pair that has the maximum sum of probabilities (Hock and Mumby, 2015). We calculated the diameter of the network as the minimum probability value of all the, most reliable paths, analogous to the maximum distance between nodes (Van Langevelde *et al.*, 2008; Rayfield *et al.*, 2011). Characteristic path length was the mean of the same set of most reliable paths (Jordán *et al.*, 2007; Rayfield *et al.*, 2011). Within the Suzuki Simulation, we adjusted the dispersal probabilities of the edges in the network by multiplying all pairwise probabilities by the parameter d , with a range of 0.001 to 100. d therefore represents dispersal strength, which we used to uniformly increase or decrease pairwise dispersal probabilities among nodes and observe the resultant effects on simulated metacommunities.

Abiotic Responses

The variance in the Gaussian distribution of each species’ fitness is uniform but was adjustable and represented by parameter h , which we varied from 0.001 to 1000. Increasing h (the Gaussian distribution of the species fitness) in turn decreases the local selection strength, therefore h is the inverse local selection strength. How the fitness of a species overlaps with the local environmental condition of the vent site dictates the proportion of dispersers that can settle, as well as the reproductive output of those settlers from that vent site. We determined the local environmental conditions of each vent site using a Gower

distance (Gower, 1971) matrix based on each vent site's depth and tectonic setting. Depth and tectonic setting are the only consistently available local environmental parameters for all vent sites in this region from the InterRidge database 4 (Beaulieu and Szafranski, 2020) and are good explanatory variables for the variance of species assemblages (Chapter 1/Brunner *et al.*, 2022). Following the advice of Legendre and Legendre (2012), we selected Gower distance to calculate environmental dissimilarity and then decomposed it into a single variable using a principal coordinate analysis (PCoA), which explained 92% of the Gower distance in its first component. We then normalized this first component of the PCoA to a value between 0 and 1, with 0 representing the deepest vent site with a back-arc tectonic setting and 1 representing the shallowest vent site with a volcanic arc tectonic setting. The numerical distance of vent sites on this axis represents their environmental dissimilarity within the Suzuki Simulation. To explore the role of environmental spatial autocorrelation in structuring the metacommunity, we carried out a second treatment of the Suzuki Simulation with the environmental conditions randomly shuffled among sites (hereafter referred to as the randomised treatment). For the empirical and randomised environmental treatments, we iterated the simulation with 8 variants of h (0.001, 0.01, 0.05, 0.1, 0.5, 1, 5, 10, 100, 500, 1000) and 10 variants of d (0.001, 0.01, 0.1, 0.5, 'ori' (1), 1.5, 2, 10, 100) resulting in a total of 110 iterations for each treatment. The output of interest from each iteration of each treatment was an independent site-by-species relative abundance matrix.

Multivariate Analyses

We compared the simulated metacommunity abundance output from each iteration of the Suzuki simulation with one another as well as the empirical metacommunity data, which was in the form of a presence-absence matrix (Chapter 1/Brunner *et al.*, 2022). We summarized the global properties as well as the internal structures of the metacommunities (*censu* Leibold *et al.*, 2022) in the form of global diversity and site-by-site dissimilarity respectively. For simulated metacommunities, we calculated the Bray-Curtis dissimilarity (Bray and Curtis, 1957) between sites. For the empirical metacommunity, we used the Sørensen's coefficient (Sorensen, 1948) to calculate between-site dissimilarity because of the binary nature of the data. We then compared the resultant pairwise dissimilarity matrices of each simulation treatment and iteration to that of the empirical dissimilarity matrix using a mantel test to return an 'r' value based on Spearman's rank correlation. We applied the statistics used in the above multivariate analyses using the 'vegan' package (Oksanen *et al.*, 2019) and visualized the metacommunities as a species assemblage networks using the 'igraph' package (Csardi and Nepusz, 2006) in R (R Core Team, 2021). We used a multiplicative partition to calculate the alpha, beta, and gamma diversity (Jost 2006; 2007; Jost *et al.*, 2010) from the Gini-Simpson calculated effective number of species (Hill, 1973). Therefore, gamma represents the effective number of species within the entire metacommunity, alpha represents the average effective number of species within each site in the metacommunity and beta is gamma divided by alpha.

Biotic Interactions

To explore potential biotic interactions in the empirical metacommunity we tested whether species co-occurrences occurred significantly more or less frequently than would be expected by chance using a probabilistic model (Veech, 2013) in the R package 'cooccur' (Griffith *et al.*, 2016). We carried out the same analysis on a simulated metacommunity as a control for comparison with the empirical results. Any significant co-occurrence within the simulated metacommunity could not be due to biotic interactions as this process is not

parameterized in the Suzuki Simulation. We then formatted the significant co-occurrences in the empirical metacommunity as edges in a network weighted by the p-value (inversed and re-scaled to values between 0 and 1 using min-max normalization) to represent the strength of co-occurrence. The structure of this weighted co-occurrence network was investigated using the ‘igraph’ and ‘rnetcarto’ (Csardi and Nepusz, 2006; Doucier and Stouffer, 2015) packages in R. We clustered the nodes in a way that would minimize between and maximize within cluster connections (maximize the network modularity). We used a simulated annealing approach to iteratively cluster nodes until we found the arrangement that maximized modularity with no a-priori assumptions of the number or size of clusters (Guimera and Amaral, 2005a; 2005b). We quantitatively assessed the relative role of each species in structuring this co-occurrence network by comparing their number of connections within and without their cluster, which defines their ‘cartographic’ role (Guimera and Amaral, 2005a, 2005b; Borthagaray *et al.*, 2014). We also assessed the centrality of species in terms of co-occurrence based on their eigencentrality (Bonacich, 1987).

Results

Dispersal

Both the 36-site and 67-site dispersal simulations returned networks where every vent site node was at least indirectly connected by weighted, directional edges representing dispersal probability (Figure 1). Both networks had a very similar structure despite their different number of nodes. The 36-site network had a characteristic path length of 26.83 and a diameter of 6.63 while the 67-site network had a characteristic path length of 27.89 and a diameter of 6.63. The results of the 67-site simulations showed similar trends to the 36-site simulations in terms of internal and global metacommunity structures across iterations. For these reasons we primarily focus upon the results of the 36-site simulations.

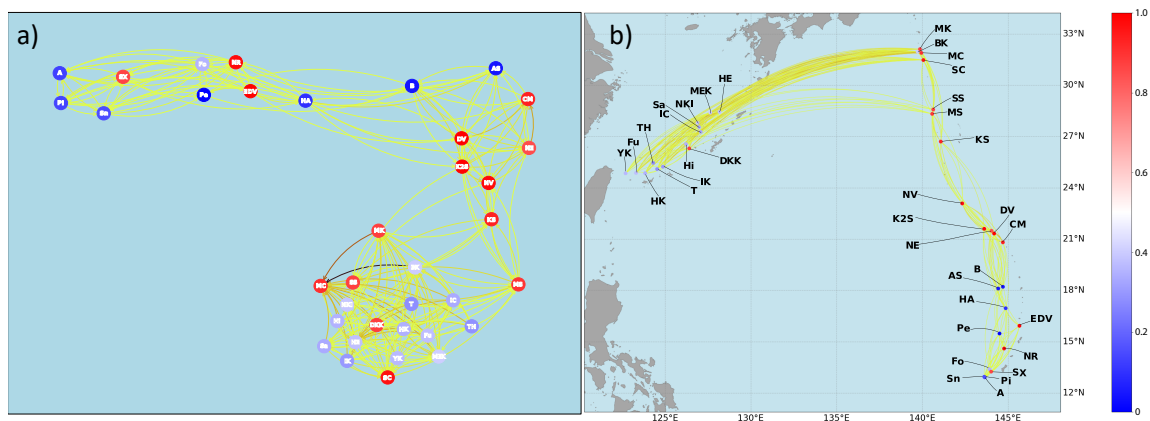


Figure 1: Dispersal probability networks among 36 vent sites in the Northwest Pacific. The darkness of the edges represents the probability of pairwise dispersal while the colour of the nodes represents the position of the environment in terms of the normalised principal component. Nodes are positioned based on the strength of their connections using a Fruchterman-Reingold force-directed algorithm (a) or based on their geographical location (c).

In terms of the pairwise dissimilarity between vent site assemblages, simulated metacommunities generally correlated more strongly with the empirical metacommunity with higher dispersal (Figure 2).

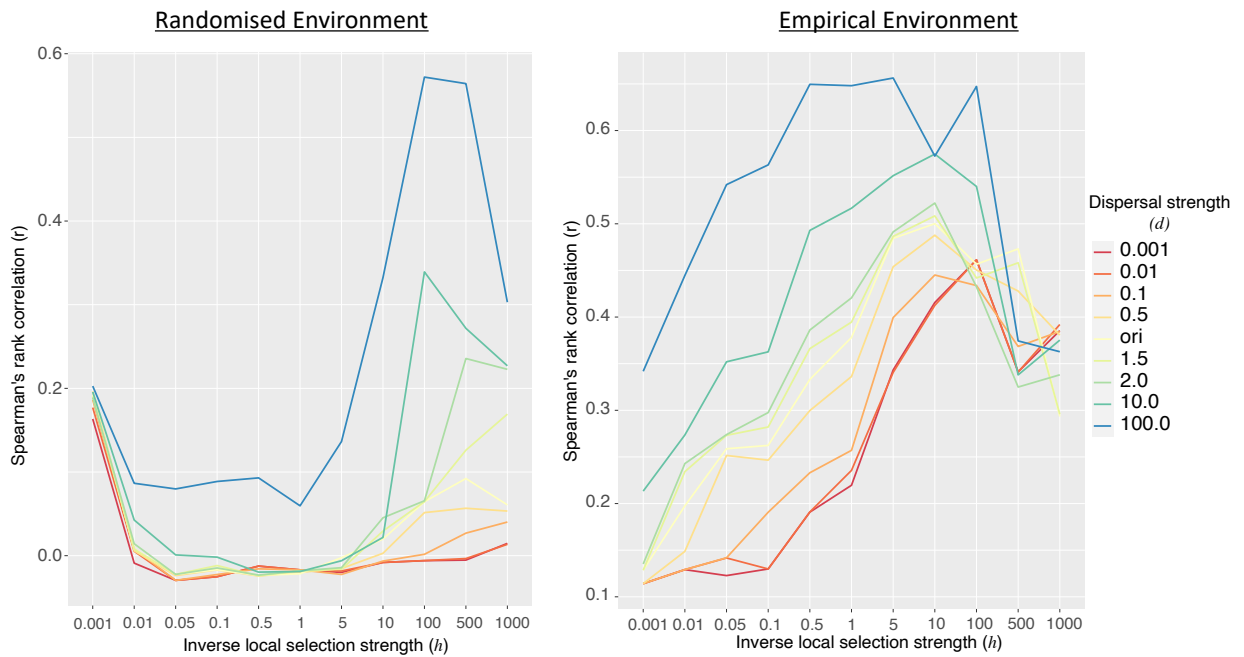


Figure 2: Spearman Rank correlation coefficients (r) between the empirical site dissimilarity (Sorensen Coefficient) and the simulated site dissimilarity (Bray-Curtis) across different treatments of dispersal strength (d) and inverse local selection strength (h).

The increase in correlation coefficient with increased dispersal was particularly evident when the pairwise dispersal among sites was multiplied by 100 ($d100$). This trend was evident in the randomised treatment also, but the increased correlation with the $d100$ iteration was markedly higher. The relationship between dispersal and diversity - partitioned into alpha, beta, and gamma - at the final step of the Suzuki Simulation was highly variable depending on the inverse local selection strength. However, there were some general trends across treatments, such as very little or no change in alpha, while gamma diversity decreased as dispersal strength increased. Due to the changes in alpha being orders of magnitude lower than gamma, beta diversity decreased comparably with dispersal (Figure 3).

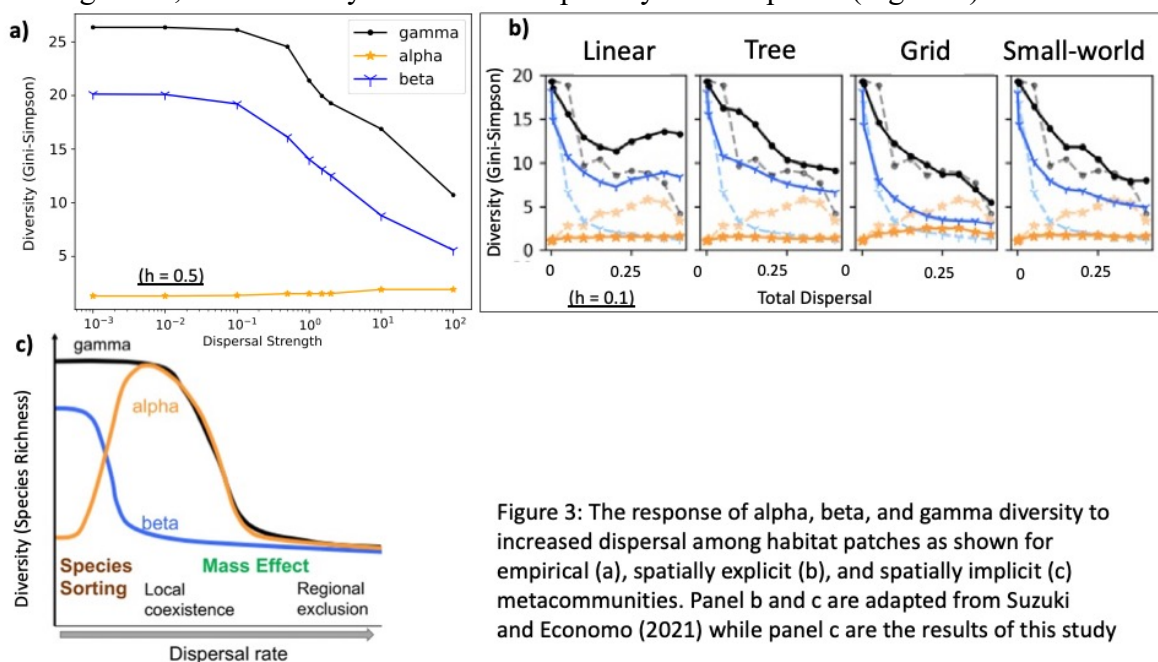


Figure 3: The response of alpha, beta, and gamma diversity to increased dispersal among habitat patches as shown for empirical (a), spatially explicit (b), and spatially implicit (c) metacommunities. Panel b and c are adapted from Suzuki and Economo (2021) while panel c are the results of this study

Abiotic Responses

The correlation between simulated and empirical site-by-site dissimilarity matrices (r) followed different trends with increasing h values depending on whether the environmental conditions were randomised or not (Figure 2). For simulations with empirical environmental conditions, r steadily increased from a minimum at low h , peaking at mid-high h (0.5 – 100 depending on d), and then decreased again at the maximum h . In the randomised treatments, r had a peak at the lowest h of 0.001, followed by a trough at intermediate h values of 0.1 before peaking again at high h (10 – 1000 depending on d). Under every combination of h and d , the metacommunity with the randomized environmental conditions had a lower r . We selected the simulated metacommunity with $h = 0.05$ and $d = 100$ for more in-depth comparisons with the empirical metacommunity based on its very high correlation coefficient ($r = 0.649$) as well as qualitative similarities in their species assemblage networks (Figure 4).

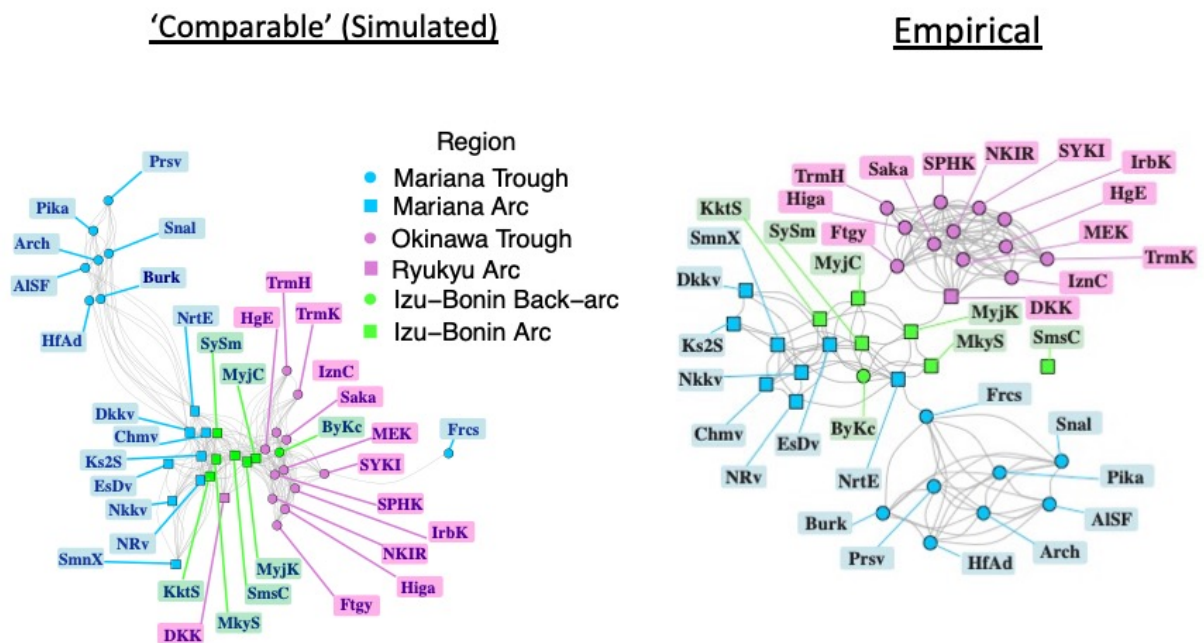


Figure 4: Species assemblage networks, where node (vent site) are linked by weighted edges (pairwise similarity) based on shared species. The nodes positions are based on Fruchterman-Reingold force-directed algorithm and so represent their relative similarity to on another.

Regardless of whether the environment was randomised, h had a strong and consistent effect on diversity. The number of species persisting at the end of the simulation (species richness) generally shows a linear increase with h and was consistent across treatments (Figure 5).

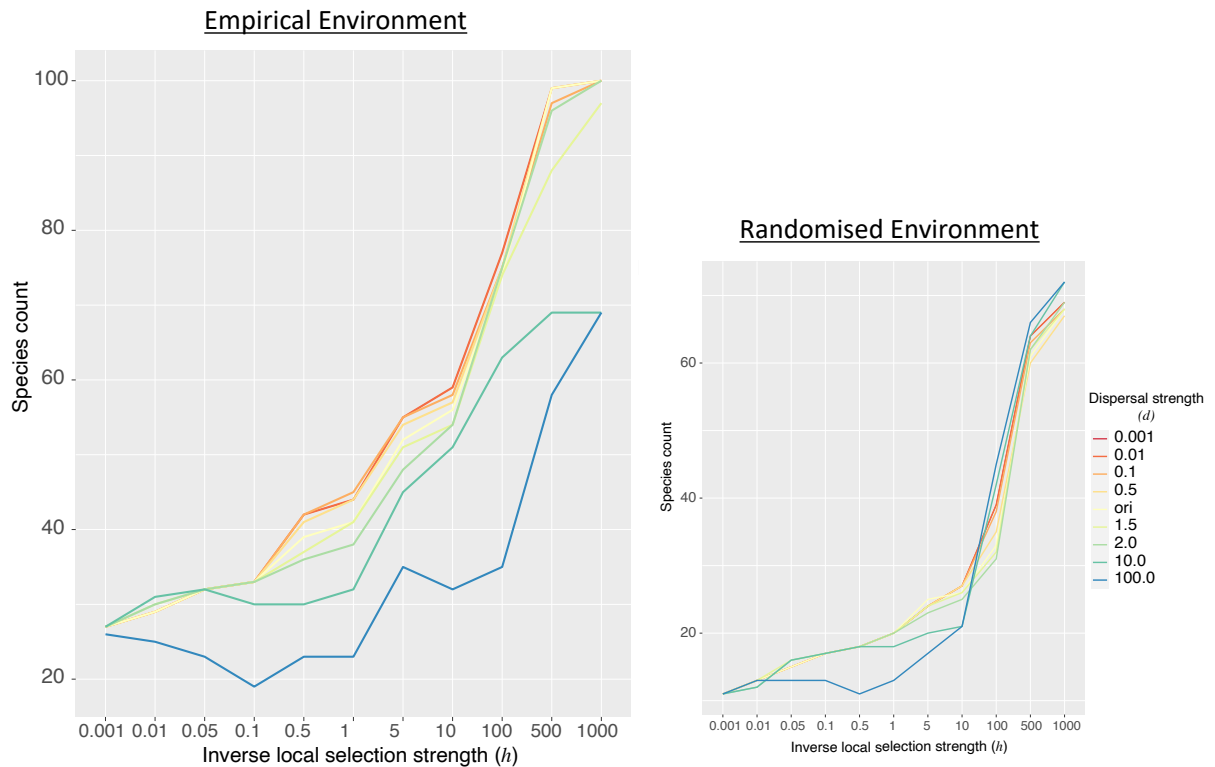


Figure 5: Species richness (count) at the end of the simulations near-uniformly increases with the inverse selection strength (h) across treatments of dispersal strength (d)

The species richness of simulated metacommunities was consistently higher in the empirical environment treatment. Alpha diversity was consistently low until $h > 1$, when it underwent an exponential increase in most iterations of dispersal strength. Beta diversity decreased with the strength of local selection and began to level out at very low local selection strengths ($\sim h100$). Gamma diversity generally increases with decreasing strength of local selection. This increase in gamma diversity is not very strong or consistent at the highest dispersal strengths and is more exponential the weaker the dispersal strength (Figure 6).

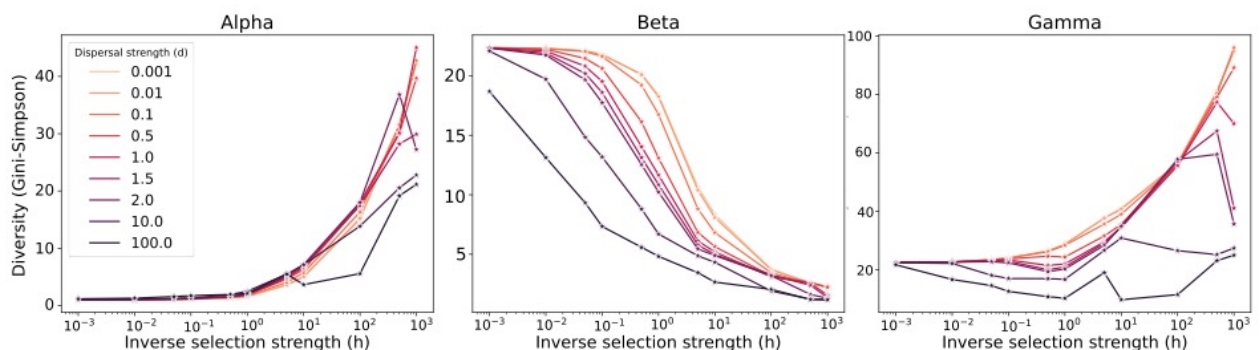


Figure 6: The response of alpha, beta, and gamma diversity to inverse selection strength is consistent across treatments of differing dispersal strength (individual line) although the 100 d treatment (dark line) does show some deviation, particularly in terms of alpha diversity at high h .

The comparable metacommunity, showed the expected trend of a correlated decrease of beta and gamma diversity, which both reached a minimum at very high levels of dispersal (Figure 7c). The randomised treatment as well as the treatment with a 67-site network show the same

trend. This trend is very similar to those found in the original simulations within spatially explicit metacommunity networks by Suzuki and Economo (2021) (Figure 7b).

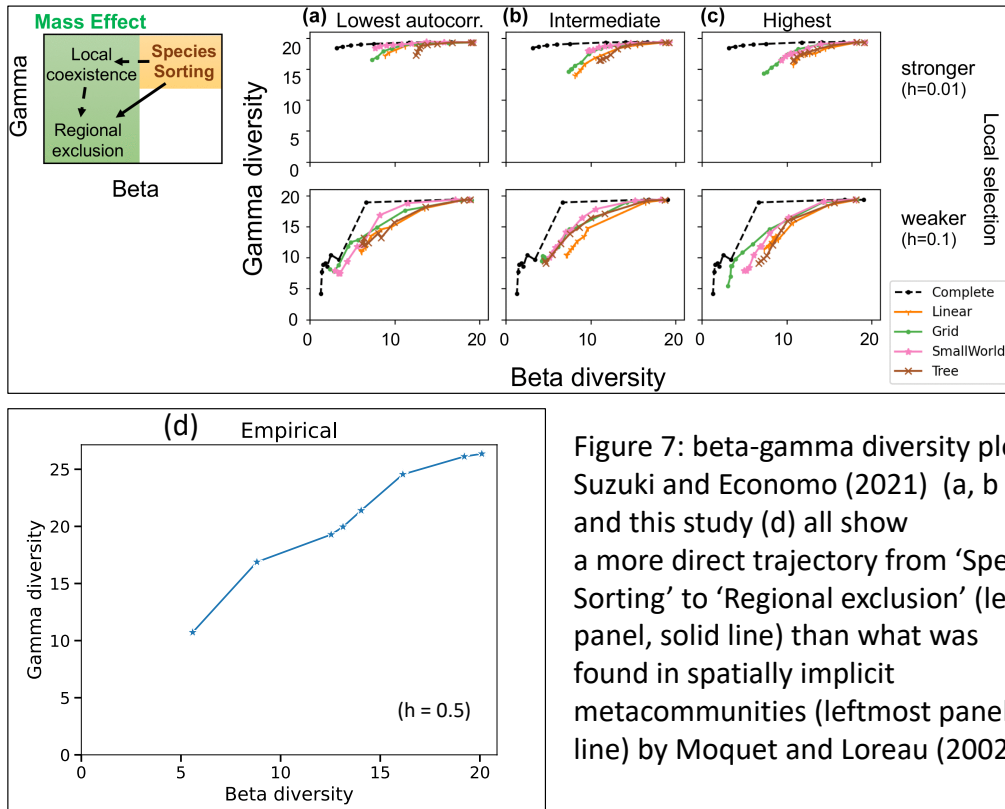


Figure 7: beta-gamma diversity plots from Suzuki and Economo (2021) (a, b and c) and this study (d) all show a more direct trajectory from ‘Species Sorting’ to ‘Regional exclusion’ (leftmost panel, solid line) than what was found in spatially implicit metacommunities (leftmost panel, dashed line) by Moquet and Loreau (2002)

Biotic interactions

Significant positive and negative co-occurrences were detected based on the distribution of species in the empirical metacommunity (Figure 8). The comparable metacommunity was checked for co-occurrence patterns and showed significant, negative and positive co-occurrence among species (though biological interactions do not occur in these simulated metacommunities).

The empirical metacommunity’s co-occurrence network was separated into four distinct modules within which significant positive interactions between species were stronger and more frequent than without. Approximately half of the species in this co-occurrence network had very low eigencentality while a small number had very high eigencentality, representing the relative number of species with which they significantly co-occur and the strength of those co-occurrences. All species were found to be peripheral in terms of their cartographic role in the co-occurrence network.

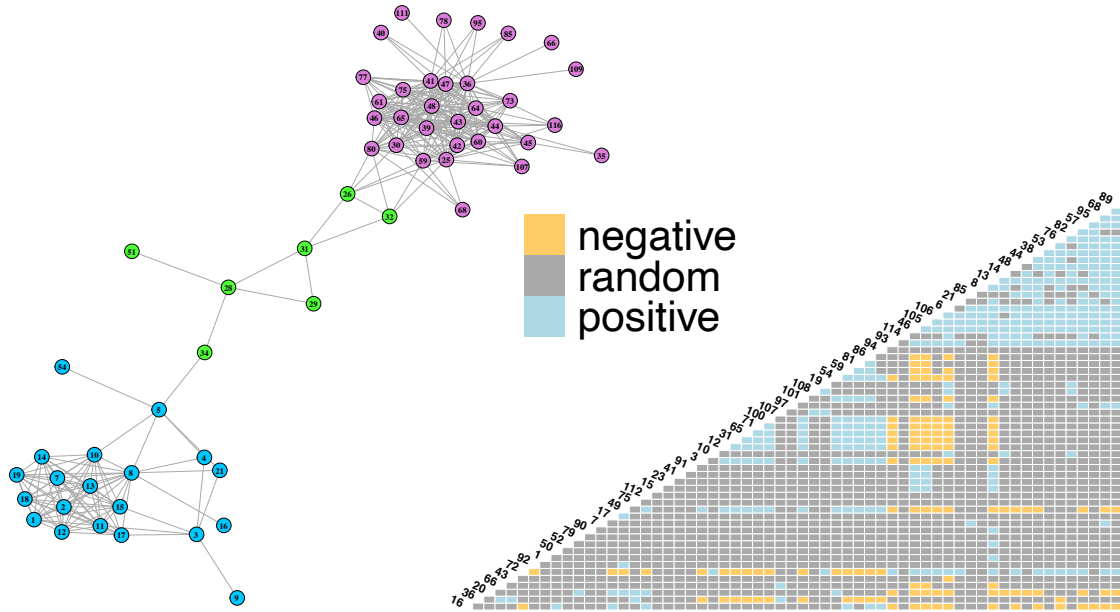


Figure 8: Co-occurrence patterns from empirical data (Brunner et al., 2022) show multiple instances of significantly negative and positive associations between species compared to random (right panel). The positive associations cluster (left panel) into three distinct groups of species that closely align with the three distinct sub-regions: Okinawa Trough (purple), Izu-Bonin-Mariana Arc (green), and Mariana Trough (blue) detected by Brunner et al. (2022). Key for species names can be found in appendices (A3).

Discussion

The Applicability of the Suzuki Simulation to Empirical data

Using empirical data of the local environmental conditions and the spatial structure of hydrothermal vent habitat patches, we were able to simulate a metacommunity comparable to the empirical metacommunity (Figure 4). Calculating the correlation coefficients was helpful for determining trends across iterations of dispersal and local selection strength (Figure 2). By visualizing the simulated metacommunities as species assemblage networks we were able to make more detailed qualitative comparisons. As with non-parametric multi-dimensional scaling (Kruskal, 1964) the position of vent sites in the species assemblage networks represent their relative similarity to one another (Figure 4). The defining attribute of the simulated metacommunity that we consider comparable to the empirical metacommunity that distinguished it from others is the low levels of similarity (shared species) between sites of the Okinawa Trough and Mariana Trough. In most other iterations, the simulated metacommunities had high similarity among the Okinawa and Mariana Trough sites, though there are currently no recorded shared species among these hydrothermal vent systems (Brunner *et al.*, 2022, Tunnicliffe *et al.*, *unpublished*). Although the simulated metacommunity with weaker local selection strength ($h=5$) and the same dispersal strength ($d=100$) had a slightly higher correlation coefficient (+0.007), it showed a complete disconnect of the Mariana Trough from the region. Additionally, in this iteration a single site in the Izu-Bonin Arc maintained shared species across all other sites in the region. Although the species assemblages of Mariana Trough vents are quite distinct from the rest of the region, they do share species (Brunner *et al.*, 2022; Tunnicliffe *et al.*, *unpublished*). The most glaring inconsistency between the ‘comparable’ and empirical species assemblage networks is the connection between a Mariana Trough and Okinawa

Trough site at the periphery of the network. This mistaken similarity between ‘Spot Yonaguni Knoll IV’ (Okinawa Trough) and ‘Forecast’ (Mariana Trough) vent sites is likely due to their near identical environmental conditions (depth and tectonic setting) as well as the strength of dispersal of this scenario ($d=100$) which enables species to travel (via steppingstones) between these two sites at opposite ends of the dispersal network (Figure 1).

While the agreements between the simulated and empirical metacommunities provide insight into the relative roles of local environmental filtering and dispersal in structuring the metacommunity, the discrepancies highlight the simulation’s assumptions as well as the role of unparameterized drivers of species distributions. For example, by including additional environmental information, the assemblages in the Okinawa Trough sites may have been more consistently distinct from those at the Mariana Trough across iterations of local selection and dispersal strength. While tectonic setting is a useful proxy for local environmental conditions such as the composition, intensity and stability of venting fluid, important local environmental conditions also vary among sites within the same tectonic setting (Juniper & Tunnicliffe, 1997; Gamo et al., 2013; Kojima & Watanabe, 2015; Mullineaux et al., 2018). One such example of a local environmental variable not parameterized here is the sediment composition. The Okinawa Trough has a high proportion of soft sediment, which may be a key contributor to the composition of the local communities (Watanabe *et al.*, 2010; Nakajima et al., 2014; Watanabe and Kojima, 2015) and would be an important distinguishing feature if such data were available across the region. With additional or more detailed environmental information we could at least improve the ‘comparable’ metacommunity by distinguishing between the environmental conditions at ‘Spot Yonaguni Knoll IV’ and ‘Forecast’.

The Role of Dispersal on Metacommunity Structure

In the treatment with empirical environmental conditions, increasing dispersal strength resulted in a stronger positive correlation between the empirical and simulated metacommunities. This increase was consistent until $h > 10$. In the randomised environment treatment, dispersal had very little effect on the correlation coefficient apart from when $d = 100$ (Figure 2). Although it has been suggested that most biophysical simulations may overestimate dispersal ability (Swearer *et al.*, 2019), our findings show that our original dispersal simulations ($d = ori$) is less able to replicate internal metacommunity structures compared to when it is uniformly multiplied by 100 ($d = 100$). The methods used here assume that all species disperse in the same way, which affects our ability to replicate the empirical metacommunity to an unknown extent. Our collective knowledge of species-specific larval dispersal behaviour is limited (Swearer *et al.*, 2019) especially in the deep sea (Hilário *et al.*, 2015). Population genetics studies have found instances of connectivity in the opposite direction expected based on simulations of larval dispersal (Breusing *et al.*, 2021), suggesting that we cannot resolve the population connectivity with dispersal simulations alone. That we could use a simulated dispersal model to approximate an empirical metacommunity supports the central role of ocean currents in dispersal among hydrothermal vents (Adams, 2011; 2012) despite species-specific differences in dispersal behaviour.

The effects of dispersal on alpha, beta, and gamma diversity here are very similar to that of Suzuki and Economo (2021) in their simulated metacommunities (Figure 3). As was the case with Suzuki and Economo (2021), our simulated metacommunities alpha diversity has a very small effect on regional gamma diversity and results in the metacommunity shifting from a state of species sorting at low dispersal strength directly to regional exclusion at high

dispersal strength (Figure 7). This contrasts with the findings of Mouquet and Loreau (2001, 2002) who showed that this transition includes a peak in alpha and gamma diversity at intermediate dispersal rates. This discrepancy is due to the spatially implicit nature of the Moquet and Loreau (2001; 2002) model versus the spatially explicit nature of our simulation (Suzuki and Economo, 2021).

The Role of Local Environmental filtering on Metacommunity Structure

The comparable metacommunity is created at an intermediate local selection strength ($h = 0.5$), while the correlation coefficient peaks at a weaker local selection strength in all dispersal strengths for the empirical environment ($h \leq 10$) and randomised environment ($h \leq 100$) treatments (Figure 2). The higher correlation coefficient at very weak local selection in the randomised environment treatment is likely an artifact of the increased species richness (Figure 5a). By decreasing the strength of local selection, the overall number of species retained within the simulated metacommunity increases sharply in all cases. This is likely driven by the accompanying increase in alpha diversity as species' range of fitness expand and overlap so that a single local environment can support more species. We also found a corresponding decrease in beta diversity with expanding ranges of fitness (Figure 6) as regionally successful species (those with a range of fitness that corresponds to many local environments) become more ubiquitous, excluding locally successful species, and causing regional homogenisation of the metacommunity (Moquet and Loreau, 2002; Suzuki and Economo, 2021). The confounding effect of species richness on the correlation coefficient demonstrates that this is not an ideal metric by which to determine a simulation's ability to replicate the empirical metacommunity and why the qualitative comparison in figure 4 is necessary.

The species richness of the simulated metacommunities from the empirical environmental treatment is generally higher than the corresponding metacommunities from the randomised environment treatment (Figure 5). As the principal difference between these treatments is the spatial arrangement (spatial autocorrelation) of local environments, the higher diversity in the empirical treatment supports the conclusion of Suzuki and Economo (2021) that intermediate-scale environmental clustering can enhance regional diversity. The importance of the spatial arrangement of habitat patches in driving beta diversity was demonstrated for islands archipelagos (Cabral *et al.*, 2014) and extended to archipelago-like systems such as hydrothermal vents (Kiel, 2016). Specifically, the volcanic arc vent sites of the Izu-Bonin-Mariana Arc may act as an environmental filter along the stepping-stone pathway of dispersal between the Okinawa and Mariana Trough, which enhances regional diversity.

The role of Biotic interactions on Metacommunity Structure

As species within a simulated metacommunity do not interact with one another, all the significant positive or negative co-occurrences can be attributed to dispersal barriers and/or the overlap between species' relative fitness. As this may be the case for the empirical metacommunity, it is important to investigate how incidences of significant co-occurrence relate to species' traits as well as environmental or dispersal barriers.

The clustering of species in the co-occurrence network mirrors the regional arrangement of vent sites with species commonly found in the Mariana Trough closely co-occurring at one end, only connected to the tight cluster of Okinawa Trough-associated species at the other end via intermediary species associated with the Izu-Bonin back-arc (Figure 8). Some species do cluster in terms of co-occurrence found outside of their sub-region. *Neoverruca intermedia* is one such example that also plays a relatively central role in the co-occurrence network. *N. intermedia* is a vent-associated barnacle that is commonly associated with vent sites in the Izu-Bonin Arc but is also frequently found at sites in the Okinawa Trough. Due to *N. intermedia*'s chemosymbiotic source of nutrition, its preference for vent-periphery habitats (Nomaki *et al.*, 2019), and its non-habitat building classification (Chapman *et al.*, 2019) there are no obvious ways to explain its strong co-occurrences through biotic interactions. This species' clustering in the Okinawa Trough and central role in the co-occurrence network may be related to its ability to disperse long distances (Watanabe *et al.*, 2006) and to colonize periphery areas of different vent ecosystems rather than any crucial biotic interactions. Those species considered foundational and/or contributors to habitat complexity (Chapman *et al.*, 2019) did not show any trend in centrality in the co-occurrence network. Because all species were considered peripheral in terms of their cartographic role in the co-occurrence network, there was no detectable role of functional traits, such as size, in connecting the different modules of the co-occurrence (e.g. Borthagaray *et al.*, 2014). In a succession and colonization experiment in the Okinawa Trough, Nakamura *et al.* (2018) suggested that the identity of pioneer species was related to their reproductive and maturity rates. Similarly, Dykman *et al.* (2021) attributed other functional traits, such as habitat building, to pioneer species. The association of functional traits related to recolonization with co-occurrence centrality depends on the occurrence of disturbance events, which are likely infrequent at vent sites in this region (German *et al.*, 2006).

The complexity of biotic interactions are overlooked in this, and previous implementations of lottery models, which implicitly incorporate density-dependent competition rather than explicitly specifying inter-species interactions (Moquet and Loreau, 2001; 2002; Suzuki and Economo, 2021). Although it is beyond the scope of this study, Thompson *et al.* (2020) were able to incorporate various levels of inter-specific competition in their metacommunity simulations to study the effects on the relationship between biodiversity and ecosystem-function. Later, Leibold *et al.* (2022) adapted patch-occupancy models to include inter-specific competition and found that the resultant simulated metacommunity exhibited increased levels of co-occurrence compared to when inter-specific competition was excluded. Based on these findings, it is reasonable to assume that explicitly incorporating biotic interactions in our lottery-based simulation would improve its predictive power. However, the interactions among species at hydrothermal vents is very poorly understood, so incorporating these interactions explicitly would introduce many assumptions of space or resource limitation that remain untested at hydrothermal vents outside of the East Pacific Rise (Mullineaux *et al.*, 2018).

Hydrothermal vents as a model for metacommunity and conservation research

As demonstrated here, hydrothermal vents can serve as natural laboratories to apply and expand upon island biogeography and metacommunity theory (Dawson and Santos, 2016;

Mullineaux *et al.*, 2018). Replicating the dispersal of individual species from hydrothermal vents via biophysical models cannot be achieved without more in-situ experimental observations (Hilario *et al.*, 2015) however, simulations of Lagrangian particle dispersal is a suitable method for quantifying the isolation of habitat patches and is strongly related to both genetic and community similarities (Chust *et al.*, 2016). By calculating isolation based on the probability of dispersal, we are effectively considering the distance between habitat patches from the organism's perspective, which is therefore more biologically relevant than any measure of geographical distance (Borthagaray *et al.*, 2015). The discrete nature of the chemical energy source that supports hydrothermal vent communities makes their definition as discrete habitat patches particularly appropriate. Although systematic surveying of local environmental parameters at hydrothermal vents is not likely in the near future, the key role of geology in determining these parameters may allow us to extrapolate the drivers of environmental variation to as yet unexplored sites. For example, Giguère and Tunnicliffe (2021) used the distance of vent sites from the Mariana volcanic arc as a proxy for hydrothermalism (Stern *et al.*, 2013; Anderson *et al.*, 2017), an important local environmental condition not otherwise available across their study sites. With limited direct observations, classifications of biotic interactions among vent-associated species are rare but these interactions are likely very important for determining community composition in such a space limited habitat (Mullineaux *et al.*, 2003). Temporal variability of community composition at hydrothermal vents can confound the role of local environmental parameters in structuring the local community (Tsurumi and Tunnicliffe, 2001; Gollner *et al.*, 2013). However, vent sites on relatively slow spreading systems such as those found in the Northwest Pacific and the Mid-Atlantic Ridge experience natural disturbances (volcanic eruptions) over periods of thousands of years (Jamieson *et al.*, 2013) and have been observed to undergo little variation in community composition over several years (Gebruk *et al.*, 2010; Cuvelier *et al.*, 2011; Sarrazin *et al.*, 2015). The geological parameters that dictate the temporal stability of a vent site's community and the large range of natural disturbance rates make hydrothermal vents an ideal model system for the exploration of stability in community composition (Mullineaux *et al.* 2018).

As well as an opportunity, there is also an impetus on applying models of metacommunity dynamics to hydrothermal vents due to the joint threats they face from deep-sea mining (Van Dover *et al.*, 2018) and climate change (Levin *et al.*, 2020). The holistic and spatially explicit framework of the metacommunity perspective complements typical objectives of conservation strategies (reviewed by Chase *et al.*, 2020) as well as the recent COP15 goals to protect global biodiversity through, in part, spatial management. The results of this study present an opportunity to simultaneously enhance our understanding of hydrothermal vent metacommunity dynamics as well as identify and prioritise key areas for which empirical data is needed to improve our models. A next step for this line of research would be to simulate disturbances caused by proposed deep-sea mining and or projected climate change models and determine the effects they have on local and regional diversity as well as community structure and resilience.

Conclusion

In this thesis I have compiled a relatively comprehensive database of hydrothermal vent associated species and their regional distribution to infer demographic connectivity for the sake of spatial management in the age of deep-sea mining. The inaccessible nature of hydrothermal vents makes direct observations of demographic connectivity or evidence of genetic connectivity at the regional scale practically impossible. Imminent mining of hydrothermal vents with unknown regional consequences for these vulnerable marine ecosystems warrants a novel combination of methods from the fields of physics and ecology to infer connectivity with the limited available data. By successfully replicating the connectivity processes via a metacommunity model, I have created a new methodological pipeline to combine empirical observations of species distributions with simulations of their dispersal to unravel the drivers of demographic connectivity and identify keystone sites for conservation. The charismatic and island-like features of hydrothermal vents make them an ideal natural laboratory to apply metacommunity theory to inform conservation priorities. This research could provide a strong foundation upon which the conservation of other patchy marine ecosystems is based. Finally, I have demonstrated the value of hydrothermal vents as a model habitat patch for use in the furtherment of metacommunity theory and its integration into applied marine conservation.

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Appendices

A1: Hydrothermal vent key and site metadata

Abbreviation	Name (InterRidge)	Latitude (InterRidge)	Longitude (InterRidge)	Depth (InterRidge)	Bathymetry (MERCATOR)	Region (InterRidge)
13N	13 N Ridge Site	13.0987	143.6886	3036	3018	Mariana Trough
AS	Alice Springs Field	18.2103	144.7073	3640	3636	Mariana Trough
BK	Bayonnaise Knoll caldera	31.9667	139.7333	900	1020	Izu-Bonin back-arc
B	Burke	18.109	144.432	3660	4196	Mariana Trough
CM	Chamorro volcano	20.81	144.705	896	1809	Mariana Arc
DAK	Daiichi-Amami knoll	28.45	128.75	350	347	Ryukyu Arc
DV	Daikoku volcano	21.324	144.194	450	1309	Mariana Arc
DKK	Daisan-Kume Knoll	26.302	126.4125	1370	1304	Ryukyu Arc
DS	Doyo Seamount	27.6833	140.8167	520	2080	Izu-Bonin Arc
EDV	East Diamante volcano	15.93	145.67	457	530	Mariana Arc
EB	Esmeralda Bank	14.9667	145.25	323	624	Mariana Arc
Fo	Forecast	13.4	143.9166	1470	3150	Mariana Arc
FR	Formosa Ridge (Site F)	22.1158	119.1186	1138	1679	South China Sea
FV	Fukujin volcano	21.93	143.47	1100	1342	Mariana Arc
Fu	Futagoyama	24.8674	123.3081	1270	1795	Okinawa Trough
HA	Hafa Adai	16.957	144.868	3294	3286	Mariana Trough
Hi	Higa	26.555	126.2233	1485	1601	Okinawa Trough
HiA	Higashi Aogashima	32.26	139.53	800	1267	Izu-Bonin Arc
HE	Higashi-Ensei	28.4393	128.1724	1220	1333	Okinawa Trough
IK	Irabu Knoll	25.23	124.88	1850	2025	Okinawa Trough

IC	Izena Cauldron	27.2667	127.0833	1610	1183	Okinawa Trough
KS	Kaikata Seamount	26.7	141.0833	930	1051	Izu-Bonin Arc
K2S	Kasuga ² Seamount	21.6	143.6167	500	2080	Mariana Arc
K3S	Kasuga ³ Seamount	21.3833	143.6	1140	2911	Mariana Arc
KI	Kueishan Island, offshore	24.8333	122	1200	216	Okinawa Trough
KK	Kuroshima Knoll	24.13	124.19	641	803	Ryukyu Arc
Ma	Makhahnas	20.53	144.8833	420	940	Mariana Arc
MM	Mariana Mounds	18.0333	144.2833	3600	3843	Mariana Trough
MT14	Mariana Trough, 14.5 N	14.487	144.094	4120	3993	Mariana Trough
MT15	Mariana Trough, 15.5 N	15.408	144.509	4196	4347	Mariana Trough
MT16	Mariana Trough, 16.5 N	16.401	144.87	3829	3792	Mariana Trough
MT18	Mariana Trough, 18.2 N	18.108	144.738	3916	4036	Mariana Trough
MTC	Mariana Trough, Central Trough	18.0467	144.7533	3676	4196	Mariana Trough
MTP	Mariana Trough, plume 2	12.761	143.473	2950	2828	Mariana Trough
MEK	Minami- Ensei Knoll	28.3917	127.6417	740	701	Okinawa Trough
MS	Mokuyo Seamount	28.32	140.58	1200	1412	Izu-Bonin Arc
MK	Myojin Knoll	32.1033	139.8683	1360	784	Izu-Bonin Arc
MC	Myojinsho Caldera	31.8833	139.95	1110	477	Izu-Bonin Arc
NK	Natsushima 84-1 Knoll	27.575	127.1417	1600	1532	Okinawa Trough
NEA	NE Anatahan submarine volcano	16.375	145.725	460	1565	Mariana Arc
NV	Nikko volcano	23.0833	142.3333	600	1306	Mariana Arc
NKI	North Knoll, Iheya Ridge	27.7908	126.8966	1100	1110	Okinawa Trough

NE	Northwest Eifuku	21.485	144.043	1604	2659	Mariana Arc
NR	Northwest Rota-1 volcano	14.601	144.775	599	2486	Mariana Arc
OT1	Okinawa Trough, Site ES1	30.3303	129.0827	521	415	Okinawa Trough
OT2	Okinawa Trough, Site ES2	28.8137	128.1028	779	910	Okinawa Trough
OH	Omuro Hole	34.5467	139.4417	200	106	Izu-Bonin Arc
Pe	Perseverance	15.4802	144.5077	3935	4022	Mariana Trough
Pi	Pika	12.9183	143.6483	2990	3406	Mariana Trough
Ru	Ruby	15.62	145.57	214	1244	Mariana Arc
SB	Sagami Bay (Off Hatsushima)	35	139.23	1100	1345	Izu-Bonin Arc
Sa	Sakai	27.5481	126.9895	1600	1484	Okinawa Trough
SX	Seamount X	13.25	144.02	1450	3505	Mariana Arc
Sn	Snail	12.9533	143.62	2880	3010	Mariana Trough
SSS	South Sarigan Seamount	16.58	145.78	240	1750	Mariana Arc
HK	SPOT, Hatoma Knoll	24.855	123.841	1520	1886	Okinawa Trough
YK	SPOT, Yonaguni Knoll IV	24.849	122.7	1385	1233	Okinawa Trough
SS	Suiyo Seamount	28.575	140.6417	1380	1712	Izu-Bonin Arc
SC	Sumisu Caldera	31.4667	140.0667	690	415	Izu-Bonin Arc
SR	Sumisu Rift	31.1	139.8917	1600	1809	Izu-Bonin back-arc
SwS	SW Syoyo	22.387	142.762	1750	2551	Mariana Arc
Ta	Tangyin	25.0667	122.5667	1206	1403	Okinawa Trough
TH	Tarama Hill	25.45388	124.310103	1973	2056	Okinawa Trough
TK	Tarama Knoll	25.0916	124.5416	1990	1984	Okinawa Trough
TC	TOTO Caldera	12.7167	143.5333	2960	2828	Mariana Arc

WS	W Syoyo	22.508	142.533	2150	2890	Mariana Arc
WR	West Rota volcano	14.325	144.833	1150	1094	Mariana Arc
Yo	Yokosuka	25.2638	124.3733	2190	2241	Okinawa Trough
YH	Yoron Hole	27.4916	127.5333	590	666	Okinawa Trough
vent	name	lat	lon	depth	bathy	region

A2: Species key and cartographic roles

Species	Key	Module	Within-module degree (zi)	Between-module degree (Pi)	Cartographic Role
<i>Alviniconcha hessleri</i>	1	MT	0.12087737	0	Ultra peripheral
<i>Austinograea williamsi</i>	2	MT	0.12087737	0	Ultra peripheral
<i>Bathymodiolus septemdierum</i>	3	IBMa	0.4292096	0.55621302	Peripheral
<i>Branchinotogluma burkensis</i>	4	MT	-0.6527378	0	Ultra peripheral
<i>Branchinotogluma marianus</i>	5	IBMa	0.11337612	0.44444444	Peripheral
<i>Desbruyeresia chamorroensis</i>	6	MT	-1.2329492	0	Ultra peripheral
<i>Desbruyeresia marianaensis</i>	7	MT	0.12087737	0	Ultra peripheral
<i>Lepetodrilus aff schrolli</i> MT	8	MT	-0.0725264	0.42	Peripheral
<i>Lepidonotopodium minutum</i>	9	MT	-0.8461416	0	Ultra peripheral
<i>Levensteiniella raisae</i>	10	MT	-0.2659302	0.375	Peripheral
<i>Marianactis bythios</i>	11	MT	-0.0725264	0	Ultra peripheral
<i>Munidopsis marianica</i>	12	MT	0.12087737	0	Ultra peripheral
<i>Neoverruca brachylepadoformis</i>	13	MT	0.12087737	0	Ultra peripheral
<i>Paralvinella hessleri</i>	14	MT	-0.2659302	0.24489796	Peripheral
<i>Phymorhynchus wareni</i>	15	MT	-0.0725264	0	Ultra peripheral
<i>Provanna nassariaeformis</i>	16	MT	-0.6527378	0	Ultra peripheral
<i>Pseudorimula marianae</i>	17	MT	-0.459334	0	Ultra peripheral

<i>Rimicaris vandoverae</i>	18	MT	0.12087737	0	Ultra peripheral
<i>Rimicaris variabilis</i>	19	MT	-0.0725264	0	Ultra peripheral
<i>Sirsoe hessleri</i>	20	MT	-1.2329492	0	Ultra peripheral
<i>Symmetromphalus regularis</i>	21	MT	-0.6527378	0	Ultra peripheral
<i>Vulcanolepas verenae</i>	22	MT	-0.8461416	0	Ultra peripheral
<i>Rimicaris falkorae</i>	23	MT	-1.0395454	0	Ultra peripheral
<i>Sericosura cochleifovea</i>	24	MT	-1.2329492	0	Ultra peripheral
<i>Alvinocaris longirostris</i>	25	OT	0.72295863	0.32	Peripheral
<i>Branchinotogluma japonicus</i>	26	IBMa	-0.5182908	0.44444444	Peripheral
<i>Desbruyeresia armata</i>	27	IBMa	-0.8341243	0	Ultra peripheral
<i>Gandalfus yunohana</i>	28	IBMa	2.64004396	0.36419753	Connector Hub
<i>Munidopsis myojinensis</i>	29	IBMa	0.4292096	0	Ultra peripheral
<i>Neoverruca intermedia</i>	30	IBMa	1.06087656	0.495	Peripheral
<i>Shinkailepas kaikatensis</i>	31	IBMa	0.11337612	0	Ultra peripheral
<i>Shinkailepas myojinensis</i>	32	IBMa	-0.8341243	0.61111111	Peripheral
<i>Alviniconcha adamantis</i>	33	IBMa	-0.8341243	0	Ultra peripheral
<i>Opaepele loihi</i>	34	IBMa	-0.2024574	0	Ultra peripheral
<i>Alvinocaris marimonte</i>	35	IBMa	-0.5182908	0.49382716	Peripheral
<i>Bathyacmaea nipponica</i>	36	OT	0.57929378	0.15277778	Peripheral
<i>Conchocele bisecta</i>	37	OT	-0.7136899	0	Ultra peripheral
<i>Enigmaticolus nipponensis</i>	38	Su	-0.5773503	0.625	Connector
<i>Gigantidas platifrons</i>	39	OT	0.43562892	0	Ultra peripheral
<i>Iheyaspira lequios</i>	40	OT	-0.5700251	0	Ultra peripheral
<i>Lebbeus shinkaiae</i>	41	OT	0.57929378	0.15277778	Peripheral
<i>Lepetodrilus nux</i>	42	OT	0.14829921	0.19753086	Peripheral
<i>Margarites ryukyuensis</i>	43	OT	0.29196406	0	Ultra peripheral
<i>Munidopsis ryukyuensis</i>	44	OT	0.29196406	0	Ultra peripheral

<i>Phreagena okutanii</i>	45	OT	-0.4263602	0	Ultra peripheral
<i>Provanna subglabra</i>	46	OT	0.43562892	0.16528926	Peripheral
<i>Shinkaia crosnieri</i>	47	OT	0.57929378	0.15277778	Peripheral
<i>Shinkaicaris leurokolos</i>	48	OT	0.43562892	0.16528926	Peripheral
<i>Deshayesiella sirenkoi</i>	49	IBMa	-0.8341243	0	Ultra peripheral
<i>Homalopoma bicolor</i>	50	IBMa	-1.1499578	0	Ultra peripheral
<i>Laeviphitus japonicus</i>	51	IBMa	0.11337612	0	Ultra peripheral
<i>Lamellibrachia satsuma</i>	52	IBMa	-0.8341243	0	Ultra peripheral
<i>Oenopota ogasawarana</i>	53	IBMa	-0.5182908	0	Ultra peripheral
<i>Paragiopagurus ventilatus</i>	54	IBMa	-0.5182908	0	Ultra peripheral
<i>Periclimenes cannaphilus</i>	55	IBMa	-0.8341243	0	Ultra peripheral
<i>Symphurus thermophilus</i>	56	IBMa	-0.5182908	0	Ultra peripheral
<i>Xenograpsus novaeinsularis</i>	57	IBMa	-0.8341243	0	Ultra peripheral
<i>Munidopsis gracilis</i>	58	MT	-1.2329492	0	Ultra peripheral
<i>Bathymodiolus aduloides</i>	59	OT	-0.1390305	0.49382716	Peripheral
<i>Lamellibrachia columna</i>	60	OT	0.14829921	0.19753086	Peripheral
<i>Leucolepas longa</i>	61	OT	-0.1390305	0	Ultra peripheral
<i>Metacrangon kaiko</i>	62	OT	-0.8573548	0	Ultra peripheral
<i>Munidopsis naginata</i>	63	OT	-0.7136899	0	Ultra peripheral
<i>Provanna clathrata</i>	64	OT	0.29196406	0	Ultra peripheral
<i>Puncturella parvinobilis</i>	65	OT	0.00463435	0.21875	Peripheral
<i>Abyssotrophon soyoae</i>	66	OT	-0.5700251	0	Ultra peripheral
<i>Archivesica kawamurai</i>	67	ME	-0.2581989	0.5	Peripheral
<i>Ashinkailepas seepiophila</i>	68	IBMa	-1.1499578	0.48	Peripheral
<i>Buccinum koshikinum</i>	69	OT	-0.8573548	0	Ultra peripheral
<i>Delectopecten vitreus</i>	70	OT	-0.8573548	0	Ultra peripheral
<i>Hanleyella henrici</i>	71	OT	-0.7136899	0	Ultra peripheral

Otukaia ikukoae	72	OT	-0.8573548	0	Ultra peripheral
Archinome jasoni	73	OT	-0.2826954	0	Ultra peripheral
Desbruyeresia costata	74	OT	-0.7136899	0	Ultra peripheral
Ophiambix kagutsuchi	75	OT	0.14829921	0	Ultra peripheral
Alvinocaris brevitelsonis	76	IBMa	-1.1499578	0.625	Connector
Branchipolynoe pettiboneae	77	OT	-0.4263602	0.32	Peripheral
Cantrainea jamsteci	78	ME	-0.2581989	0.44444444	Peripheral
Margarites shinkai	79	OT	-0.8573548	0	Ultra peripheral
Paralvinella n sp	80	OT	-0.2826954	0.53125	Peripheral
Puncturella rimaizenaensis	81	OT	-0.7136899	0	Ultra peripheral
Gigantidas horikoshii	82	IBMa	-1.1499578	0	Ultra peripheral
Monilea cocoa	83	IBMa	-1.4657913	0	Ultra peripheral
Alvinocaris dissimilis	84	ME	-0.2581989	0	Ultra peripheral
Bathymodiolus japonicus	85	ME	-0.2581989	0.44444444	Peripheral
Cantrainea nuda	86	ME	-0.2581989	0	Ultra peripheral
Chaceon granulatus	87	ME	-0.2581989	0	Ultra peripheral
Eunice masudai	88	ME	-0.2581989	0	Ultra peripheral
Eunice northioidea	89	ME	-0.2581989	0	Ultra peripheral
Lepetodrilus japonicus	90	ME	-0.2581989	0.5	Peripheral
Munidopsis longispinosa	91	ME	-0.2581989	0.5	Peripheral
Mytilidiphila enseiensis	92	ME	-0.2581989	0	Ultra peripheral
Mytilidiphila okinawaensis	93	ME	-0.2581989	0.5	Peripheral
Paralomis jamsteci	94	ME	-0.2581989	0	Ultra peripheral
Provanna lucida	95	ME	-0.2581989	0.44444444	Peripheral
Shinkai semilonga	96	ME	-0.2581989	0.5	Peripheral
Astyris thermophilus	97	OT	-0.8573548	0	Ultra peripheral
Branchinotogluma elytropapillata	98	OT	-0.7136899	0	Ultra peripheral

Lepidonotopodium okinawae	99	OT	-0.7136899	0	Ultra peripheral
Levensteiniella undomarginata	100	OT	-0.7136899	0	Ultra peripheral
Metacrangon ryukyu	101	OT	-0.8573548	0	Ultra peripheral
Paraescarpia echinospica	102	OT	-0.8573548	0	Ultra peripheral
Phreagena nankaiensis	103	OT	-0.8573548	0	Ultra peripheral
Placiphorella okutani	104	OT	-0.8573548	0	Ultra peripheral
Protomystides hatsushimaensis	105	OT	-0.8573548	0	Ultra peripheral
Shinkai longipedata	106	OT	-0.7136899	0	Ultra peripheral
Thermochiton undocostatus	107	OT	-0.4263602	0	Ultra peripheral
Iheyomytilidicola tridentatus	108	OT	-0.8573548	0	Ultra peripheral
Leptochiton tenuidentatus	109	OT	-0.5700251	0	Ultra peripheral
Nicomache ohtai	110	OT	-0.8573548	0	Ultra peripheral
Provanna fenestrata	111	OT	-0.5700251	0	Ultra peripheral
Solemya flava	112	OT	-0.8573548	0	Ultra peripheral
Lurifax japonicus	113	Su	-0.5773503	0	Ultra peripheral
Pyropelta yamato	114	Su	-0.5773503	0	Ultra peripheral
Thermomya sulcata	115	MT	-1.2329492	0	Ultra peripheral
Pyropelta ryukyuensis	116	OT	-0.4263602	0	Ultra peripheral
Stylodactylus major	117	OT	-0.8573548	0	Ultra peripheral

A3: Lagrangian particle tracking simulation details

Supporting Information: Larval Dispersal Simulation with PARCELS

An example of the methods described below and all those used in the associated manuscript can be found at:

https://github.com/otistwo/hydrothermal_thesis/tree/main/PARCELS

Ocean Model (Fieldset)

Three oceanographic variables were used in these simulations (Eastward Ocean Current, Northward Ocean Current and Seawater Temperature) and were freely downloaded from the 'MOI GLORYS12_FREE' MERCATOR product. These variables are in the Arakawa C-grid format (ORCA 1/12deg). Additional information on this product can be found at <https://www.mercator-ocean.eu/en/solutions-expertise/accessing-digital-data/product-details/?offer=4217979b-2662-329a-907c-602fdc69c3a3&system=4f9a6cea-7bb0-e4d7-f56d-5dde805195e0>

The horizontal extent of the oceanographic variables and entire simulation was approximately 104°E - 62°W and 0.04°N - 359.95°N, therefore included most of the North Pacific Ocean. The temporal resolution was daily and the extent was five years from 1997/01/01 - 2002/01/01. 'Ocean PARCELS' (<https://oceanparcels.org/>), a series of methods in the python programming language, were used to combine environmental variables into a 'fieldset', within which simulated particles were released.

Simulating dispersal with PARCELS

Simulated particles that represent infinitesimally small parcels of water were released and given behaviours to make them approximate dispersing larvae. Particles were released every six hours from each source site (Appendix A1) for a period and density dictated by the periodicity of the scenario (see methods). Once released into the oceanographic model, particle positions were modified by advection (a 4th order Runge-Kutte implementation) as well as diffusion (Smagorinsky, 1963). The implementation of Smagorinsky diffusion was modified from the tutorial in PARCELS (https://nbviewer.org/github/OceanParcels/parcels/blob/master/parcels/examples/tutorial_diffusion.ipynb) to reduce diffusion to 0 at each cell bordering the landmask.

Custom behaviour kernels were attributed to each particle in order to record the distance travelled, average temperature experienced and age at termination. Termination occurred at the end of the Planktonic Larval Duration (PLD), determined by implementing the model of O'Connor *et al.* (2006) as implemented by Mitarai *et al.* (2016). $\ln(\text{PLD}) = B_0 - 1.34 \times \ln(T/T_c) - 0.28 \times [\ln(T/T_c)]^2$ where T= temperature experienced by the particle at each hourly timestep, T_c was set to 15 and B₀ = 4.56 as the maximum magnitude of PLD - temperature relationship that fits with the unified model.