



Earth Sciences
New Zealand

Review study of benthic thresholds for dissolved oxygen and particle deposition

Gigablue Threshold Study

Prepared for Gigablue

August 2025

Prepared by:

Jeroen Ingels

For any information regarding this report please contact:

Jeroen Ingels

Deep-Sea Ecologist

Marine Benthic Ecosystems

+64 4 386 0300

jeroen.ingels@niwa.co.nz

New Zealand Institute for Earth Science Limited

Private Bag 14901

Kilbirnie

Wellington 6241

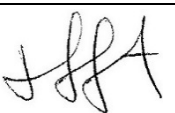
Phone +64 4 386 0300

Client Report No: 2025252WN

Report date: August 2025

Project No: GIG25306

Revision	Description	Date
Version 1.0	Final version sent to client	06 August 2025

Quality Assurance Statement		
	Reviewed by:	Scott Nodder (Principal Scientist – Marine Geology)
	Formatting checked by:	Jess Moffat
	Approved for release by:	Mike Williams

© New Zealand Institute of Earth Science Limited (“Earth Sciences New Zealand”) 2025. All rights reserved. This publication may not be reproduced or copied in any form without the permission of the copyright owner(s). Such permission is only to be given in accordance with the terms of the client’s contract with Earth Sciences New Zealand. This copyright extends to all forms of copying and any storage of material in any kind of information retrieval system.

Whilst Earth Sciences New Zealand has used all reasonable endeavours to ensure that the information contained in this document is accurate, Earth Sciences New Zealand does not give any express or implied warranty as to the completeness of the information contained herein, or that it will be suitable for any purpose(s) other than those specifically contemplated during the project or agreed by Earth Sciences New Zealand and the client.

Contents

Executive summary	6
1 Introduction	8
1.1 Background and general methodology	8
1.2 Gigablue MCFS activities	9
1.3 Main objectives	11
1.4 Methods, considerations, and dependencies	12
2 Oxygen at the deep-sea floor	15
2.1 Global oxygen dynamics	15
2.2 Deep-Sea Floor Oxygen off East New Zealand (1000–2000 m)	15
3 Organic matter and particle supply to deep-sea sediments	20
3.1 Organic matter supply in the AOI and adjacent areas	22
3.2 Responses of deep-sea fauna to organic matter supply and resulting oxygen decline	24
4 Thresholds	30
4.1 Threshold frameworks	30
4.2 Applicability of thresholds under New Zealand law	33
4.3 MCFS pressures on benthic ecosystems	37
4.4 Sensitivities and thresholds for specific taxa	37
5 Summary and conclusions	87
6 References	89

Tables

Table 1-1:	Comparison of typical sinking rates between natural marine particles vs. the rate specified in the MCFS Methodology.	9
Table 2-1:	Bottom-water oxygen concentrations (1000-2000 m water depth range) for the east New Zealand/Chatham Rise Region highlighting the spatial and vertical variations in O ₂ and associated water masses.	19
Table 3-1:	POC fluxes in oceanic areas east-southeast of Aotearoa New Zealand.	23
Table 3-2:	Summary of present-day POC flux to the seabed across the Aotearoa New Zealand region.	23

Table 3-3:	Hypothesized scenario of extra oxygen demand from a 25 g m ⁻² organic matter pulse	26
Table 3-4:	Generalized differences between organic matter pulses and sedimentation effect on benthic communities	29
Table 4-1:	Examples of threshold variables with numerical values based in science conducted in deep-sea environments that have been applied in Aotearoa New Zealand EEZ consenting processes.	34
Table 4-2:	Examples of New Zealand EPA provisions and regulatory effects in relation to empirical thresholds.	35
Table 4-3:	Example of three EPA decisions/consents that set numerical limits for activities in deep-sea environments within Aotearoa New Zealand EEZ.	36
Table 4-4:	Parameter values for deep-sea brachiopod health index models.	44
Table 4-5:	Optimum and threshold values for O ₂ , POC, and sedimentation for different brachiopod species, threshold effects, and supporting literature.	44
Table 4-6:	Summary of the sensitivity of deep-sea brachiopods (bathyal New Zealand taxa) to oxygen, organic matter pulses, and sedimentation/turbidity.	47
Table 4-7:	O ₂ , POC, and sedimentation threshold values and biological effects for deep-sea coral species <i>Solenosmilia variabilis</i> and <i>Goniocorella dumosa</i>	53
Table 4-8:	Summary of sensitivity of deep-sea corals to key environmental factors in New Zealand's bathyal zone. Citations indicate supporting research findings	55
Table 4-9:	Thresholds and optima are based on experimental and field data	61
Table 4-10:	Summary of sensitivities and responses of deep-sea sponges (Hexactinellidae, Demospongiae, Calcarea) to dissolved oxygen, organic matter supply, and sedimentation.	66
Table 4-11:	Environmental thresholds and health index response for deep-sea polychaetes (1000-3000 m, New Zealand Region)	73
Table 4-12:	Qualitative sensitivity of major deep-sea infaunal groups to low oxygen, organic matter supply, and sedimentation disturbances.	76
Table 4-13:	Qualitative environmental information for deep-sea xenophyophores	81
Table 4-14:	Summary of xenophyophores' sensitivity to oxygen availability, organic matter supply, and sedimentation.	82
Table 4-15:	Sensitivity of deep-sea bryozoans to oxygen availability, organic matter pulses, and sedimentation	84
Table 4-16:	Optimum and threshold values for O ₂ and POC flux applied to deep-sea bryozoans	85
 Figures		
Figure 1-1:	Spatial extent of the study area.	10
Figure 2-1:	Oxygen patterns in waters around New Zealand.	17
Figure 4-1:	Three-dimensional surface plot for deep-sea brachiopod health index as a function of dissolved oxygen and sedimentation rate.	45

Figure 4-2:	Three-dimensional surface plot for deep-sea brachiopod health index as a function of dissolved oxygen and POC flux.	46
Figure 4-3:	3D (left) and 2D (right) surface plot for deep-sea coral <i>Solenosmilia variabilis</i> health index as a function of dissolved oxygen and suspended sediment concentration	53
Figure 4-4:	3D (left) and 2D (right) surface plot for deep-sea coral <i>Solenosmilia variabilis</i> health index as a function of dissolved oxygen and POC flux	54
Figure 4-5:	3D (left) and 2D (right) surface plot for deep-sea coral <i>Goniocorella dumosa</i> health index as a function of dissolved oxygen and suspended sediment concentration.	54
Figure 4-6:	3D (left) and 2D (right) surface plot for deep-sea coral <i>Goniocorella dumosa</i> health index as a function of dissolved oxygen and POC flux.	55
Figure 4-7:	3D surface plot of the health index of the sponge <i>Ecionemia novaezealandiae</i> as a function of oxygen concentration and POC flux.	62
Figure 4-8:	3D surface plot of the health index of the sponge <i>Ecionemia novaezealandiae</i> as a function of oxygen concentration and suspended sediment concentration.	63
Figure 4-9:	3D surface plot of the health index of a deep-sea sponge cluster as a function of oxygen concentration and POC flux.	64
Figure 4-10:	3D surface plot of the health index of a deep-sea sponge cluster as a function of oxygen concentration and suspended sediment concentration.	65
Figure 4-11:	3D surface plot of the polychaete health index as a function of bottom-water dissolved oxygen and POC flux.	74
Figure 4-12:	3D surface plot of the polychaete health index as a function of bottom-water dissolved oxygen and sedimentation.	75
Figure 4-13:	Xenophyophore observed abundance across O ₂ and POC flux ranges.	82
Figure 4-14:	3D surface plot showing modelled bryozoan health index as a function of POC flux and dissolved oxygen.	86

Executive summary

Earth Sciences New Zealand was commissioned to undertake a threshold study for Gigablue's Microalgae Carbon Fixation and Sinking (MCFS) project. Gigablue's request was that Earth Sciences New Zealand review scientific literature for limits on bottom-water dissolved oxygen (DO) drawdown and particulate deposition within an agreed Area of Interest (AOI) within Subantarctic waters in Aotearoa New Zealand's Exclusive Economic Zone (EEZ). These waters are characterised by High-Nutrient Low Chlorophyll (HNLC) conditions and have water depths mainly between 1000–2000 m.

Specifically, Earth Sciences New Zealand was requested to:

1. Review international literature around benthic DO in deep-water basin environments relevant to the area of interest, and natural variability (keeping in mind that there are dependencies that may not be resolved such as benthic and pelagic consumption, adaptations, and biotic interactions with organic matter arrival and mineralisation) (Task 2).
2. Assess reduction in DO from background levels before adverse benthic impacts are likely to occur (Task 3.1).
3. Assess particle accumulation rate before adverse smothering causes benthic impacts (Task 3.2).

To achieve this goal, we carried out a desktop review to: (i) first characterise the prevailing environmental conditions in the project area, then (ii) identify the levels of oxygen reduction and sediment or organic carbon flux that could lead to adverse effects in key benthic taxa, and (iii) finally situate these thresholds within New Zealand's legal and regulatory framework.

To quantify the natural variability and baseline conditions for DO and particulate flux, we conducted a desktop review of published CTD (conductivity, temperature, depth) profiles, sediment-trap measurements, and benthic chamber experiments published in the scientific literature relevant to the AOI. This review indicates that bottom-water DO in the study area typically ranges from 150 to 200 $\mu\text{mol O}_2 \text{ kg}^{-1}$, with a seasonal-stable minimum of approximately 130–160 $\mu\text{mol O}_2 \text{ kg}^{-1}$ at 1200–1500 m, reflecting the influence of Upper Circumpolar Deep Water. Particulate organic carbon (POC) fluxes to the seabed average 3–4 $\text{mg C m}^{-2} \text{ d}^{-1}$ in this HNLC region, punctuated by episodic peaks up to 8–10 $\text{mg C m}^{-2} \text{ d}^{-1}$ during phytoplankton blooms. Sedimentation rates at the seafloor are generally below 1 mm yr^{-1} , with occasional pulses tied to surface productivity events.

Building on these baselines, we synthesized taxon-specific sensitivity to DO and sedimentation using data from published laboratory and field studies on deep-sea corals, sponges, brachiopods, xenophyophores, bryozoans, and infauna (focusing on polychaetes). Due to the lack of NZ-species specific information, we had to rely mostly on studies of species that may not be typical for New Zealand waters or that presented data that served as proxies for the taxa under investigation. It is worthy of note that no information was available on species that originated from the AOI. For deep-sea corals (stony corals), DO limitations below 40–50 $\mu\text{mol O}_2 \text{ kg}^{-1}$ and suspended sediment concentrations exceeding 50–100 mg L^{-1} have been linked to tissue degradation and elevated mortality. Sponges show optimal health at 200–220 $\mu\text{mol kg}^{-1}$

but begin to decline below $\sim 150 \mu\text{mol O}_2 \text{ kg}^{-1}$, and they experience sub-lethal stress when exposed to sediment concentrations above $\sim 55 \text{ mg L}^{-1}$. Brachiopods and general infauna exhibit critical DO thresholds around $40\text{--}50 \mu\text{mol O}_2 \text{ kg}^{-1}$, with POC flux “optima” in the $3\text{--}10 \text{ mg C m}^{-2} \text{ d}^{-1}$ range and adverse effects when fluxes drop below $2 \text{ mg C m}^{-2} \text{ d}^{-1}$ or exceed $12 \text{ mg C m}^{-2} \text{ d}^{-1}$. Xenophyophore densities occupy a broad envelope of O_2 concentrations, and densities decline below roughly $100 \mu\text{mol O}_2 \text{ kg}^{-1}$ and moderate sedimentation, although no single numeric cutoff applies. These values should be considered indicative only.

When assessed against New Zealand legislation—including the EEZ Act 2012, Continental Shelf Act 1964, and Wildlife Act 1953—these thresholds suggest that MCFS operations should avoid DO drawdowns exceeding 20–30% of background (i.e., to maintain concentrations above $\sim 120 \mu\text{mol O}_2 \text{ kg}^{-1}$ which is 20% below the observed $150 \mu\text{mol O}_2$). This is a conservative approach to minimize risk. Particulate deposition events should be limited to levels below established taxon-specific sedimentation thresholds (typically $50\text{--}100 \text{ mg L}^{-1}$ suspended sediment pulses or $<0.5 \text{ mm yr}^{-1}$ accumulation). While definitions of hypoxia (e.g., $<60 \mu\text{mol O}_2 \text{ kg}^{-1}$) fall well below the levels at which sensitive taxa are impacted, a precautionary approach would set project limits more conservatively to safeguard the most vulnerable benthic communities.

Due to the significant uncertainties, and the absence of information on thresholds for specific taxa implementation of a monitoring program is likely needed to detect early signs of ecological stress. Conclusive evidence should be gathered on the presence of sensitive taxa and environments in the AOI so that their distributions are known and potential MCFS impacts can be assessed. Furthermore, Targeted *in situ* and *ex situ* loading experiments and experiments on organic matter remineralisation and benthic community responses to sedimentation are critical to refining the thresholds and reducing uncertainty.

1 Introduction

1.1 Background and general methodology

The client, Gigablue, proposes to fix atmospheric carbon and sequester it in the deep ocean within New Zealand's EEZ waters. The method by which Gigablue aims to achieve this is by Microalgae Carbon Fixation and Sinking (MCFS) (Puro.Earth, 2025). This method is considered one of many ways in which atmospheric carbon is captured and stored for prolonged periods of time. MCFS is categorized as a marine Carbon Dioxide Removal (mCDR) technique (Levin et al., 2023). The method uses a pathway of capturing and sequestering carbon through additional photosynthetic activity of local phytoplankton in the surface ocean on Gigablue's specific substrates. Summarized, MCFS activity recommended in [Puro Earth's Microalgae and Carbon Fixation and Sinking Methodology for CO₂ Removal](#) (Puro.Earth, 2025) consists of the following general steps:

1. Deployment of engineered substrates in regions of the ocean which have high nutrient, low chlorophyll (HNLC) conditions;
2. Growth of additional local microalgae (phytoplankton) on the substrate, consuming CO₂ dissolved in the ocean, that are then incorporated into the substrate;
3. Sinking of the substrates and the attached microalgae to the deep ocean;
4. Storage of the carbon in the slow carbon cycle of the deep ocean;
5. Re-capturing consumed CO₂ in surface waters: The microalgae-captured (fixated) carbon was already dissolved in the surface ocean, and by removing that new biomass allows for additional carbon uptake by the ocean through gas-exchange with the atmosphere and re-equilibration processes.

The induced increase of photosynthetic carbon fixation in the photic zone can also increase local oxygen production. However, as it sinks through the water column, the remineralisation of natural organic matter (OM) produced at the surface may increase oxygen consumption in the water column, at the seafloor and in the ocean sediments. Low concentrations of dissolved oxygen (DO), especially below the near-bottom "hypoxia" threshold of 60 $\mu\text{mol O}_2 \text{ kg}^{-1}$, can affect organisms, their ecology (Diaz & Rosenberg, 1995) and biogeochemical cycles. The MCFS method prescribes that decreases in deep-water DO concentration in excess of a 30% threshold (here understood to be a 30% reduction from natural background values) should be avoided as a consequence of the MCFS activity (Puro.Earth, 2025). However, the threshold value of 30% (reduction) stated in the methodology does not appear related to any ecological threshold, national regulatory requirement, or any international regulations or agreements.

In addition to the concerns related to oxygen consumption, consideration needs to be given to the physical arrival of the particles on the seafloor when the sinking process has been completed. MCFS, by design, causes the relatively rapid descent of particulates and associated organic carbon to deep depths, likely reducing remineralisation in the upper ocean by shortening its residence time in the water column compared to naturally sinking OM (Table 1-1). This will likely result in larger quantities of relatively undegraded particles and OM being exported from the surface ocean to the seafloor. These particles and associated OM can be

seen as a pressure on the deep benthic ecosystem in what is usually recognized as a relatively oligotrophic, food-limited system, where organisms have ecologically and evolutionarily adapted to the episodic deposition of euphotic production with inter- and intra-annual changes driving the input of that production to the deep-sea (Gooday, 2002; Ruhl & Smith, 2004; Smith et al., 2009).

Table 1-1: Comparison of typical sinking rates between natural marine particles vs. the rate specified in the MCFS Methodology.

Particle Type	Typical Sinking Rate	Compared to 20 m/hr (MCFS Methodology Draft)(Puro.Earth, 2025)	References
Marine snow/aggregates	10–200 m/day (0.4–8.3 m/h)	Slower	McDonnell and Buesseler (2010); Turner (2015a)
Small phytoplankton	<1 m/day (<0.04 m/h)	Much slower	Turner (2015a)
Large diatoms	~1–10 m/day (0.04–0.4 m/h)	Much slower	Turner (2015a)
Zooplankton faecal pellets	50–1000+ m/day (2–40+ m/h)	Similar–faster (for fastest pellets)	Turner (2015a)
Foraminifera	~100 - 1300 m/day	Faster	Caromel et al. (2014); Fok-Pun (1981); Takahashi and Allan (1984); Walker et al. (2021)
Ballasted particles – polyacrylamide gel	10-150 m/day; 5 – 2700 m/day (8–30 m/h)	Slower-similar-faster	McDonnell and Buesseler (2010 and references therein)
MCFS (minimum)	480 m/day (20 m/hr)	—	MCFS Methodology Draft ⁴

Therefore, two environmental risks associated with the MCFS activity that warrant detailed investigation and lie within the scope of this report, are:

1. Smothering of benthic organisms owing to the arrival of particles and associated OM at the seafloor; and
2. Perturbations of dissolved oxygen budgets in the benthic environment in response to the influx of this carbon-rich material.

1.2 Gigablue MCFS activities

Gigablue is developing a technology that aims to capture carbon dioxide through growth of phytoplankton on particles released into the marine environment, more specifically in high-nutrient, low-chlorophyll (HNLC) waters. At the time of report preparation this is based on a 9(2)(b)(i), 9(2)(b)(ii)

Particles are expected to remain at or near the sea surface for up to approximately 21 days during which time it is envisaged that phytoplankton will grow on and within the particles. The particles will then sink into deep water and settle on seafloor sediments, and benthic communities, sequestering carbon into deep-sea sediments.

The Area of Interest (AOI) proposed by Gigablue for these activities, and considered in these reports, comprises an area roughly 107,000 km² off the southeastern coast of Te Waipounamu South Island, Aotearoa New Zealand Figure 1-1. The water depth in this area is mainly bathyal (between 1000 and 3000 metres), but the seabed within the direct AOI lies mostly between 1000 and 2000 m water depth. However, there are still uncertainties about where the release of particles will occur and how the particles may be dispersed, and what the range of the dispersal area will be. These uncertainties are likely to be addressed in other studies and reports.

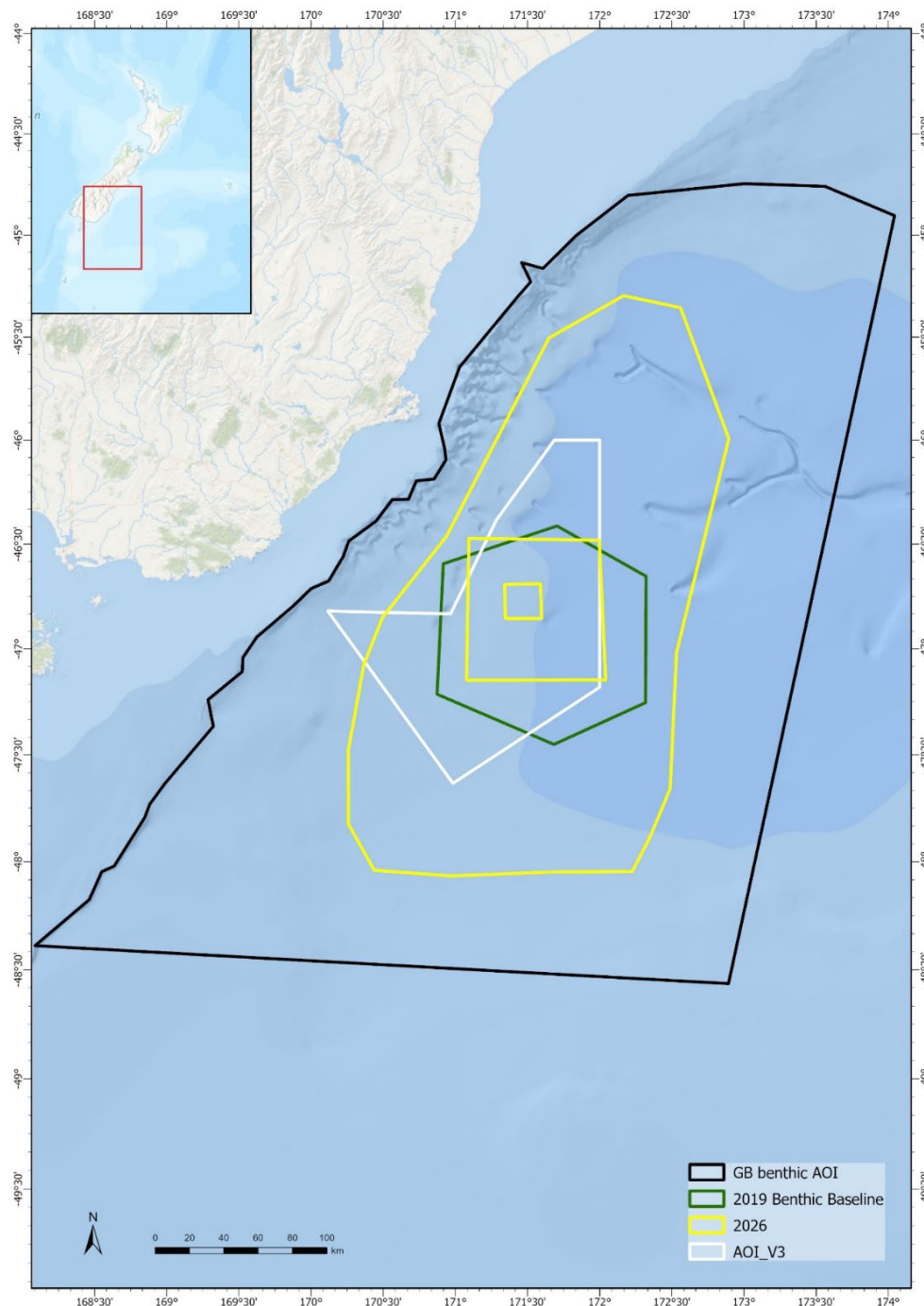


Figure 1-1: Spatial extent of the study area. Black line indicates the benthic Area of Interest (AOI), which provides a buffer zone around the areas of interest provided by Gigablue. Yellow lines indicate areas of interest (2026), the white line indicates Gigablue's area of interest (AOI_v3) and the green line indicates the extent of a 2019 benthic baseline survey conducted for OMV New Zealand Ltd. Inset map indicates spatial extent of main map.

It is unclear at the time of writing this report what the growth potential or realized growth of these particles are when they are deployed in the HNLC waters found in the AOI. We understand that growth of phytoplankton (and associated micro-organisms) attached or associated with the particles has been demonstrated and indeed forms one of the critical premises of the MCFS method (Puro.Earth, 2025). We currently, however, lack scientific data on the rate or magnitude of the organic matter growth, the composition of the particle's phyto-microbial communities, and remineralisation (of the organic matter) and degradation (9(2)(b)(i), 9(2)(b)(ii)) potential and realized rates, either *in vitro* or *in situ*, although it is expected that the activities may result in a deposition of up to ~25 g of organic matter m⁻² (Gigablue pers. comm.). Other caveats in our understanding concern the specific particle volumes, and the area of expected release and dispersal. These uncertainties have shaped our methodology and have helped define how we addressed the objectives in the present report as described below.

1.3 Main objectives

In consideration of the above, Earth Sciences New Zealand was requested to conduct a desktop review study of relevant international literature that addresses: 1) the issues around benthic dissolved oxygen in deep-water basin environments, and 2) the issues around exposure of organisms to particulates in the marine environment. Both objectives are to be considered in the context of proposed MCFS activities in the Gigablue AOI.

More specifically, these objectives encompassed the following activities:

1. Review international literature that can inform on sensitivity of deep-sea benthic fauna (relevant to the AOI) to dissolved oxygen variations;
2. Review literature that can inform on sensitivity of deep-sea benthic fauna (relevant to the AOI) to particulate exposure;
3. Review literature that can inform on the level of reduction in DO from background levels before adverse benthic impacts are likely to occur (sensitivity, impact level, uncertainty); and
4. Review literature that can inform on particulate accumulation rate before adverse smothering causes benthic impacts (sensitivity, impact level, uncertainty).

The objectives were to consider each of the following:

1. Natural variability in baseline conditions (notably DO and POC/sedimentation);
2. The relevant legal framework in terms of protected taxa or definition of sensitive environments;
3. Dependencies such as pelagic and benthic consumption, and organic matter arrival and mineralisation;
4. The potential of cumulative impacts from longer-term likelihood of increased particle flux to the seabed; and
5. What additional data might be needed to assess benthic impacts and threshold levels.

Note that for this report Gigablue was requested to supply the following information in sufficient time that it could be considered:

1. Data and information on the biogeochemical and specific physical characteristics of the particles and their associated biota (detrital, planktonic/algal, microbiological) to allow us to constrain our work and set boundaries as to what literature is relevant for the desktop study.
2. Outcomes of particle dispersal model, including estimated particle accumulations rates (mass per unit area and time), and a more constrained definition of where the AOI is situated.
3. A conceivable “worst case scenario” with respect to particle settling. This is needed to consider impacts, through net increase in particle dispersal mass and frequency or combination of natural events. Gigablue informed Earth Sciences New Zealand that a mass flux event arriving at the seafloor resulting from an MCFS activity may amount to 25 g m⁻² within the currently modelled dispersal area. It is our understanding that this is based on the total mass of the predicted particle and OM flux.

The absence of certain types of information has limited our ability to constrain our findings, leaving several caveats in our ability to interpret potential impacts, including their magnitude, frequency, and extent.

1.4 Methods, considerations, and dependencies

1.4.1 Scientific considerations

1. To achieve above objectives, three types of literature were reviewed: 1) Literature that can give context to the development of a threshold framework that could support the threshold development for MCFS; 2) Literature that offers information on natural conditions of O₂, sedimentation, organic matter or POC flux, and benthic fauna; and 3) Literature that offers information on impacts or responses to variation in O₂, POC, and sedimentation.
2. To constrain the breadth of the study, we focused the desktop search on the AOI to the extent possible and only broadened the search when there was not sufficient information.
3. In the absence of limited information on the characteristics and *in situ* behaviour of the particles and the composition of the associated biota (detrital, planktonic/algal, microbiological) upon arrival at the seafloor, we had to consider a generalized view of the pressures and effects these particles and associated OM would have on the benthic environment. On one hand, there is the MCFS substrate, 9(2)(b)(i), 9(2)(b)(ii), which will comprise about 1/5th of the total carbon efflux arriving at the seafloor (Gigablue, personal communication). Considering what we know about natural sinking processes of OM from euphotic waters to the deep seafloor and the transformations and remineralisation it undergoes, and extending such processes to the MCFS particles and their deployment and sinking, we posit that the main

pressures to consider in this threshold study are oxygenation effects, the effects of sedimentation (proxy for particle load), and the effects of OM/POC flux arriving at the seafloor. However, it is important to note that the particles will not behave the same as sediments. With the information we currently have about the particles we cannot assess how similar or dissimilar they might be; and so how relevant the review of sedimentation sensitivities is to the MCFS methodology.

4. Where possible or necessary, particularly when making assumptions, we included considerations related to broader scientific knowledge of pelagic and benthic processes. In each instance, the relevant scientific studies were cited.

1.4.2 Legal framework considerations

To constrain the amount of scientific information we reviewed, we considered their relevance to protected benthic taxa based on knowledge from existing New Zealand legal frameworks and regulations. For instance, when determining the types of organisms to consider for developing a threshold review for deep-sea benthic taxa in a MCFS context, we restricted ourselves to those taxa that have a likelihood of occurring in the AOI and are mentioned or referenced in the Continental Shelf Act 1964 and the Exclusive Economic Zone and Continental Shelf (Environmental Effects) Act 2012 (commonly referred to as the EEZ act), see also Beaumont et al. (2025) for other relevant legislation.

The [Continental Shelf Act 1964](#) primarily focuses on the exploration and exploitation of New Zealand's continental shelf. The Act includes provisions related to the management and protection of marine resources, including oysters, other shellfish, and sponges. Specifically, it states under the definition of natural living resources: "living organisms belonging to sedentary species, that is to say organisms which, at the harvestable stage, either are immobile on or under the seabed or are unable to move except in constant physical contact with the seabed or subsoil."

The [Exclusive Economic Zone and Continental Shelf \(Environmental Effects\) Act 2012](#) on the other hand comprises much more detail on the nature of sensitive environments and provides a list of taxa or groups of taxa that are seen as indicators of the existence of sensitive environments, and the criteria for when indicator taxa observations can be classified as a sensitive environment (see also Beaumont et al., 2025). These include:

- Stony coral thickets or reefs
- Xenophyophores (sessile protozoan) beds
- Bryozoan thickets
- Calcareous tube worm thickets
- Chaetopteridae worm fields
- Sea pen field
- Rhodolith (maerl) beds
- Sponge gardens
- Beds of large bivalve molluscs

- Macro-algae beds
- Brachiopods
- Deep-Sea Hydrothermal vents
- Methane or cold seeps

The [Wildlife Act of 1953](#) (2018 Reprint) is another piece of legislation that provides protective measures for selected animals in Aotearoa New Zealand. Marine species declared to be protected animals in Schedule 7 of this Wildlife Act include:

- Anthozoa (corals and sea anemones)
 - Black corals – all species in the order Antipatharia
 - Gorgonian corals – all species in the order Gorgonacea
 - Stony corals – all species in the order Scleractinia
- Hydrozoa (hydra-like animals)
 - Hydrocorals – all species in the family Stylasteridae

Many of the taxa mentioned in these legislative works are likely present in the AOI; data availability and habitat suitability models are available in Beaumont et al. (2025).

- Stylasterid corals (Stylasteridae)
- Bryozoans (Bryozoa)
- Cup corals (Scleractinia)
- Gorgonian corals (Gorgonaceae)
- Sponges (Porifera)
- Sea pens (Pennatuloidae)
- Reef-forming stony corals (Scleractinia (colonial))
- Xenophyophores (Xenophyophorea)

In addition to this information, preliminary determinations could be made as to which sensitive environments are present in the AOI, based on whether they meet the thresholds stated in legislation (i.e., present but not in sufficient densities to be classified as sensitive environments). Note that these determinations are based on limited observational data and may change if additional surveys are conducted to cover more of the AOI. The organisms most relevant here are:

- Stony coral thickets or reefs
- Xenophyophore beds
- Brachiopods beds

Furthermore, several protected taxa have been confirmed as present in the AOI based on data available to Earth Sciences New Zealand. These include Scleractinia (both branching and cup corals), Antipatharia, stylasterids, and Gorgonacea; these are all protected cnidarian groups under New Zealand and international legislation and regulations. Taxa that are covered in New Zealand's legislative framework helped us constrain our literature search and data collection and interpretation to develop an informative threshold study.

2 Oxygen at the deep-sea floor

2.1 Global oxygen dynamics

Deep-sea bottom water oxygen concentrations are governed by the interplay of large-scale circulation (ventilation by deep- and bottom-water formation), local benthic respiration (sediment, microbial, and faunal oxygen uptake), and biogeochemical processes at the seafloor. These processes produce pronounced spatial heterogeneity - from near-anoxic oxygen minimum zones (OMZs) at mid-depths to well-oxygenated abyssal plains – and temporal variability on scales from tidal and diurnal oscillations to seasonal, interannual, and decadal trends.

Benthic O₂ dynamics span spatial scales from millimetres (diffusive boundary layers) to hundreds of kilometres (water mass fronts) and temporal scales from seconds (turbulent bursts) to decades (climate-driven deoxygenation). Resolving these multiscale variations requires complementary methods, such as benthic chambers and landers, eddy correlation techniques, *in situ* optode and electrode techniques and long-term observatories, as well as modelling approaches. Spatial variability of oxygen is driven by water-mass structure and circulation. OMZs at 200–1000 m in eastern boundary regions exhibit bottom water concentrations as low as <20 $\mu\text{mol kg}^{-1}$, whereas ventilated Southern Ocean waters can exceed 300 $\mu\text{mol kg}^{-1}$ at abyssal depths. Temporal variability on the other hand arises from tidal and internal wave forcing (daily to weekly cycles), seasonal changes in productivity and ventilation, and interannual-decadal trends linked to climate modes and global warming. Recent observations indicate an average deoxygenation of $\sim 2 \mu\text{mol kg}^{-1} \text{ decade}^{-1}$ in the upper 2000 m, with pronounced regional differences driven largely by changes in water-mass age and solubility (Stramma et al., 2008a; Stramma et al., 2008b).

2.2 Deep-Sea Floor Oxygen off East New Zealand (1000–2000 m)

2.2.1 Oceanographic setting and oxygen distribution

The deep waters off New Zealand's east coast are shaped by water masses with distinct oxygen signatures. Antarctic Intermediate Water (AAIW), formed north of the polar front, predominantly in the eastern south Pacific (Sloyan & Rintoul, 2001), occupies ~ 600 – 1000 m depths and is relatively oxygen-rich (often $>200 \mu\text{mol kg}^{-1}$) due to recent ventilation in cold southern surface waters (Russell & Dickson, 2003). Beneath this, Upper Circumpolar Deep Water (UCDW) and North Pacific Deep Water (NPDW) intrude at ~ 1200 – 2000 m. These older waters carry the region's low-oxygen layer, with dissolved O₂ dropping to ~ 130 – $160 \mu\text{mol kg}^{-1}$ (the lowest values at the deep-seafloor) (Russon et al., 2009). By contrast, Lower Circumpolar Deep Water (LCDW) and deep waters from the Southern Ocean, which flow into the region below ~ 2000 m, have higher oxygen (~ 180 – $200 \mu\text{mol kg}^{-1}$) since they originate in well-ventilated polar zones (Russon et al., 2009). In summary, waters south of the Chatham Rise transition from oxygen-rich in the

upper layers (0-500 m) to an oxygen-minimum at ~1500 m, then modestly higher O₂ in deeper layers, reflecting the layered water-mass structure (Johnson, 2008). This vertical O₂ distribution is characterised by sparse hydrographic observations collected over the last few decades and include RV *Tangaroa* Voyages and data from the World Ocean Circulation Experiment (Russon et al., 2009; Wijffels et al., 2001). Spatial variations occur across the Chatham Rise itself, a submarine ridge (~43°S) that separates subtropical and subantarctic waters. The southern flank and HNLC Subantarctic Zone side of the rise are bathed in subantarctic waters that carry the mid-depth relative O₂ minimum. In the central and western Chatham Rise crest (~450–1300 m) – near the Subtropical Front – benthic foraminiferal assemblages indicate chronically depleted O₂ conditions (Hayward et al., 2007). This corresponds to the oxygen minimum layer impinging on the crest at these depths (O₂ concentrations on the order of ~150 µmol kg⁻¹ in some areas)(Thiagarajan et al., 2013). In contrast, the eastern crest of Chatham Rise shoals to ~300–600 m, lying above the lower-oxygen zone; bottom waters there remain well-oxygenated (near saturation)(Hayward et al., 2007; McCave et al., 2008). Thus, east-west differences along the rise reflect depth and water-mass influences: shallow eastern sites have plentiful O₂, whereas deeper central/western sites experience the depleted O₂ of intermediate-depth NPDW/UCDW. Further south in the open subantarctic Pacific (south of Chatham Rise, ~45–50°S), O₂ levels at the seafloor are fairly homogeneous horizontally, governed by the broad water-mass patterns. Here, recent observational programs (CTD sections and autonomous profiling floats) confirm that bottom waters ~1000 m deep remain oxygen-rich (typically 85–95% saturation), while those ~1500 m deep approach the Pacific O₂ minimum (roughly 150 µmol kg⁻¹), with slight O₂ increases again toward ~2000 m and deeper.

Oceanographic measurements essentially reinforce the above-mentioned understanding of the vertical O₂ structure: high O₂ (~220–240 µmol kg⁻¹) in the 0–1000 m layer influenced by high-oxygen AAIW (700–1200 m), a pronounced minimum around 1200–1500 m (~150–170 µmol kg⁻¹; intrusion of the low-oxygen UCDW), and higher values below (influenced by the LCDW) – see Figure 2-1. O₂ concentrations at ~1000 m depth in the subantarctic zone experiences minimal seasonal fluctuation (variations on the order of only a few µmol kg⁻¹), which is expected because deep waters are removed from direct seasonal forcing; small O₂ changes largely reflect slow advection of water masses or minor consumption by remineralisation. Consistent with this, a recent report found no significant long-term deoxygenation trend in intermediate waters around New Zealand – observed O₂ changes over the past few decades have been minor (Law et al., 2016; Oschlies et al., 2018). Climate projections likewise suggest only a minor (<3–5%) O₂ decline in deep waters south of NZ by 2100 (Law et al., 2016), implying that the deep seafloor in this region has so far been relatively buffered from global ocean deoxygenation (Oschlies et al., 2018).

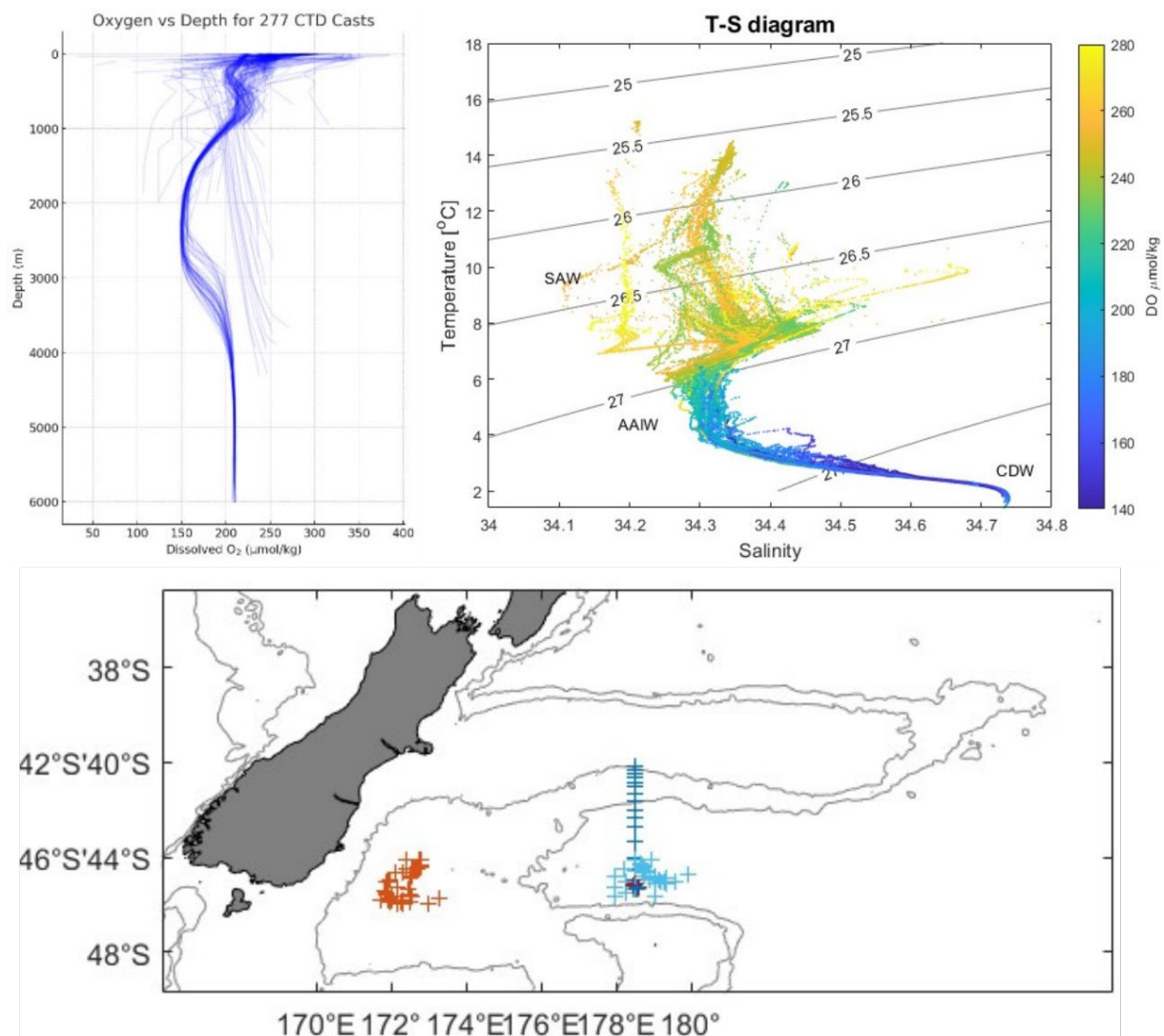


Figure 2-1: Oxygen patterns in waters around New Zealand. (Upper left) Dissolved oxygen vertical profiles from 277 CTD casts in waters off New Zealand as used for species distributions models (see Beaumont et al. (2025)) and retrieved from NOAA World Ocean Atlas, 2013, volume 3. These casts span depths of 0 - 6000 m. Each blue line represents an individual cast, with the ensemble illustrating a well-oxygenated surface layer (250 - 300 $\mu\text{mol kg}^{-1}$), a pronounced subsurface minimum near 200–300 m in summer, a secondary maximum at 500–800 m due to Antarctic Intermediate Water, and a gradual decline to $\sim 150\text{--}200 \mu\text{mol kg}^{-1}$ at abyssal depths. (Upper right) Salinity-Temperature plot based on CTD casts specifically from waters southeast of New Zealand, indicating high-oxygen subantarctic surface waters (SAW), Antarctic Intermediate Water (AAIW), and the lower-oxygen Circumpolar Deep Water (CDW) (Fernandez, in prep.). (Bottom) Map of locations (red and blue crosses) of CTD casts used to generate the T-S diagram in top right panel; these locations include sites in the AOI.

2.2.2 Ecological and biogeochemical variations

Even moderate variability in seafloor oxygen can have notable biological and biogeochemical consequences. Oxygen concentrations at the levels observed ($\sim 150\text{--}250 \mu\text{mol kg}^{-1}$) are well above “hypoxic” thresholds for most marine life, but they still influence the distribution and activity of deep-sea organisms. For example, benthic foraminifera assemblages on Chatham Rise respond to O_2 differences: the west/central crest communities (exposed to the O_2 -minimum water) are dominated by taxa tolerant of low- O_2 , episodic-food conditions, whereas the eastern-crest communities (in higher O_2 water) host different species more adapted to well-

oxygenated settings (Hayward et al., 2007). This indicates that even a drop from near-saturation to ~60–70% saturation (as occurs from east to west across the rise) can act as an environmental filter for benthic fauna. Similarly, deep-sea corals are sensitive to oxygen levels. Studies of cold-water corals south of New Zealand have revealed a depth band (~1200–1500 m) where coral abundance is low – precisely corresponding to the low O₂ levels (~165 $\mu\text{mol kg}^{-1}$) in the water column (Thiagarajan et al., 2013). Laboratory experiments show that coral respiration and growth slow markedly once O₂ falls to ~100–150 $\mu\text{mol kg}^{-1}$ (Lunden et al., 2014). *In situ*, once bottom-water O₂ increases again below the low-O₂ zone, corals reappear in greater numbers (Thiagarajan et al., 2013). This “gap” in coral distribution at intermediate depths highlights how the O₂ trough limits high-metabolism organisms, effectively acting as an oxygen constraint on habitat availability in the deep sea.

Seafloor carbon cycling is also tied to oxygen availability. On Chatham Rise, sediment community oxygen consumption (SCOC) – a measure of benthic metabolic rate – varies with food supply and faunal activity but is not O₂-limited under present conditions (Leduc et al., 2020a; Nodder et al., 2007; Pilditch et al., 2015). Benthic incubation studies in 2015 (at sites 450–1200 m on Chatham Rise) showed SCOC differences between winter and summer linked to OM input and macrofauna abundance, not to O₂ changes (Leduc et al., 2020a). This suggests that as long as bottom water remains well-oxygenated (>~150 $\mu\text{mol kg}^{-1}$), the seafloor biota can obtain enough O₂ to fuel respiration of sinking organic carbon. Nonetheless, oxygen does modulate remineralisation pathways: in lower-O₂ zones, microbial communities may operate closer to suboxic conditions in the sediment, potentially affecting nutrient fluxes (e.g. releasing phosphate or promoting denitrification in extreme cases) (Glud, 2008; Middelburg, 2019). The Chatham Rise phosphorite deposits have been hypothesized to form at the fringes of an ancient oxygen-minimum zone (Nielsen et al., 2015), indicating that sustained low-O₂ conditions over geologic time (i.e., millions of years – Middle-Late Oligocene to Early Pliocene; see Frontin-Rollet et al. (2022) and references therein) can drive significant chemical authigenesis. In the modern era, however, seafloor O₂ concentrations off east New Zealand are high enough that aerobic processes dominate carbon remineralisation. Macrofauna (e.g. polychaetes, echinoderms) actively bioturbate the sediments, enhancing oxygen penetration a few centimetres into the seabed (Leduc et al., 2020a). Only in very fine-grained pockets of sediment with high organic content might oxygen get locally depleted in the sedimentary microenvironment. Overall, the benthic ecosystem is well adapted to the prevailing oxygen regime: DO concentrations are low enough to exclude the most O₂-sensitive corals from mid-depths, yet high enough to support diverse invertebrate communities and vigorous carbon processing. If future climate change were to push the O₂ levels down (even slightly), we might expect further shifts – e.g. reduced habitat for corals and changes in macrofaunal composition – but current projections suggest minimal O₂ decline in this region by 2100 (Law et al., 2016).

2.2.3 Summary of bottom-water oxygen levels and regional variations relevant to the AOI

The deep waters off the east coast of New Zealand’s South Island are shaped by a complex interplay of Southern Ocean water masses and mid-ocean circulation, resulting in a distinct vertical layering of. Despite this mid-depth oxygen minimum, the deep seafloor east of the South Island is not presently oxygen-limited in a functional sense. Macrofaunal bioturbation, sediment oxygen consumption, and microbial remineralisation processes all continue effectively, supported by bottom-water oxygen concentrations generally above 150 $\mu\text{mol kg}^{-1}$. Sensitive

organisms like deep-sea corals, however, do respond: cold-water coral distributions show a relative gap around 1200–1500 metres, corresponding directly to this lower oxygen zonation. Coral presence resumes below these depths where oxygen increases again, suggesting a physiological threshold shaping habitat availability.

At intermediate depths (roughly 1000–1500 metres), waters are typically lower in oxygen relative to surface and abyssal layers, due to the presence of aged Upper Circumpolar Deep Water (UCDW). These older water masses, which have been removed from surface ventilation for extended periods, carry the region’s lowest oxygen concentrations—falling to ~130–170 $\mu\text{mol kg}^{-1}$. Though these values are not hypoxic by strict biological definitions, they represent an oxygen minimum for the New Zealand region and form a bottleneck for oxygen-sensitive deep-sea life.

This low-oxygen midwater layer interacts strongly with regional topography. Along the Chatham Rise, the oxygen minimum impinges most clearly on the central and western crest, where depths between 450 and 1300 metres lie within this depleted layer. In these areas, benthic foraminiferal assemblages show clear adaptation to episodic food availability and low-oxygen conditions, indicating long-term ecological sorting based on oxygen gradients. In contrast, the eastern crest of the Chatham Rise, which shoals to 300–600 metres, remains above the oxygen-depleted layer and retains well-oxygenated bottom water, close to saturation. This east–west contrast reflects both the vertical position of the oxygen minimum and the influence of subantarctic versus subtropical water masses.

Table 2-1: Bottom-water oxygen concentrations (1000-2000 m water depth range) for the east New Zealand/Chatham Rise Region highlighting the spatial and vertical variations in O_2 and associated water masses. Sources: Oxygen concentrations compiled from hydrographic measurements and analyses in (Bostock et al., 2010; Chiswell et al., 2015; Hayward et al., 2007; Law et al., 2016; Lawrence et al., 2016; Leduc et al., 2020a; Russell & Dickson, 2003; Stramma et al., 2010; Thiagarajan et al., 2013). All values are approximate; regional variability and measurement conditions can cause minor deviations.

Location / Water Mass (Depth)	Dissolved O_2 ($\mu\text{mol kg}^{-1}$)	Characteristics / Source
Antarctic Intermediate Water (AAIW) Subantarctic Zone south of Chatham (~1000 m)	~200–250 (high)	Well-ventilated cold intermediate layer; oxygen-rich.
Low Oxygen Minimum Layer (UCDW/NPDW) Intermediate depth (~1200–1500 m) south/east of Chatham Rise	130–170 (minima)	Aged deep waters from Pacific; lowest O_2 in region.
Lower Circumpolar Deep Water (LCDW) Deep inflow (>~1800–2000 m) from Southern Ocean	~180–200 (moderate)	More recently ventilated deep water; higher O_2 content.
Chatham Rise crest – west/central (450–1300 m on rise, STF zone)	~150 (at lowest)	Low O_2 by mid-depth; benthic fauna adapted.
Chatham Rise crest – east (300–600 m on rise, east end)	>250 (near saturated)	Shallow crest bathed in well-oxygenated waters; higher O_2 .

Further south and offshore in the subantarctic Pacific, bottom-water oxygen conditions become more uniform, with values at ~1000 metres generally ranging from 85–95% saturation, and only dipping to ~150 $\mu\text{mol kg}^{-1}$ at ~1500 metres. Below this, oxygen levels rise again as deeper inflows of Lower Circumpolar Deep Water (LCDW)—well-ventilated water from polar regions—replenish the abyss.

Long-term observations indicate no significant trend of deoxygenation in intermediate waters around New Zealand in recent decades, and climate projections suggest only a modest decline (<5%) in deep oxygen levels by 2100. Thus, compared to many other global regions, the continental slope east of the South Island remains relatively buffered from the more severe impacts of global ocean deoxygenation—at least for now. However, small future declines may tighten the environmental envelope for sensitive benthic fauna, potentially altering the structure and function of slope ecosystems.

3 Organic matter and particle supply to deep-sea sediments

The delivery of organic matter (OM) from the photic surface ocean to the deep-sea floor is a fundamental process that sustains life at great depths and shapes global carbon cycling. At depths of 1000–2000 metres, where photosynthetic production ceases, this downward flux of organic particles to the seafloor becomes the main energy and carbon source for benthic ecosystems. It drives benthic functioning, microbial activity, and carbon sequestration in the ocean. Although chemosynthetic ecosystems may exist in the AOI, this report focuses on the dominant heterotrophic deep seafloor.

The supply rate and composition of OM reaching the deep sea are strongly influenced by surface productivity, particle transport mechanisms, and water column processes, such as degradation and remineralisation. Surface-derived OM can aggregate into larger particles such as marine snow, faecal pellets, and phytodetritus that sink rapidly (Table 1-1), while other carbon components remain dissolved or are recycled by zooplankton and microbial organisms. The vertical transfer of this organic carbon, the "biological carbon pump," is most efficient in the upper ocean but declines with depth due to remineralisation (Turner, 2015a, b). The transfer of carbon from the surface ocean to the ocean interior is facilitated by other biological and physical processes, termed "particle injection pumps" (Boyd et al., 2019), including mixed-layer shoaling (Gardner et al., 1995), eddy subduction (Stukel et al., 2017) and diurnal to seasonal vertical migration through the water column by zooplankton (Jónasdóttir et al., 2015; Steinberg & Landry, 2017) and mesopelagic organisms, such as fish (Davison et al., 2013).

Ocean sedimentation includes both the descent of OM and inorganic particles such as lithogenic material from terrestrial runoff and biogenic minerals like calcium carbonate and opal. Sinking rates depend on particle size and density: larger aggregates and faecal pellets can reach bathyal depths in days to weeks, while smaller particles descend more slowly unless ballasted by denser materials (Miklasz & Denny, 2010; Waite et al., 1997). Particle transformation during descent – via microbial colonisation, zooplankton repackaging, or aggregation – further influences the rate and depth of OM delivery.

By 1000–2000 m, only $1\text{--}5\text{ mg C m}^{-2}\text{ day}^{-1}$ — around 1–2% of the original export — remains (Lampitt & Antia, 1997; Martin et al., 2010), though typical global POC fluxes range from $1\text{--}10\text{ mg C m}^{-2}\text{ d}^{-1}$ at 1000 m to $0.5\text{--}5\text{ mg C m}^{-2}\text{ d}^{-1}$ at 2000 m (Lutz et al., 2007). The remaining OM is more refractory and often mineral-associated due to the loss of labile components during descent (Martin et al., 1987; Yang et al., 2022). Sediments typically contain 0.1 – 1% total organic carbon, with only a small labile fraction available for benthic consumption (Arndt et al., 2013; Glud, 2008; Middelburg, 2019).

Although vertical POC flux is the main carbon source to the deep sea, other sedimentation processes—including lateral transport via nepheloid layers and boundary currents—enhance

deep-sea accumulation. Gravity-driven turbidity flows, and sediment resuspension can redistribute both OM and inorganic matter, particularly near topographic features such as canyons and seamounts (Carter & McCave, 1997; Wilks et al., 2021). In the New Zealand region, the East Cape Current and the Southland Current and associated flows contribute to such lateral particle movement (Chiswell et al., 2015).

In the AOI, the seafloor at 1000-2000 m lies within a HNLC region with iron-limited primary production, leading to lower surface productivity and smaller phytoplankton (Boyd et al., 1999; Bradford-Grieve et al., 1999). Consequently, POC fluxes are relatively modest—averaging 3.5-4 mg C m⁻² d⁻¹ (Décima et al., 2023; Nodder & Alexander, 1999)—and significantly lower than fluxes observed along the Chatham Rise (Nodder et al., 2016). Nevertheless, episodic events and mineral ballasting can augment sinking rates and enhance deep-sea delivery (Armstrong et al., 2002b; Honda & Watanabe, 2010).

Sinking particle fate depends on particle size, density, composition (e.g., whether they are mineral ballasted or easily degradable), local oceanographic conditions, and aggregation and disaggregation processes (Burd et al., 2010; Collins et al., 2015; De La Rocha & Passow, 2007; Giering et al., 2014; Soviadan et al., 2024). Mineral ballast (e.g., CaCO₃, opal) can reduce mineralisation time by speeding up descent (Passow & De La Rocha, 2006), and thus enhancing the transfer of OM to depth (Armstrong et al., 2001; Cram et al., 2018; Iversen & Poulsen, 2007; Nodder & Northcote, 2001). Faecal pellets, varying in size, composition, and sinking speed depending on the consumer, are an important but highly variable component of POC export (e.g. Table 1-1). Organic matter retention in the upper ocean (e.g., through coprophagy (Iversen & Poulsen, 2007) and microbial recycling (Steinberg et al., 2008)) often limits transfer to depth with reported retention rates of 30 – 98 % (Turner, 2015b). Repackaging and transformation by zooplankton and microbial communities alter particle characteristics, with microbial colonisation further modifying particle density and cohesion (Cram et al., 2022; Dithugoe et al., 2023).

Export flux is controlled by three key processes (Lampitt et al., 2023): 1) primary production, almost all of which takes place in the euphotic zone, and which sets the ultimate “input” to the biological carbon pump; 2) export efficiency (fraction of surface production exported below the euphotic zone (Buesseler et al., 2020)), isolating this organic carbon from further contact with the atmosphere; and 3) transfer efficiency, involving processes which determine how much of this export flux reaches depths below which the material remains for a climatically relevant period, i.e., 100s to 1000s of years (Archer, 2011). A myriad of inter-connected processes affect both export and transfer efficiency (Baetge et al., 2020; Boyd et al., 2019; Cavan et al., 2019; Henson et al., 2022) which can vary regionally (Honjo et al., 2008; Lampitt & Antia, 1997; Lutz et al., 2007) and are affected by community structure, ballasting, and physical mixing (Boyd et al., 2019; Henson et al., 2022).

The result of the modifications of OM in the ocean, and the magnitude and spatial variability of the biological carbon pump on global scales also has implications for the structure and functioning of deep-sea benthic and mesopelagic communities (Billett et al., 1983; Graf, 1989; Siegel et al., 2023; Smith et al., 2013). However, based on ~30 years of observational data in the Northeast Atlantic, Lampitt et al. (2023) have shown that the composition of the upper ocean biological community may be a determinant in how much and at what depth in the water column carbon can be sequestered, as a consequence of different sinking efficiencies.

3.1 Organic matter supply in the AOI and adjacent areas

The ocean region east of Aotearoa New Zealand, including the Chatham Rise, Hikurangi Margin, and Bounty Trough, illustrates how local oceanography shapes surface productivity and OM delivery to the deep sea. The Subtropical Front and nutrient-rich surface waters over the Chatham Rise generate strong seasonal phytoplankton blooms (Murphy et al., 2001; Pinkerton et al., 2024), resulting in higher OM export than adjacent Subtropical and Subantarctic waters (Nodder et al., 2016; Nodder & Northcote, 2001). Seasonal blooms dominate POC export in the region, with mineral ballasting – especially carbonate, biogenic silica and lithogenic mineral components – likely playing a crucial role in accelerating POC sinking rates (Nodder et al., 2016; Nodder & Northcote, 2001), supporting the paradigm where episodic, heavily ballasted biogenic particle aggregates drive deep carbon flux (Armstrong et al., 2002a; Armstrong et al., 2009; Honda & Watanabe, 2010; Klaas & Archer, 2002; Ziveri et al., 2007).

However, the AOI lies southwest of the Chatham Rise and covers the upper channels of the Bounty Trough system that lie beneath mainly Subantarctic waters (Chiswell et al., 2015). It falls within a HNLC zone, where iron limitation, vertical mixing, light and microzooplankton grazing regulate phytoplankton productivity and taxonomic composition (Boyd et al., 1999; Bradford-Grieve et al., 1999; Gutiérrez-Rodríguez et al., 2023). Algal populations here are dominated by small cells (Boyd et al., 1999; Bradford-Grieve et al., 1997) and heterotrophic bacteria make up substantial proportions of total community biomass (Bradford-Grieve et al., 1999). Due to weak seasonal chlorophyll variation (Banse & English, 1997) and strong eastward advection (Nodder & Northcote, 2001), POC fluxes are expected to be low.

Near-surface total mass fluxes (upper 550 m) within and around the AOI range from 200–700 mg m⁻² d⁻¹ (Nodder & Alexander, 1998; Nodder & Alexander, 1999), with POC fluxes of ~10–150 mg m⁻² d⁻¹ (Décima et al., 2023; Nodder & Alexander, 1999). These are typically lower than in the Subtropical Front and Subtropical zones, depending on season (Nodder & Alexander, 1998; Nodder & Gall, 1998), consistent with the HNLC region's low chlorophyll and productivity (Bradford-Grieve et al., 1999; Décima et al., 2023). The dominance of small phytoplankton also leads to their increased presence in marine aggregates and faecal pellets (Waite et al., 2000).

Sediment trap data on Chatham Rise flanks show near-bed POC fluxes of ~5–20 mg C m⁻² day⁻¹, with seasonal peaks during diatom blooms exceeding those values (see Table 3-1 Table 3-2) (Nodder and Northcote, 2001; Wilks et al., 2021). Across the New Zealand EEZ, average primary productivity is 525.1 ± 6.5 mg C m⁻² d⁻¹ with particle fluxes of 22.6 ± 5.5 mg C m⁻² d⁻¹ at release depth, and 4.9 ± 6.8 mg C m⁻² d⁻¹ at the seabed (Pinkerton et al., 2016), see Table 3-2). Within the AOI, seabed POC fluxes are typically ~3.5 – 4 mg C m⁻² d⁻¹, reflecting HNLC conditions (Décima et al., 2023; Nodder & Alexander, 1999).

Besides marine OM, sediments also receive occasional terrestrial inputs — average 1.2 mg m⁻² d⁻¹ lithogenic-derived fluxes in Subantarctic waters vs. 12 mg m⁻² d⁻¹ in Subtropical waters (Nodder et al., 2016) — and near-shore material like benthic diatoms (Wilks et al., 2021). Episodic “food falls” of macroalgae or wood may also contribute, especially near canyons and continental margins (Harrold et al., 1998; Vetter & Dayton, 1999).

Table 3-1: POC fluxes in oceanic areas east-southeast of Aotearoa New Zealand. Values marked “*” are regional inferences based on broader deep-water and margin global syntheses in the absence of site-specific trap data. “bloom peaks” refer to episodic, spring–summer pulses. Values from different studies may have different underlying calculations, inter- or extrapolations, and should be used as approximate values only.

Area	Depth (m)	POC Flux (mg C m ⁻² d ⁻¹)	Source
North Chatham Rise	300	10.1	(Nodder & Northcote, 2001)
	1000	20.5	
South Chatham Rise	300	4.1	
	1000	4.9	
Subtropical E of NZ	1500	6	(Nodder et al., 2016)
Subantarctic E of NZ	1500	3	
Chatham Rise	1500–2000	~2–5 (annual mean); ~8–10 (bloom peaks)	(Nodder et al., 2007)
Chatham Rise (average over larger area)	410–995	~10	(Leduc et al., 2020a)
Hikurangi Margin	1000–2000	1–5 (estimated)*	(Lutz et al., 2007)
Bounty Trough	1500–2000	1–12 (seasonally* variable)	(Lutz et al., 2007)

Table 3-2: Summary of present-day POC flux to the seabed across the Aotearoa New Zealand region. Based on the refitted Lutz et al. (2007) model forced by satellite Net Primary Production and oceanographic data (mean of 1997 - 2015), modified from Pinkerton et al. (2016).

Region / Depth band	Mean fluxSeabed (mg C m ⁻² d ⁻¹)	Interannual range (±2 SD, mg C m ⁻² d ⁻¹)
Entire EEZ	4.9	6.8
Chatham Rise (STF)	9.8	8.5
Tasman Sea (west)	5.2	9.2
Subtropical waters (STW)	4.4	7.1
Subantarctic waters (SAW)	4.0	14.1
250–800 m (shelf/rise)	7.6	13.0
800–1500 m (upper slope)	4.0	11.2
1500–3000 m (deep slope)	3.5	6.4
>3000 m (abyssal)	3.0	6.6

3.2 Responses of deep-sea fauna to organic matter supply and resulting oxygen decline

Deep-sea benthic organisms between 1000 and 2000 m water depth (upper to mid-bathyal zone) respond to pulses of OM such as phytodetritus or marine snow; this has been amply documented in global literature (e.g. Smith et al., 2008; Snelgrove et al., 2018). In general, the benthos will respond quickly and actively to OM pulses, with increases in respiration, changes in community behaviour, such as feeding and reproduction, and enhanced nutrient cycling.

Deep-sea OM pulses can drive substantial increases in sediment oxygen consumption and lead to transient depletion of oxygen at the sediment-water interface, with important consequences for benthic community structure and function. The exact magnitude of oxygen drawdown depends on the magnitude of the flux, the composition of the OM, local hydrodynamics, and baseline conditions. Studies from the Chatham Rise in New Zealand waters and other deep-sea regions allow us to frame rough estimates and expected biological responses for a pulse of ~ 25 g of OM m^{-2} (i.e. maximum modelled MCFS scenario; GB pers. comm.) deposited over a few days at 1000-2000 m depth. Measurements from the Chatham Rise at ~ 1000 -2000 m depth indicate background sediment community oxygen consumption (SCOC) on the order of a few $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, typically around 2-6 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ under background organic flux conditions (Leduc et al., 2020a). These baseline rates reflect steady-state mineralization of the slow, seasonal or episodic supply of particulate organic carbon (Nodder et al., 2007).

Diagenetic models and empirical compilations show a non-linear relationship between POC flux to the seafloor and SCOC (Jahnke, 1996). Benthic oxygen demand can be related to the organic carbon flux using empirical exponential or power laws derived from *in situ* chamber incubations and sediment cores (Christensen, 2000; Jørgensen et al., 2022). For moderate to large pulses, SCOC can increase by an order of magnitude above background levels for several days to weeks, depending on the size of the pulse and the reactivity, driven by the local benthic communities (Billett et al., 1983; Smith et al., 2018).

Fresh phytodetritus or labile organic substrates are rapidly utilized by bacteria and, to a lesser degree, macrofauna and meiofauna, often with high respiration efficiency, i.e., a large fraction of supplied carbon is respired to CO_2 , consuming O_2 (Stratmann et al., 2018; Stratmann et al., 2019). The responses to OM supply in the deep sea is not uniform, a complex myriad of trophic interactions and different feeding behaviours and food preferences means that different benthic components may respond differently to the OM pulse, depending on the magnitude and composition of the OM arrival. It is also important to note that time lags between changes in observations of POC flux and SCOC can vary dependent on the environmental conditions (Smith et al., 2018). Studies have shown that for a deposition event, a large fraction (e.g., 90%) of labile carbon can be respired within ~ 1 -2 days in eutrophic or moderately eutrophic settings. In more oligotrophic deep-sea sites, it may take somewhat longer, but still within days to a couple of weeks (review of many SCOC studies in Stratmann et al., 2019).

One can calculate the estimated oxygen consumption for a 25 g OM m^{-2} pulse, based on carbon content and respiratory stoichiometry. If the OM is fresh phytodetritus or similarly labile material, carbon content might be ~ 40 -50% by weight; hence 25 g OM would translate into 10-12.5 g C m^{-2} , which, in turn, equates to ~ 830 -1040 mmol C m^{-2} . Aerobic respiration of this amount of carbon would consume the same amount of O_2 , ~ 830 -1040 mmol C m^{-2} (i.e., 1 mol C as CH_2O consumes ~ 1 mol O_2). If the pulse is respired over, say 3-5 days, the additional SCOC

would be $\sim 166\text{--}350 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ above background – an increase of $\sim 30\text{--}70$ times above baseline ($2\text{--}6 \text{ mmol m}^{-2} \text{ d}^{-1}$). Even if only part of this OM is rapidly respired (e.g. 50–60%), the added demand still likely exceeds tens of $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$. Of course, this preliminary calculation assumes rapid respiration of the OM being all labile carbon. If the OM is more refractory, respiration may be slower, spreading O_2 demand over weeks and lowering the daily peak. Conversely, fresh phytodetritus (such as the OM associated with rapidly sinking catalyser particles in an MCFS scenario) often show rapid bacterial uptake within a few days (Moodley et al., 2002; Moodley et al., 2005).

The critical question of course is how this increased oxygen demand translates to DO concentration gradients in bottom waters and within sediments. Such calculations are more complex and subject to several variables, such as boundary layer dynamics and the oxygen diffusion from overlying bottom water into sediments.

Oxygen diffuses from overlying bottom water into sediments. The flux J ($\text{mol m}^{-2} \text{ s}^{-1}$) is related to the concentration gradient ΔC across a diffusive boundary layer thickness δ :

$$J = D \frac{\Delta C}{\delta}$$

where D (molecular diffusivity) $\approx 1\text{--}2 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$ for oxygen in seawater (Boudreau, 1997; Glud, 2008; Yuan-Hui & Gregory, 1974). For an oxygen demand of $200 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (within the range of $\sim 166\text{--}350 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ described above) and assuming a diffusive boundary layer thickness of 0.5 cm, the flux $\approx 67 \text{ } \mu\text{mol L}^{-1}$, suggesting that bottom water DO concentrations near the sediment could be drawn down by tens of $\mu\text{mol L}^{-1}$ compared to ambient. For pulses causing several hundred $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in oxygen demand the drawdown could exceed ambient bottom-water concentrations ($\sim 200\text{--}250 \text{ } \mu\text{mol L}^{-1}$ at 1000–2000 m), potentially driving near-sediment to near-anoxic conditions at the sediment water interface (see Table 3-3).

Initially, bottom water may buffer some demand, but as the SCOC is heightened over 3–5 days (see calculation above) oxygen may be severely depleted. Afterwards, diffusion would gradually restore oxygen over days to weeks. Enhanced consumption also reduces oxygen penetration depth into sediments affecting redox-sensitive processes such as nitrification and denitrification. Of course, bottom currents and bioturbation can enhance oxygen supply, but in very quiescent deep-sea settings, boundary layers may be thicker and exacerbate O_2 drawdown.

The responses from the benthic biota will likely vary among microbial, meio-, macro-, and megafaunal components. Bacteria and protozoa are likely to rapidly respire labile organic carbon, rapidly colonizing and multiplying on the phytodetritus, driving most of the immediate oxygen consumption (e.g. Cecchetto et al., 2023; up to 98%, de Jonge et al., 2024), which can lead to bloom-like heterotrophic responses in surface sediments (Gooday, 2002; Gooday et al., 1990). As oxygen is depleted, suboxic, hypoxic, and anoxic processes become more prominent in deeper sediment layers, and accumulation of reduced metabolites such as ammonium and sulphides may occur if anoxia persists (Glud, 2008). Some meiofauna and small macrofauna groups can exploit the fresh detritus, increasing feeding activity and growth if oxygen remains sufficient. Pulse chase tracer studies show uptake of ^{13}C -labeled detritus (although limited in some cases) by meiofauna within days (e.g. de Jonge et al., 2024; Ingels et al., 2011; Ingels et al., 2010; Middelburg et al., 2000; van Oevelen et al., 2011; Witte et al., 2003b), but some studies that have investigated natural POC fluxes indicated potential increased activity but not necessarily increased abundances (Veit-Köhler et al., 2011). In contrast, infaunal foraminifera –

a diverse group of prokaryotes that is well represented within the same size range as meiobenthos - are likely more efficient at exploiting newly arrived OM (Gooday et al., 1996; Gooday et al., 1990). Of interest here, particularly with regards to the AOI, is the study by Nodder et al. (2007) on the Chatham Rise, where episodic phytodetrital deposition did not seem to have promoted bacterial biomass; possibly attributable to: 1) low local bacterial abundance in some cases, 2) the potential predation of bacteria by meiofauna and macrofauna, and 3) time delays in the bacterial biomass response (Witte et al., 2003a; Witte et al., 2003b). The role of macrofauna in phytodetritus processing has been observed to be variable in different studies, with some observations showing a rapid and important macrofaunal contribution to initial carbon degradation (Witte et al., 2003a; Witte et al., 2003b) and others not (de Jonge et al., 2024). Deep-sea megafauna (organisms visible on the seafloor through imagery or video) are also known to respond to POC changes through significant alterations in abundance or community changes, although often such changes are delayed relative to the arrival of the flux (Bett et al., 2001; Billett et al., 2010; Ruhl, 2008; Ruhl & Smith, 2004).

Table 3-3: Hypothesized scenario of extra oxygen demand from a 25 g m⁻² organic matter pulse

Step	Assumption
Organic C fraction	40 % of dry mass $\Rightarrow$ 10 g C m⁻² ($\approx$ 830 mmol C) m ⁻²
Aerobic stoichiometry	1 mol C $\Leftrightarrow$ 1 mol O ₂ $\Rightarrow$ 830 mmol O₂ total demand
Reactivity scenario	60 % of the carbon is labile and respired within 4 days (based on pulse-chase experiments) (Witte et al., 2003b)
Extra SCOC	$(0.60 \times 830 \text{ mmol m}^{-2}) \div 4 \text{ d} \approx$ 125 mmol O₂ m⁻² d⁻¹ ($\approx$ 20–40 $\times$ background)

Many larger infauna and epifauna have limited tolerance to low oxygen. If near-sediment oxygen drops below species-specific thresholds (often $<60 \mu\text{mol L}^{-1}$), they reduce activity, may migrate vertically (if possible). Prolonged hypoxia can cause mortality or reduced bioturbation and feeding (Diaz & Rosenberg, 1995). A feedback mechanism in the sedimentary environment that should also be considered is that under low-oxygen conditions bioturbation by infauna is often reduced. This would limit sediment-water exchange and potentially exacerbate local oxygen depletion and slow benthic community recovery. Megafaunal filter feeders (sessile organisms, sponges, corals) may benefit initially from enhanced particulate supply, but if oxygen decline persists, they will experience stress. Deep-sea corals and sponges typically require well-oxygenated waters; even moderate declines can impair respiration and growth, potentially leading to sublethal stress or mortality if prolonged.

In a scenario where the OM flux to the seabed is of such magnitude that enhanced respiration of the OM evokes suboxic or hypoxic conditions, we can hypothesize that successional processes and longer-term effects may take place. Initially (within a matter of days), microbial respiration is likely to dominate, resulting in oxygen drawdown near the sediment surface, with opportunistic taxa exploiting the detritus. Within the weeks that follow, oxygen diffusion and currents are likely to restore oxygen levels and redox conditions in the sediments are likely to normalize. Microbial taxa will continue processing the refractory matter, the remineralisation of nutrients will peak, and benthic fauna will gradually resume baseline activities if sub- or hypoxic conditions did not deleteriously impact the resident benthic communities. It is important to

note, however, that repeated, or very large pulses can lead to organic accumulation, altered community composition favouring tolerant species, or even anoxia at the scale of the deposition (i.e., the scale of the MCFS activity) causing long-lasting changes. However, single moderate pulses often result in resilient, transient responses, especially where bottom-water oxygen replenishment is adequate and pulses are not too frequent (See Results from NIWA project “Resilience of deep-sea benthic communities to the effects of sedimentation (ROBES)” presented during research webinar, Thu 30 June 2022. Results from the project are being published in a special issue “Effects of sedimentation in the deep sea” in the New Zealand Journal of Marine and Freshwater Research. The webinar presentation slides can be found [here](#)).

Specific considerations for the AOI - New Zealand waters at 1000 – 2000 m water depth

At 1000-2000 m around New Zealand, bottom waters are typically well-ventilated (e.g., $>200 \mu\text{mol L}^{-1}$), which offers some buffer against natural pulses of OM. However, a very large additional pulse (e.g. 25 g OM m^{-2} as hypothesized in the ‘worst case scenario’ for GB’s MCFS activities) could still deplete the oxygen levels and affect all benthic components. Natural pulses of phytodetritus may be seasonal but generally smaller than the hypothesized maximum MCFS scenario (Natural: $\sim 1\text{--}20 \text{ mg C m}^{-2} \text{ d}^{-1}$, see Table 3-1 and Table 3-2, vs estimated $10\text{--}12 \text{ g C m}^{-2}$ for maximum MCFS scenario, which is a three to four order of magnitude difference), the latter being more akin to the mass flux observed for significant seafloor sediment disturbance such as the one conducted for the ROBES (Resilience of deep-sea benthic communities to the effects of sedimentation) Project on the Chatham Rise (Nodder et al., 2025). Note also that the AOI is situated mainly south of the Chatham Rise, in a HNLC area where POC fluxes are likely lower than observed for natural events at the Chatham Rise (Nodder et al., 2016; Nodder & Northcote, 2001).

Summary points

- Spatial and temporal variation in sediment community oxygen consumption (SCOC) on Chatham Rise indicates background SCOC of $\sim 2\text{--}6 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in 1000–2000 m depths (Leduc et al., 2020a)
- Diagenetic models relating organic carbon flux to benthic oxygen demand show that large pulses can drive SCOC to tens or hundreds of $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Christensen, 2000; Jørgensen et al., 2022)
- *In situ* pulse-chase experiments globally demonstrate that $\sim 90\text{--}96\%$ of labile detritus can be respired within $\sim 1.5\text{--}2$ days, with bacteria dominating short-term uptake (SCOC database by Stratmann et al., 2019 and references therein)
- Hypoxia effects on benthic fauna: many macrofauna and megafauna show stress or mortality when O_2 falls below $\sim 60 \mu\text{mol L}^{-1}$, with severe impacts $<20\text{--}30 \mu\text{mol L}^{-1}$ (Diaz & Rosenberg, 1995)
- NZ-focused disturbance studies (NIWA ROBES project) note changes in seafloor community oxygen consumption with disturbance, highlighting resilience but also sensitivity to large perturbations
- A pulse of $\sim 10\text{--}12 \text{ g C m}^{-2}$ ($\approx 25 \text{ g OM m}^{-2}$ with 40-50% C) over a few days at 1000–2000 m is expected to raise SCOC by tens to hundreds of $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$,

dwarfing background rates ($\sim 2\text{--}6 \text{ mmol m}^{-2} \text{ d}^{-1}$) and potentially depleting oxygen near the sediment interface to very low concentrations ($< 50 \text{ } \mu\text{mol L}^{-1}$) for the duration of the pulse.

- Microbial communities will rapidly respire the labile fraction within 1–2 days, but oxygen replenishment via diffusion and advection may lag, causing transient hypoxia in the boundary layer.
- Benthic fauna: small and opportunistic organisms may exploit the pulse if oxygen remains above their tolerance; larger and more oxygen-sensitive fauna (e.g., sponges, corals) may experience stress, reduced feeding, or even mortality if exposure to low oxygen is prolonged.
- Recovery: Once the pulse subsides, oxygen levels may gradually recover over days to weeks; microbial processes continue processing refractory matter. Community composition may shift slightly if some sensitive species suffer during the pulse, but in a well-ventilated setting (i.e. currents, bioturbation). It is reasonable to expect some resilience unless pulses are frequent or larger.

Uncertainties and caveats

- The organic composition of the OM arriving at the seafloor plays an essential role in determining how the benthos will respond and how it will affect oxygen consumption. Labile vs. refractory fractions greatly affect respiration rates. Our estimates of C-content of the OM (40 – 50% C) were based on fresh organic material that originated in euphotic surface waters and sank rapidly to the seafloor. Moreover, 9(2)(b)(i), 9(2)(b)(ii) [REDACTED]
[REDACTED]. A higher refractory content would smear demand over weeks, lowering peak O_2 demand.
- Substantial spatial heterogeneity may occur in the distribution of the particles on the seafloor as deposition is seldom uniform, creating local hotspots that see steeper O_2 reductions, interspersed with low-activity areas which will be less affected.
- Bottom currents, internal waves, and bioturbation modulate oxygen supply and stronger currents mitigate oxygen drawdown. *In situ* observations and data should be gathered to document these processes.
- The boundary layer thickness may vary from general averages and those used above, which is likely to affect estimated oxygen demand calculations
- Empirical data forms the backbone of accurate predictions. These estimates are approximate and based on available literature from New Zealand and analogous deep-sea settings. For site-specific assessments within the AOI, direct measurements (e.g., *in situ* benthic chamber incubations, oxygen micro-profiles) following experimental addition of known organic quantities would provide more precise oxygen consumption rates and concentration changes. However, from the literature a 25 g OM m^{-2} pulse at 1000–2000 m is large enough to likely cause

substantial transient oxygen drawdown and measurable impacts on benthic communities, with potentially longer lasting effects.

- Current estimates are based on information available mostly from areas outside the AOI which are likely to have different environmental characteristics (e.g., from the more productive Chatham Rise compared to the HNLC waters to its south).

It is worth considering pressures that may be caused by sedimentation in the context of MCFS activities, since the particles used as catalyser for the growth of phytoplankton in surface waters will descend to the seafloor together with the phytoplankton and associated microbial organisms. Depending on the nature of the particles, different kinds of impacts can occur. Based on what we know at the time of report writing, we can assume that the particle under consideration is cellulose based, and hence of an organic but refractory nature. It is considered biodegradable, but not as labile as fresh phytoplankton or fresh detritus that arrives at the seafloor quickly through rapid sinking rates and may therefore cause additional pressure beyond the arrival of OM alone.

Organic matter pulses and sedimentation events can both cause physical smothering by burying or covering benthic organisms and habitats, especially small or sessile fauna such as sponges, corals and foraminifera; and they both can affect oxygen dynamics at the sediment-water interface. Organic matter increases microbial oxygen demand, while thick sediment layers can create oxygen barriers. However, they do differ in several different aspects:

Table 3-4: Generalized differences between organic matter pulses and sedimentation effect on benthic communities

Factor	Organic Matter Pulse	Sedimentation Event
Nature	Biogenic (nutrient-rich)	Abiotic (inorganic, often nutrient-poor)
Effect on Food	Increases food supply for benthos	No food value (often dilutes food quality)
Microbial Respiration	Stimulates bacterial activity, O ₂ demand rises	Less direct effect, may suppress activity
Short-Term Respiration	Can cause rapid blooms in opportunists (e.g. certain polychaetes, holothurians, foraminifera)	Can cause stress or mortality, slow recovery
Long-Term Respiration	Boosts productivity, but risk of hypoxia if pulse is large	May lead to chronic stress, habitat loss, reduced biodiversity
Recovery	Often rapid (weeks to months), unless hypoxia occurs	Can be slow (years), depends on sediment thickness and type

4 Thresholds

4.1 Threshold frameworks

Thresholds are defined levels of key environmental drivers, such as dissolved oxygen, organic loads, sedimentation, or turbidity, beyond which ecological harm has occurred or is likely to occur (Glasson, 2008; Groffman et al., 2006). In addition, thresholds can refer to a tipping point where beyond which a small change in environmental conditions can cause a significant and often abrupt shift in the ecosystem's state or function. The establishment of thresholds is helpful to environmental management, but determining a threshold requires multiple research components coming together under a framework from where realistic scenarios can be considered. Three general response types can be identified (Foley et al., 2015).

1. **Linear response:** gradual, proportional change with increasing pressure from the driver.
2. **Continuous threshold** response (abrupt): a sudden shift once a critical driver level is reached.
3. **Discontinuous threshold** response (hysteresis): alternative stable states where returning the driver to pre-disturbance levels does not immediately restore the original state. Hysteretic systems are of particular concern because recovery often requires reducing multiple pressures and can follow a different, slower pathway than degradation, or recovery to the original state may not occur at all.

Other key points about ecological thresholds that should be considered include:

1. **Abrupt Changes:** When a threshold is crossed, the ecosystem can shift rapidly from one state to another. For example, a coral reef might suddenly shift to an algal-dominated state due to changes in water quality or temperature.
2. **Resilience and Stability:** Ecosystems have a certain level of resilience, meaning they can absorb disturbances without changing state. However, if the stress exceeds a certain point, the system's resilience is overwhelmed, leading to a new stable state.
3. **Non-linear Dynamics:** Thresholds are often associated with non-linear responses, meaning the ecosystem's response to stress is not always proportional to the amount of stress applied. This non-linearity makes predicting and managing thresholds challenging.

Understanding thresholds is vital for resource management. It helps in setting targets and developing strategies to avoid crossing these critical points (e.g., maintaining water quality and controlling fishing pressures can help prevent undesirable shifts in marine ecosystems (Foley et al., 2015)).

Regulatory thresholds and threshold-based frameworks already exist to support science-based environmental management and help manage levels of human impacts on aquatic ecosystems (Glasson, 2008; Groffman et al., 2006). Regulatory thresholds are often implemented, however, as a response to a dramatic observed change in an ecosystem that can have harmful

consequences. Conversely, thresholds can also be developed prior to such impacts occurring, pre-empting damage to the environment (Groffman et al., 2006). Thresholds can be:

1. **Science-based:** thresholds based on empirical ecological data.
2. **Precautionary:** thresholds that incorporate levels of uncertainty and adopt conservative limits.
3. **Socially and Regulatorily acceptable:** thresholds that align with different stakeholder values.

One interesting example of where ecologically relevant thresholds are being developed is for the emerging industry of deep seabed mining, where national and international regulatory frameworks are being developed to manage the risks, impacts, and outcomes of resource extraction in the deep sea (Kaikkonen et al., 2025). Importantly, the regulatory framework is being developed before any extraction will occur, following the principles of the precautionary approach and to pre-empt ecological damage and prevent the occurrence of serious or irreversible harm prior to extraction taking place (Hitchin et al., 2023). In addition, the definitions of ecological damage and serious or irreversible harm need careful consideration in accordance with the establishment of threshold levels, so that realistic pressure scenarios can be linked with regulatory language. For deep-sea mining, Leduc et al. (2024) recently defined the term “serious harm” based on existing documentation and ecological criteria, and proposed a three-tier traffic light scheme with detectable harm (green), significant harm (orange), and serious harm (red). In this process, threshold frameworks can be of great use and provide template approaches to newly developing threshold frameworks.

Notable similarities can be drawn between deep-sea mining and mCDR; both operate in environments with limited baseline ecological knowledge and high uncertainties about potential impacts (Levin et al., 2023; Smith et al., 2020). Because of this lack of information, a structured, adaptive approach is needed, whereby initial precautionary (conservative) thresholds are developed that can be revised as knowledge improves, instead of waiting for the perfect data to be collected. The lack of ecological information and general data scarcity result in uncertainty about baseline ecological conditions needed to determine effective thresholds. Both require the identification and monitoring of thresholds; but this can be complicated by the high variability in different kinds of pressures operating simultaneously, hampering translation of ecological impacts to threshold values (Hillebrand et al., 2020). An additional challenge is to reconcile the different perspectives of the different stake holders, which may have conflicting views on what levels of harm or deterioration are acceptable and the degree of precaution.

A hypothetical threshold-setting framework for mCDR, structured around the deep-sea mining approach (Hitchin et al., 2023), could be as follows:

1. Defining clear objectives and environmental values: identifying what needs protection, such as benthic community integrity, oxygen levels, food web stability, water column chemistry, ecosystem services; and setting ecosystem and social goals, such as “no serious or irreversible harm to deep-sea fauna”, “no persistent hypoxia”, the “preservation of essential ecological functions”.

2. Assessing baseline ecological conditions: establishing baselines for key variables before intervention, such as dissolved oxygen, pH and carbonate chemistry, benthic biodiversity and abundance, and sedimentation rates.
3. Developing a monitoring plan: Developing a robust monitoring strategy that covers the relevant spatial and temporal resolution, indicators species, and the types of technology that should be used.
4. A dual system approach to identifying thresholds, beginning with
 - a. Warning or “soft” thresholds, with conservative limits that, if exceeded, trigger increased scrutiny, adaptive management, or temporary halts, based on, for instance: dissolved oxygen (e.g., drop of O₂ by >10% from baseline conditions at any monitoring site for >7 days); or a pulse of OM deposition (e.g., that exceeds historical maximum by 20%).
 - b. Action or “hard” thresholds, with more stringent, non-negotiable limits that, if exceeded, would require suspension of activity and management intervention, based on, for instance: dissolved oxygen <1.5 mg/L for >24 hours in benthic zones; pH drop below the regional minimum tolerance for key benthic species; or a >30% reduction in sentinel species abundance vs. baseline over three consecutive monitoring periods.
5. SMART threshold characteristics
 - a. Specific: e.g., O₂ concentration at 1000 m depth at a particular site.
 - b. Measurable: “mg/L daily mean values”.
 - c. Achievable: Based on best-available monitoring technology.
 - d. Relevant: Tied to biological/ecosystem function.
 - e. Time-bound: Exceeding thresholds defined over clear periods, e.g. sustained for 7 days.
6. A system based on decision triggers and response actions
 - a. If warning threshold crossed: increase monitoring frequency; implement pre-agreed mitigation (e.g., scale back the activities, deploy recovery measures); independent expert review.
 - b. If action threshold crossed: Immediate halt of mCDR activity; investigate cause of exceedance and remediate where possible; a comprehensive review before activity may resume.
7. Put in place adaptive management and iterative review
 - a. Review thresholds and monitoring data at regular intervals (e.g. annually or after major activities or event).
 - b. Refine thresholds as new data, technology, and ecological understanding emerge.

- c. Stakeholder involvement in reviews of the activity and thresholds, considering scientific evidence, regulatory priorities, indigenous importance, and public consultation.
8. Engage with stakeholders, by early, transparent consultation with regulators, independent scientists, local and indigenous communities, NGOs, and Industry.
9. Documentation and Accountability: Thresholds, rationale, monitoring results, and management responses must be transparent and publicly reported in conjunction with a third-party audit or independent oversight.

The hypothetical framework described above is **precautionary** (limits unintended consequences), **adaptable** (allows for improvement as science and knowledge advances), and **accountable** (ties action to transparent, measurable outcomes). In this scenario, threshold values for environmental variables in a deep-sea context like mCDR or deep-sea mining are typically based on a combination of published ecological studies (field or lab data on organism tolerances), monitoring data (from previous projects or reference sites), regulatory precedents (from similar industries, e.g., oil and gas, fisheries), precautionary values (where data is scarce, thresholds are met more conservatively, sometimes using “expert elicitation”), and ecosystem function modelling (e.g. biogeochemical models predicting oxygen depletion effects).

4.2 Applicability of thresholds under New Zealand law

The Exclusive Economic Zone & Continental Shelf (Environmental effects) Act 2012 (“EEZ Act”) is effects-based and does not contain “hard” numbers for key variables, such as dissolved oxygen or sediment organic carbon. Instead, it says the EPA decision makers should “avoid, remedy, or mitigate” adverse effects and give special weight to “sensitive environments” (such as cold-water corals, hydrothermal vents, etc.) that are listed in the Permitted-Activities Regulations 2013. Applicants must file a Sensitive-Environments Contingency Plan, that sets trigger values for key stressors (EPA’s Form 3: Initial environmental assessment and sensitive environments contingency plan). This allows the EPA decision-makers to borrow the best available national guidelines (e.g., the [ANZECC & ARMCANZ 2000 Water Quality Guidelines](#)) and the latest peer-reviewed science when it writes site-specific consent conditions. A brief synthesis is provided below of numeric values that have been used in consent conditions or environmental-effects assessments for deep-sea projects (e.g., mining, dredge dumping, oil-and-gas discharges) inside the Aotearoa New Zealand EEZ (Table 4-1). Where the legislation itself is non-specific, the EPA guideline that is usually cited can be provided, as well as the supporting data from New Zealand studies that have convinced the EPA those numbers are ecologically relevant.

The EPA typically uses the above-mentioned numbers in assessing pre-consent modelling of proposed activities in the deep sea, with, for instance, predicted sediment plumes or organic discharges that should be kept within the threshold values. Moreover, numeric limits (e.g., “DO shall not fall below 5 mg L⁻¹ for more than 2 hours”) and monitoring frequencies can be written directly into consents as conditions, and breaches can trigger a shutdown and activation of a contingency plan based on adaptive management. Furthermore, if mapping shows that vulnerable marine ecosystems (e.g., cold-water corals, sponge gardens, vent fields) lie within the footprint of the activity, the EPA can require a sensitive-environment buffer (e.g., 250 m) and modelling output that demonstrates that the thresholds will not be exceeded. Finally, the [2013](#)

[EEZ and Continental Shelf \(Environmental Effects\) Amendment Act](#), entered into force in 2015, excluded the application of adaptive management to marine discharge consents; i.e., requiring a priori evidence that thresholds will be met instead of relying on adaptive management based on more relaxed limits in an iterative process.

Table 4-1: Examples of threshold variables with numerical values based in science conducted in deep-sea environments that have been applied in Aotearoa New Zealand EEZ consenting processes.

Variable	Working trigger used in EEZ consents	Scientific basis for deep-sea environments
Bottom-water dissolved oxygen (DO)	$\geq 6 \text{ mg L}^{-1}$ target; never below 5 mg L^{-1} in the mixing zone (ANZECC “high value” default)	Live reef-forming stony corals (<i>Solenosmilia variabilis</i> , <i>Madrepora oculata</i> , <i>Goniocorella dumosa</i>) disappear where DO drops to $\approx 3.8 \text{ mg O}_2 \text{ L}^{-1}$ on seamounts (Graves et al., 2022a; Thresher et al., 2014) but found at $\sim 5.9 \text{ mg O}_2 \text{ L}^{-1}$ in AAIW (Bostock et al., 2015). Canyon/slope meio- and macro-fauna tolerate much lower DO, but species richness reduces substantially at $< 1 \text{ mg O}_2 \text{ L}^{-1}$ in Kaikōura Canyon (Leduc et al., 2014)
Particulate organic-carbon (POC) flux to seafloor	No fixed legal limit: EPA asks for modelling to show any activity keeps flux $\leq 0.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ on nearby coral reefs	Habitat-suitability models for 12 protected coral taxa show occurrence probability falls sharply when long-term flux exceeds $0.6\text{--}0.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Anderson et al., 2018, 2020; Anderson et al., 2014)
Sediment total organic carbon (% TOC)	Consent conditions typically require that TOC in the top 5 cm does not rise $> 40\%$ above baseline outside a 250 m mixing zone.	(i) Significant macro-faunal biomass associated with $> 0.6\%$ TOC in Kaikōura Canyon, cf. $< 0.4\%$ on open slope; (ii) experimental mining plume on Chatham Rise caused measurable biodiversity loss when surficial TOM hit $\approx 4.8\%$; recovery began once it fell back $< 3\%$ (Hale et al., 2025; Mountjoy et al., 2018)
Chloroplastic Pigment Equivalents (CPE) – freshness of deposited phytodetritus	Not used in legislation; research trigger for canyon effects: $\geq 10 \mu\text{g CPE g}^{-1}$ marks switch to eutrophic conditions, opportunistic nematode assemblages	Kaikōura Canyon sediments averaged $18\text{--}45 \mu\text{g CPE g}^{-1}$, cf. open-slopes $2\text{--}8 \mu\text{g CPE g}^{-1}$ (Leduc et al., 2014)

In practical terms this could mean that bottom DO must exceed $5 \text{ mg O}_2 \text{ L}^{-1}$ and that long-term organic inputs fall below $0.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ (i.e., taking the most stringent constraints based on cold-water coral reef findings; Table 4-1). In a similar fashion, determination that canyon and slope sediments can accommodate more OM, but once surficial TOC rises past $\sim 5\%$ or DO falls $< 1 \text{ mg O}_2 \text{ L}^{-1}$ benthic communities’ transition suddenly to low-diversity, opportunistic assemblages that regulators may flag as ecological degradation. The derived threshold numbers (based on suitable empirical evidence) may be used as design targets when seeking EPA marine consent (since the EPA may use these as expected threshold values) unless stronger, site-specific evidence is provided.

The NZ EPA’s structural conditions across several recent deep-sea consents can be paraphrased as a compliance architecture that recurs in EPA decisions. In practice, a tiered compliance approach is applied, with limits commonly divided into: (1) “alert” levels that trigger extra monitoring or operational tweaks, and (2) “compliance” levels that, if breached, force activity to stop while an adaptive management response is developed and implemented. Limits are also tied to determined spatial scales around impacted locations so that measuring efforts can be positioned spatially to assess compliance in the appropriate areas. In addition, numeric values, such as used for Chatham Rock Phosphate and Trans-Tasman Resources, can be based on laboratory or field-derived stress-thresholds for key taxa (e.g., cold-water corals, demersal fish, infaunal worms). Evidence-based information on thresholds gathered during the first 1-2 years of operations can be used to update the conditions set within the consent, allowing this to be refined and adapted to the latest evidence. These ideas – based on EPA consent schedules and decisions – can be summarized as shown in Table 4-2. Based on EPA decisions the use of numerical limits for activities in deep-sea environments within New Zealand’s EEZ is demonstrated, using the wording of the relevant condition or schedule excerpt, and how the limit is designed to protect benthic or pelagic communities (Table 4-3).

Table 4-2: Examples of New Zealand EPA provisions and regulatory effects in relation to empirical thresholds.

Consent (EPA file-code)	Where the ideas appear	Reference
Chatham Rock Phosphate mining consent (EEZ000006, decision Feb 2015)	<i>Tiered compliance & spatial tying</i> —Schedule 1 sets a 50 mg L ⁻¹ Total-Suspended-Solids (TSS) “monitoring threshold” and a 1 mm sediment-blanket trigger, both tied to 5 km or 7 km guard-ring distances; exceedance initiates extra sampling and, if repeated, adaptive-management actions.	(EPA, 2014)
	<i>Ecological linkage</i> —the Decision-Making Committee (DMC) notes that the numbers in Schedule 1 come from lab/field thresholds for fish eggs (2–3 mg L ⁻¹ TSS), corals, and infauna, then rounded to practical monitoring values.	(EPA, 2014)
	<i>Periodic review</i> —Condition 40-42 let Schedule 1 be “rolled forward” after the first 1-2 years once validation data show whether triggers are “too tight or too loose.”	(EPA, 2014)
Trans-Tasman Resources iron-sand mining consent (EEZ000011, Aug 2017)	Confirms the same alert vs. compliance logic: experts recommend 2–3 mg L ⁻¹ for eggs/larvae, while Schedule 1A keeps a higher 50 mg L ⁻¹ operational trigger that, if exceeded twice, forces a stop-work and adaptive response.	(EPA, 2017)
OMV Taranaki Basin marine-discharge consent (EEZ300011, 2019, amended 2025)	Uses the identical template but for chemical discharges: Schedule 1 lists per-well caps for caustic soda, lime, barite, etc.; any breach triggers an immediate report and EPA-certified mitigation plan.	(EPA, 2019)

Table 4-3: Example of three EPA decisions/consents that set numerical limits for activities in deep-sea environments within Aotearoa New Zealand EEZ.

Consent & date	Parameter & limit written into the consent	Where it applies & why
Chatham Rock Phosphate draft marine-consent conditions (Nov 2014 version circulated during the hearing)	Total Suspended Solids (TSS) “50 mg L ⁻¹ ... measured at ≥ 5 km from the edge of the mined block or ≥ 50 m above the seabed at any location.” (Schedule 1, Ref 1A in Proposed Marine Consent Conditions, Chatham Rock Phosphate Limited)	Intended to verify plume-model predictions and cap far-field turbidity so that light attenuation and clogging do not exceed levels that benthic filter-feeders can tolerate.
	Sedimentation thickness “No observed adverse impacts on benthic organisms beyond the distance predicted for 1 mm sedimentation from the mining of one block (trigger point set at ~7 km).” (Schedule 1, Ref 1C in Proposed Marine Consent Conditions, Chatham Rock Phosphate Limited)	Links a simple measurable parameter (1 mm-thick sediment blanket) to expert evidence that most Chatham Rise infauna can re-emerge through ≤ 1 mm of new material.
Trans-Tasman Resources iron-sand mining decision (Aug 2017 decision later overturned on appeal, but conditions still illustrate EPA practice)	Fine-grained plume thresholds for fish – expert trigger values written into the Decision-Making Committee (DMC) report: 3 mg L ⁻¹ TSS ⇒ likely fish avoidance zone. 2 mg L ⁻¹ TSS ⇒ threshold to protect eggs & larvae. Decision of marine consent application, Chatham Rock Phosphate Limited, to mine phosphorite nodules on the Chatham Rise	The DMC agreed these should be the “alert/compliance” levels in any operational Environmental Monitoring and Management Plan, even though the applicant had proposed a higher 50 mg L ⁻¹ verification threshold.
	Adaptive-management “compliance” value proposed by applicant – 50 mg L ⁻¹ TSS (Schedule 1A). The DMC remarked this was too high to give confidence that the 2–3 mg L ⁻¹ ecological triggers would be met. Decision of marine consent application, Chatham Rock Phosphate Limited, to mine phosphorite nodules on the Chatham Rise	Shows how the EPA tests whether proposed numbers really translate expert ecological advice into enforceable conditions.
OMV Taranaki Basin marine-discharge consent EEZ300011 (granted Oct 2019; amended Mar 2025)	Chemical-specific mass/volume caps per well (Schedule 1 extract): Caustic soda ≤ 2.4 t site; Performatrol shale-stabiliser ≤ 40 m ³ site; Lime ≤ 2 t site with similar caps for 18 other drilling additives and trace hydrocarbons. Decision on marine discharge consent application, OMV New Zealand Limited, EEZ300011m October 2019; available	Numeric caps ensure the cumulative toxic-loading (especially metals & biocides) from water-based mud discharges remains below ANZECC-trigger concentrations once mixed in the water column. EPA audits actual volumes against these maxima after each drilling campaign.

Considering all the above, the logical next step is to establish a threshold matrix for each taxon, sensitive habitats, and communities, in the AOI of the planned MCFS activities, whereby the tolerance, recoverability, sensitivity, and evidence/confidence levels are determined relative to each of the relevant pressures caused by the specific MCFS activity. This could be used to identify a set of definable pressure pathways for which specific responses from the benthic ecosystem, individual taxa or groups of taxa, as well as from functional groups or even ecosystem functions and services can be quantified. Below we have constructed such an approach for sensitive environments and specific taxa in the AOI, based on field, experimental, and available regional and international data.

It is important to note is that the preliminary results presented here will require significant additional survey data to be gathered as well as a range of experiments to test MCFS specific products and processes *in vitro* and *in situ*, which can then be followed up on by using modelling approaches as well as survey-based ground truthing. The information presented below with regards to thresholds is heavily reliant on inferences from international literature and case studies that may not directly apply to the AOI. The current empirical knowledge required to develop suitable thresholds for sensitive environments, representative species, groups of taxa, habitats, and ecosystems within the AOI is insufficient to support reliable application into practical or regulatory consent development.

4.3 MCFS pressures on benthic ecosystems

As a result of MCFS activities it is expected that the benthos will be subject to several pressures associated with the arrival of substrates and OM which will affect their behaviour or elicit changes in benthic species, populations and communities and their ecological functioning. MCFS is a new technology, which remains - to our knowledge - untested in terms of assessing the realistic *in situ* impacts on the environment where the particles will be released and ultimately deposited. We therefore identified to our best ability the most similar analogues for the expected pressures on benthic ecosystems resulting from MCFS activities, namely: 1) the arrival of pulses of relatively fresh OM on the seafloor, 2) the arrival of physical particles on the seafloor, in the absence of *in situ* data on MCFS-specific particle depositional characteristics, we used sedimentation as an analogous pressure, and 3) oxygen decline at the seafloor as a result of the respiration and remineralisation of sizeable quantities of newly deposited OM.

Note that this exercise is limited by the fact that we did not have details on the biogeochemical characteristics of the particles, particle behaviour in-situ during the proposed MCFS activity (e.g., growth, flotation, sinking, remineralization and degradation), particle accumulation rates, and definitive information on particle settling worst-case scenario.

4.4 Sensitivities and thresholds for specific taxa

Below, we review several key taxa that bear importance to New Zealand's legislative environmental framework (described in Section 1.4.2 Legal framework considerations) and for which we have observational evidence of their presence in the AOI.

For each taxon, we provide information on how they may be referred to in relevant legislation, a brief overview of their ecology, and their sensitivities to deoxygenation, OM pulses, and sedimentation/turbidity. Their occurrence in the AOI is described in Beaumont et al. (2025). We then use available literature and data to assess whether taxon-specific thresholds can be

modelled around the taxon's identified sensitivities, presenting visual representations of the 'health' of each taxon under different magnitude or intensity levels for each pressure.

The resulting information can facilitate the development of a threshold framework to identify under which MCFS scenarios negative impacts on these taxa can be expected, although we note – as above – that substantial caveats and uncertainties remain in the development of all the here presented health or sensitivity models. Caveats are caused by the unavailability of data specific to the relevant taxa, sensitive environments, AOI, and limited understanding about the pressure-response processes of relevant taxa. For instance, for species included in this review below, there is limited information on ecological impacts of changing environments, and any lab studies generally manipulate one parameter (so we don't know about multiple stressor impacts) and don't provide info on responses across the whole life cycle (generally only the adult stages are used in the experiments, and these are naturally more resilient). The threshold models are therefore based on limited information and often not known for New Zealand-specific species.

Moreover, the health or sensitivity model output does not consider any temporal aspects of the pressure and response dynamics, e.g., a taxon may show resilience in its health model to low oxygen, but this may only be valid for short periods of time, whereas prolonged exposure to low oxygen levels may be detrimental but not visualized in the model outputs. In addition, information on sensitivities, thresholds, and pressure responses for specific taxa, does not imply that similar sensitivities, thresholds, and pressure responses are valid at other levels of biological or ecological organization, such as the population and community levels, as well as at the level of the habitat or ecosystem.

4.4.1 Deep-sea brachiopods (Bathyal 200-3000 m, New Zealand)

Legislation: Under New Zealand's legal framework, brachiopods are specifically recognized—not within the Continental Shelf Act 1964 itself—but within the species- and habitat-based regulations that sit beneath the EEZ Act. Specifically, Schedule 6 defines a “brachiopod bed” as an area containing one or more live brachiopods per square metre. Therefore, any permitted activity within the EEZ or maritime continental shelf must consider impacts on brachiopod habitats.

Ecology: Brachiopods (lamp shells) are marine lophophorates with a rich fossil history, represented today by both articulate (hinged calcite-shelled) and inarticulate (non-hinged, e.g. phosphatic or cemented) groups. New Zealand waters host about 38 living brachiopod species (26 genera), ranging from the intertidal zone to abyssal depths (MacDiarmid et al., 2013). Many species are concentrated on the continental shelf and upper slope (<500 m), but several cosmopolitan taxa extend into the bathyal zone (>1000 m) (MacFarlan et al., 2009). These sessile suspension-feeders usually attach to hard substrates (rock, gravel, shell debris) via a pedicle or cementation, and favour areas of strong water movement and low silt accumulation (MacDiarmid et al., 2013). Brachiopods tend to live in environments where natural sedimentation rates are low (e.g. rock outcrops, current-swept slopes), so they are evolutionarily unprepared for high sediment loads. In New Zealand's relatively oligotrophic deep seas, brachiopods likely rely on the steady but low flux of marine snow and availability of nutrients, thriving in currents that keep food particles in suspension (MacDiarmid, 2007; MacDiarmid et al., 2013; MacFarlan et al., 2009).

Brachiopod aggregations create three-dimensional structure on otherwise flat or rocky seabed (Angeletti et al., 2020; Toma et al., 2022). While they do not form large reefs like corals or

sponges, dense brachiopod beds (“carpets”) can reach densities of several hundred to ~1000 individuals per m², especially in regions like New Zealand and the Mediterranean (Angeletti et al., 2020; MacDiarmid, 2007). These carpets, including multiple layers of live and dead shells, enhance habitat heterogeneity by providing micro-refuges and attachment sites for other organisms. Accumulated empty shells create biogenic gravel, further increasing substrate complexity and offering shelter for small invertebrates and juvenile fish. Thus, brachiopods act as ecosystem engineers on hard bottoms by maintaining structured habitats analogous to oyster or mussel beds in shallow waters.

The physical complexity of brachiopod beds supports a diverse assemblage of benthic life. Brachiopod shells serve as attachment surfaces for encrusting sponges, bryozoans, and small corals, and provide habitat for mobile fauna such as brittle stars, crustaceans, and polychaetes. In dense assemblages, brachiopods co-occur with other habitat-forming species (e.g., sponges, corals), forming mosaics that boost local species richness. Although brachiopods lack obligate symbionts, their presence is correlated with increased faunal diversity and biomass compared to adjacent bare substrate (MacDiarmid et al., 2013).

As filter feeders, brachiopods process suspended organic particles, converting them to biomass and detritus (faecal pellets and pseudo-faeces) that transfer carbon and nutrients to the seabed. Their shell production contributes to long-term calcium carbonate accumulation, forming shell hash deposits that are eventually buried in marine sediments, thus aiding local carbon sequestration (MacDiarmid et al., 2013). Additionally, brachiopod beds may facilitate further carbon burial by baffling currents and enhancing the deposition of fine OM, and their shells provide substrate for microbial colonization.

Brachiopod beds may serve as nursery grounds for juvenile invertebrates and fishes, with shell crevices offering protection from predation and strong currents. These beds contribute to the resilience and stability of benthic communities by maintaining habitat continuity; even after death, brachiopod shells persist and continue to provide structural and ecological value.

Sensitivity to oxygen availability and deoxygenation

Deep-sea brachiopods generally exhibit a high tolerance for low-oxygen conditions relative to many benthic animals (Jackson, 2000). They have very low metabolic rates – roughly half the oxygen consumption of equivalently sized bivalve molluscs (Jackson, 2000). Experimental observations show brachiopods can sustain anaerobic metabolism for 3–5 days when oxygen is extremely limited (Jackson, 2000). In fact, some articulate brachiopods are known to inhabit oxygen-poor environments; for example, *Terebratulina unguicula* has been found in settings where dissolved O₂ frequently falls below 0.1 mg L⁻¹ (Jackson, 2000). Brachiopods lack specialized gills, instead absorbing oxygen across the lophophore and mantle surface, and they often possess the respiratory pigment hemerythrin in coelomic cells to aid oxygen transport (Ruppert et al., 1994). Their “oxygen minimum” requirement is so low as to be nearly unmeasurable – a reflection of their ancient, energy-efficient physiology (Ruppert et al., 1994). This means that short-term hypoxic episodes (days to perhaps a few weeks) can be endured by brachiopods with minimal mortality (Ballanti et al., 2012; Shumway, 1982). Individuals respond to oxygen stress by reducing activity (e.g., pausing feeding and movement) to conserve energy (Ballanti et al., 2012; Shumway, 1982).

However, prolonged or chronic deoxygenation still poses a serious threat. If dissolved oxygen remains very low for extended periods beyond their anaerobic endurance, brachiopods will

weaken or die off (Jackson, 2000). For instance, clamping the shell closed allows a brachiopod to shut in water and slow its metabolism, but it can only delay oxygen depletion for a limited time (Jackson, 2000). Extended hypoxia or anoxia (lasting many days to weeks) would eventually exhaust their anaerobic capacity and lead to mortality. In sum, deep-sea brachiopods are tolerant of episodic low-oxygen events (giving them an advantage in fluctuating environments), but persistent deoxygenation beyond a threshold will cause reduced feeding, slowed growth, and death if oxygen is not replenished. Environmental records from past ocean anoxic events and modern OMZs suggest brachiopods likely vacate or perish in regions where O₂ falls below viable levels for long periods, despite their short-term resilience.

Sensitivity to organic matter pulses

As suspension feeders, brachiopods rely on particulate organic matter (POM) suspended in seawater (seston) for nutrition (Jackson, 2000). They use a ciliated lophophore to capture phytoplankton, microzooplankton, and detrital particles from passing currents. In the deep sea, food supply is often driven by seasonal pulses of sinking OM from surface productivity (e.g., phytodetritus from algal blooms) and sporadic events like algal bloom sedimentation or carcass falls. Deep-sea brachiopods likely benefit from moderate OM pulses, which increase the concentration of edible particles in bottom waters. During such flux events, brachiopods can feed more actively, fuelling reproduction and growth when food is available. Studies have noted that brachiopod growth rates and gamete development can be linked to seasonal cycles in food availability, with higher activity during productive periods and a quiescent state during lean periods (Williams, 2022). For example, populations of *Liothyrella neozelanica* in New Zealand fjords show very low metabolism in winter (when plankton input is minimal) and higher activity in summer, indicating an adaptation to fluctuating food supply (Williams, 2022).

While periodic POM inputs are ecologically important for deep brachiopods, excessive organic loading can have negative effects. A large pulse of organic detritus that rapidly accumulates on the seafloor (e.g., from mass algal die-off or upstream pollution) may lead to bacterial decay and oxygen depletion in bottom waters, indirectly stressing brachiopods. These animals do not directly ingest big deposits of detritus; they require the material to be broken into suspended particles. If a pulse is too intense, it can form a fluff layer on the seabed that brachiopods cannot feed on, while the microbial breakdown of that material consumes oxygen. Thus, extreme organic enrichment could create a twin stress: physical smothering by organic sediments and localized hypoxia from microbial respiration. Brachiopods' tolerance for low oxygen may allow brief survival in such conditions, but if the situation persists (low O₂ and clogged feeding apparatus), they will suffer starvation or asphyxia. Generally, OM pulses within natural ranges (such as seasonal marine snow) are a net positive for deep-sea brachiopods by providing food, whereas chronic eutrophication or dense organic deposition (as might occur near fish farms or sewage outfalls) would overwhelm their feeding and respiration capacity. (MacDiarmid, 2007; MacDiarmid et al., 2013; MacFarlan et al., 2009).

Sensitivity to sedimentation and turbidity

Brachiopods are highly sensitive to sedimentation and turbidity (fine sediments in suspension). In their preferred habitats, bottom currents keep fine sediments from accumulating, and brachiopods attach to clean hard surfaces (MacDiarmid, 2007). Excess suspended sediment can interfere with feeding: brachiopods filter particles in a narrow size range, and a sudden influx of silt or clay-sized particles can clog the lophophore or be inadvertently ingested, leading

to stress. When faced with rapid turbidity increases, brachiopods exhibit active behaviours to cope. Experiments on two New Zealand brachiopods (*Calloria inconspicua* and *Liothyrella neozelanica*) showed they respond to silt by rapid valve snapping (quick closures of their shells) up to 40 times per hour, presumably to eject sediments and clear their feeding apparatus (Williams, 2022). This indicates some short-term tolerance: brachiopods can endure brief sediment influx by adjusting behaviour (closing valves, producing mucus to trap and expel particles). Both species in the study survived several days of elevated turbidity (up to 100 Nephelometric Turbidity Unit (NTU)) with only moderate metabolic changes, demonstrating resilience to transient events (Williams, 2022). Such events might include resuspension of bottom sediments by storms or internal waves even at depth.

Nevertheless, brachiopods cannot withstand prolonged or heavy sedimentation. Unlike motile animals, they cannot escape burial – they are fixed in place and must either endure or perish. If a brachiopod is smothered by a layer of sediment for an extended period, it is effectively cut off from food and oxygen. According to research on *Novocrania* (present in NZ), clamping the dorsal valve can protect against silt briefly and low oxygen can be managed for a few days, but being buried in sediment for a month would prevent feeding and respiration to the point of likely death (Jackson, 2000). Fine sediment blanketing the shell blocks the lophophore from filtering water and limits oxygen diffusion to the animal. Brachiopods show clear intolerance to such conditions – even a thin film of silt can be fatal if not removed, given enough time. In experiments, chronic exposure to moderate turbidity over weeks led to reduced growth and condition in *C. inconspicua*, confirming that sustained sediment stress is metabolically costly and detrimental in the long run (Williams, 2022). In summary, deep-sea brachiopods require clear, well-ventilated water. They can tolerate short bursts of turbidity by valve closure and reduced activity, but continuous sedimentation or muddy conditions are lethal. This sensitivity explains why brachiopod beds are found in areas free of fine sediment deposition. Any increase in sediment runoff from land, or sediment plumes from human activities, directly threatens these animals by smothering them or clogging their delicate feeding structures (MacDiarmid, 2007; MacDiarmid et al., 2013; Williams, 2022).

Visualization of deep-sea brachiopod health and environmental thresholds

Rationale. Brachiopods represent an ecologically significant group in deep-sea hard-bottom environments, including on the bathyal slopes around New Zealand (Bitner et al., 2008; Lee et al., 2022). Their sensitivity to changes in environmental conditions—such as dissolved oxygen (O_2), particulate organic carbon (POC) flux, and sedimentation—makes them important indicators of ecosystem health and vulnerability to anthropogenic impacts like mining or altered carbon cycling (Bitner et al., 2008; Emig, 1997; Logan, 2007). Brachiopods remain understudied, especially in the South Pacific. Here we combine New Zealand-specific field data with information from global studies to create a set of environmental thresholds for deep-sea brachiopods, focusing on bathyal to upper abyssal depths (>200 m, prioritizing 1000–2000 m where possible). This is relevant to regulatory and management frameworks seeking to define thresholds for environmental change in deep-sea habitats.

Methods. We searched peer-reviewed literature, New Zealand government and Earth Sciences New Zealand (formerly NIWA) reports, and global ecological works to extract available data on the environmental tolerances and distributions of extant deep-sea brachiopods. Species prioritization was given to those confirmed from New Zealand waters: *Laqueus*, *Macandrevia*, *Terebratulina*, *Liothyrella*, and *Waldheimia* (Bitner, 2011; Bitner et al., 2008; Foster, 1974; Lee et

al., 2022). Thresholds were derived from direct field observations of bathymetric and habitat occurrence, paired with CTD or regional modelled data for O₂ and POC flux (Bitner et al., 2008; Lee et al., 2022; NZODN, 2022). We also included global reviews on brachiopod ecological tolerances (Emig, 1997; Logan, 2007). In the absence of direct data, proxies were inferred from related hard-substrate invertebrate studies and global brachiopod studies.

All species were assigned threshold and optimum values for O₂, POC flux, and sedimentation. Effects of crossing thresholds (e.g., reduced density, local extinction, stress responses) were documented from field or review sources.

All available site-specific empirical values for O₂, POC flux, and sedimentation associated with brachiopod records were compiled for NZ (and global where needed). These were used both for documentation and as overlays on modelled response surfaces.

Health index modelling and plotting were conducted based on the expectation that a Gaussian (bell-curve) models are appropriate for taxa adapted to relatively narrow, non-linear optima and sensitive to declines beyond a threshold (Emig, 1997). However, there is biological justification to adopt a sigmoidal response to O₂. For many benthic and deep-sea organisms, health or survival remains high across a broad O₂ range (well above the lower threshold) but declines steeply once O₂ falls below a species-specific critical value (the hypoxia/anoxia threshold). For deep-sea corals, sponges, and other invertebrates, O₂ suitability is often modelled as a step sigmoid function (Gage & Tyler, 1992). A Gaussian curve implies health is highest at an intermediate optimum and drops off on both sides, which fits better with sedimentation and POC-flux since there is an optimum value under which brachiopods do specifically well, and values below or above that optimum likely affect brachiopods. The equivalent sedimentation rate on the other hand is not necessarily a biological optimum, but more the centre of a tolerated range, or the midpoint of the observed non-detrimental sediment range. Many deep-sea taxa generally do not require a specific amount of suspended sediment for maximum health.

Surfaces were modelled using the following parameter ranges (see Table 4-4 and Table 4-5)

- O₂: Threshold ~40-45 µmol/kg (health rapidly declines below), optimum ~75 µmol/kg.
- POC flux: Minimum survival ~2 mg C/m²/d, optimum ~3-4 mg/C/m²/d
- Sedimentation: Rapid health decline at 0.5 mm/year, optimum ~0.2 mm/year

Equations for Deep-Sea Brachiopod Health Index. The health index for deep-sea brachiopods as a function of environmental drivers was modelled as follows:

$$\text{Health Index } (O_2, \text{POC}) = \frac{1}{1 + \exp(-k \times (O_2 - O_2^{\text{thr}}))} \times \exp\left(-0.5 \times \left(\frac{(\text{POC} - \text{POC}^{\text{opt}})^2}{\sigma_{\text{POC}}}\right)\right)$$

where:

- O_2 = Dissolved oxygen concentration ($\mu\text{mol/kg}$)
- POC = Particulate organic carbon flux ($\text{mg C m}^{-2} \text{d}^{-1}$)
- O_2^{thr} = Oxygen threshold ($\mu\text{mol/kg}$)
- POC^{opt} = POC optimum ($\text{mg C m}^{-2} \text{d}^{-1}$)
- σ_{POC} = Standard deviation for POC response
- k = Steepness parameter for the sigmoid

Health Index (O_2 , Sedimentation)

$$= \frac{1}{1 + \exp(-k \times (O_2 - O_2^{\text{thr}}))} \times \exp\left(-0.5 \times \left(\frac{(\text{Sed} - \text{Sed}^{\text{opt}})}{\sigma_{\text{Sed}}}\right)^2\right)$$

where:

- Sed = Sedimentation rate (mm/year)
- Sed^{opt} = Sedimentation optimum (mm/year)
- σ_{Sed} = Standard deviation for sedimentation

Parameter Values Used (see Table 4-4 and Table 4-5):

$$O_2^{\text{thr}} = 40 \mu\text{mol/kg}$$

$$O_2^{\text{opt}} = 75 \mu\text{mol/kg}$$

$$k = 0.25$$

$$\text{POC}^{\text{opt}} = 3.5 \text{ mg C m}^{-2} \text{d}^{-1}$$

$$\text{POC}^{\text{thr}} = 2 \text{ mg C m}^{-2} \text{d}^{-1}$$

$$\sigma_{\text{POC}} = 0.75 \text{ mg C m}^{-2} \text{d}^{-1}$$

$$\text{Sed}^{\text{opt}} = 0.2 \text{ mm/yr}$$

$$\text{Sed}^{\text{thr}} = 0.5 \text{ mm/yr}$$

$$\sigma_{\text{Sed}} = 0.15 \text{ mm/yr}$$

Table 4-4: Parameter values for deep-sea brachiopod health index models.

Parameter	Description	Value (O ₂ -POC)	Value (O ₂ - Sedimentation)	Unit	Reference/Notes
O ₂ ^{thr}	Oxygen threshold (inflection point for sigmoid)	40	40	μmol/kg	Bitner et al. (2008); Emig (1997); Lee et al. (2022)
O ₂ ^{opt}	Oxygen optimum (visual reference)	75	75	μmol/kg	Bitner et al. (2008); Lee et al. (2022)
k	Sigmoid steepness parameter (O ₂)	0.25	0.25	—	Model fit; steep drop near threshold
POC ^{opt}	POC flux optimum (Gaussian mean)	3.5	—	mg C m ⁻² d ⁻¹	Bitner et al. (2008); Emig (1997)
POC ^{thr}	POC flux threshold (Gaussian minimum)	2	—	mg C m ⁻² d ⁻¹	Bitner et al. (2008); Emig (1997)
σ _{POC}	POC flux Gaussian std. dev.	0.75	—	mg C m ⁻² d ⁻¹	(POC ^{opt} -POC ^{thr})/2
Sed ^{opt}	Sedimentation rate optimum (Gaussian mean)	—	0.2	mm/yr	Emig (1997); Logan (2007)
Sed ^{thr}	Sedimentation rate threshold (Gaussian minimum)	—	0.5	mm/yr	Emig (1997); Logan (2007)
σ _{Sed}	Sedimentation Gaussian std. dev.	—	0.15	mm/yr	(Sed ^{thr} -Sed ^{opt})/2

Table 4-5: Optimum and threshold values for O₂, POC, and sedimentation for different brachiopod species, threshold effects, and supporting literature. POC = particulate organic carbon; OM = organic matter. Caveats: NZ or global indicates where NZ or global records were used, proxy indicates values were inferred from non-brachiopod literature, such as hard-substrate deep-sea benthic studies; O₂ thresholds are from observed field occurrences (habitat, not experiments).

Taxon	O ₂ Threshold (μmol/kg)	POC/OM Flux (mg C/m ² /d)	Sedimentation (mm/yr)	Effect When Threshold Crossed	Source/Reference
Laqueus sp.	>45–60 (NZ)	>2 (opt. >3– 4, global)	<0.5 (proxy)	Decline/absence, burial if threshold exceeded	Bitner et al. (2008); Lee et al. (2022)
Macandrevia sp.	>45 (NZ)	>2 (opt. >3– 4, global)	<0.5 (proxy)	Absent if O ₂ < threshold, burial	Bitner et al. (2008); Emig (1997)
Terebratulina sp.	>50 (NZ)	>2 (opt. >3– 4, global)	<0.5 (proxy)	Stress/mortality below O ₂	Bitner et al. (2008); Emig (1997)
Liothyrella sp.	>45 (NZ)	>2 (opt. >3– 4, global)	<0.5 (proxy)	Absent in low O ₂ , siltation	Bitner et al. (2008); Foster (1974)
Waldheimia sp.	>40–50 (NZ)	>2 (opt. >3– 4, global)	<0.5 (proxy)	Stress below O ₂ , burial	Lee et al. (2022)
All (proxy)	>40–60 (global)	>2 (opt. >3– 4, global)	<0.5 (proxy)	Reduced density/stress/absence	Emig (1997); Logan (2007)

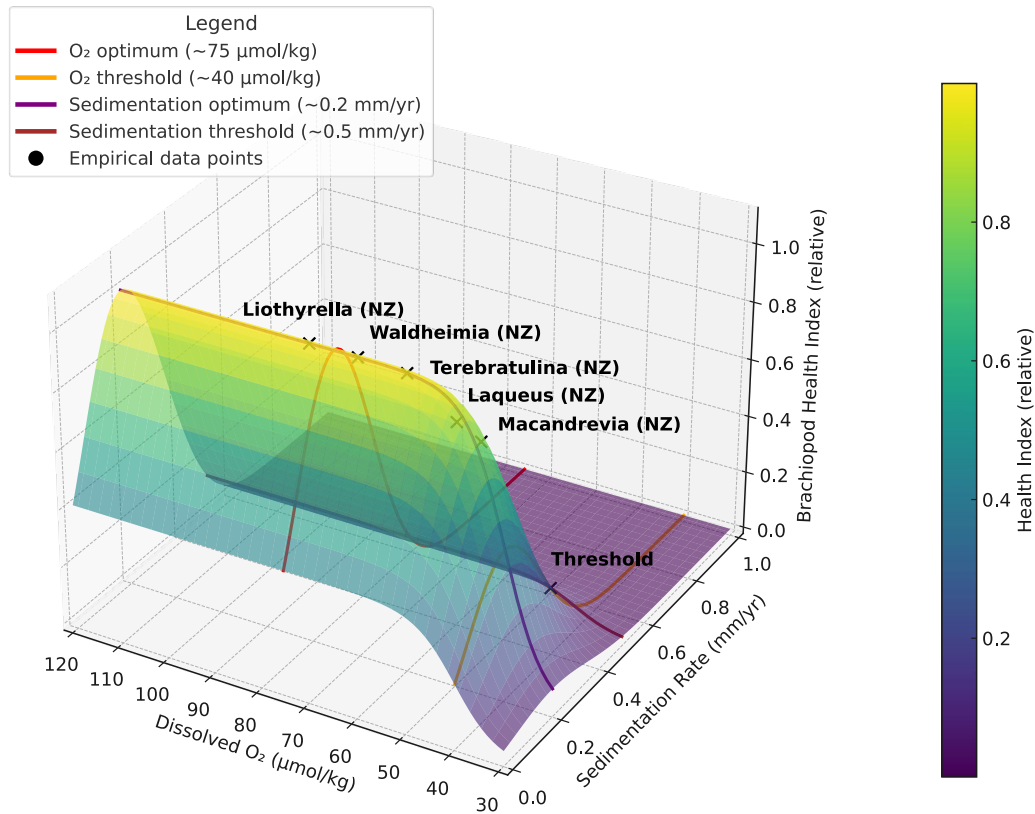


Figure 4-1: Three-dimensional surface plot for deep-sea brachiopod health index as a function of dissolved oxygen and sedimentation rate. The brachiopod health index combines a sigmoidal response to O_2 (with a steep decline below $40 \mu\text{mol/kg}$) and a Gaussian response to sedimentation (optimum at 0.2 mm/yr , threshold at 0.5 mm/yr). The colour scale on the surface indicates relative health index values, with higher (yellow/green) values corresponding to optimal environmental conditions. Red and orange lines denote O_2 optimum and threshold; purple and brown lines represent sedimentation optimum and threshold. Black markers with foreground labels show empirical records for *Laqueus*, *Macandrevia*, *Terebratulina*, *Liothyrella*, and *Waldheimia*, plus a global threshold value. This figure illustrates that brachiopod health is highest at moderate sedimentation rates and sufficient oxygen but declines markedly with excessive sediment burial or low oxygen concentrations. Empirical data sources: (Bitner et al., 2008; Emig, 1997; Foster, 1974; Lee et al., 2022; Logan, 2007). Model parameters: O_2 threshold = $40 \mu\text{mol/kg}$, O_2 optimum = $75 \mu\text{mol/kg}$, $k = 0.25$, Sedimentation optimum = 0.2 mm/yr , Sedimentation threshold = 0.5 mm/yr , $\sigma_{\text{Sed}} = 0.15 \text{ mm/yr}$.

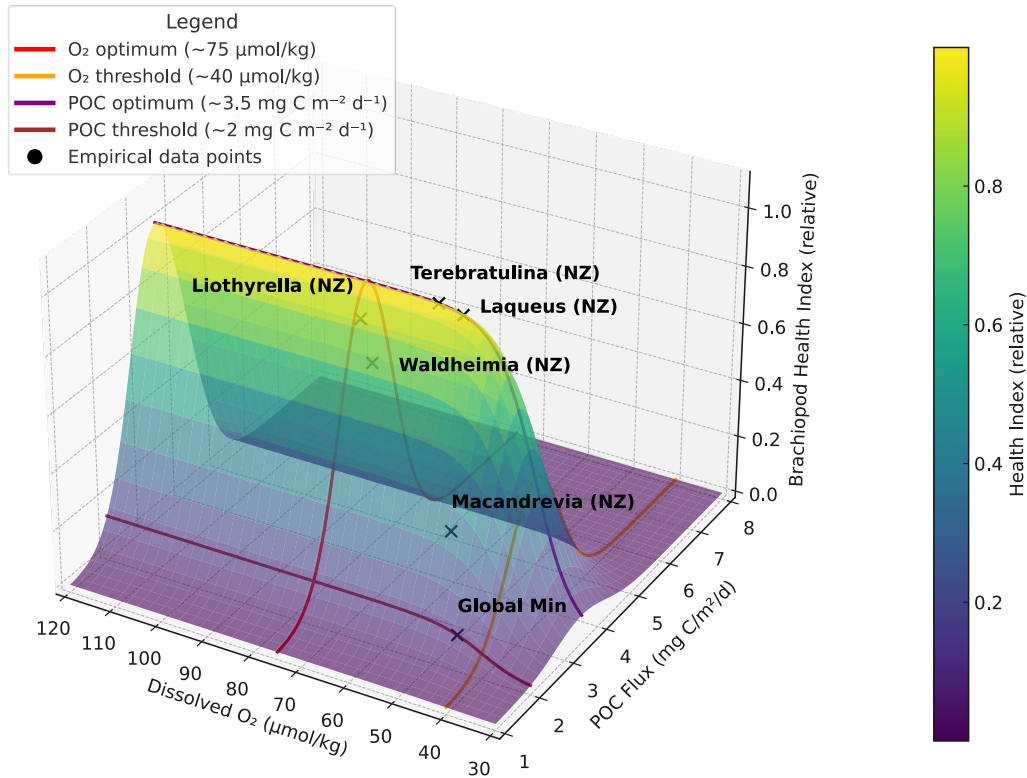


Figure 4-2: Three-dimensional surface plot for deep-sea brachiopod health index as a function of dissolved oxygen and POC flux. The health index is calculated as the product of a sigmoidal (logistic) response to O_2 —showing a sharp decline below the critical threshold of $40 \mu\text{mol/kg}$ —and a Gaussian response to POC flux, with an optimum at $3.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ and a threshold at $2 \text{ mg C m}^{-2} \text{ d}^{-1}$. The colour gradient on the surface represents relative health index values (from 0 = unsustainable to 1 = optimum). Red and orange lines mark O_2 optimum ($\sim 75 \mu\text{mol/kg}$) and threshold ($\sim 40 \mu\text{mol/kg}$), respectively, while purple and brown lines mark POC optimum and threshold. Black markers on the surface denote empirical records for *Laqueus*, *Macandrevia*, *Terebratulina*, *Liothyrella*, and *Waldheimia* (all from New Zealand), as well as a global minimum/threshold value. Labels correspond to genus or threshold status. This plot demonstrates that deep-sea brachiopod health is maximized under moderate to high oxygen concentrations and intermediate POC flux but declines rapidly when either environmental factor falls below threshold levels. Empirical data sources: (Bitner et al., 2008; Emig, 1997; Foster, 1974; Lee et al., 2022; Logan, 2007). Model parameters: O_2 threshold = $40 \mu\text{mol/kg}$, O_2 optimum = $75 \mu\text{mol/kg}$, $k = 0.25$, POC optimum = $3.5 \text{ mg C m}^{-2} \text{ d}^{-1}$, POC threshold = $2 \text{ mg C m}^{-2} \text{ d}^{-1}$, $\sigma_{\text{POC}} = 0.75 \text{ mg C m}^{-2} \text{ d}^{-1}$.

Summary and conclusion of deep-sea brachiopod environmental sensitivities

Table 4-6: Summary of the sensitivity of deep-sea brachiopods (bathyal New Zealand taxa) to oxygen, organic matter pulses, and sedimentation/turbidity. Note: “Low sensitivity” implies high tolerance, whereas “high sensitivity” implies low tolerance. Brachiopods’ sensitivity also depends on duration of exposure: they handle short-term stress better than long-term persistent change.

Environmental Factor	Brachiopod Sensitivity and Response
Oxygen Availability	Low sensitivity to short-term drops; high sensitivity to prolonged lack of DO. Brachiopods have very low O ₂ demand and can tolerate hypoxia for days. They sustain anaerobic metabolism for ~3–5 days and even occur in environments with <0.1 mg L ⁻¹ O ₂ . Activity is reduced under low O ₂ , and they can “wait out” brief hypoxic events. However, extended deoxygenation beyond their limit causes condition decline and mortality. Recovery is possible if oxygen is restored, but severe or long-lasting hypoxia is lethal.
Organic Matter (Food) Pulses	Generally beneficial in moderation; harmful if excessive. Brachiopods are suspension feeders on seston, so moderate pulses of particulate OM (e.g. seasonal phytodetritus) enhance their food supply and can boost growth/reproduction. They often show seasonal activity patterns tied to food availability. Excessive organic input, however, can lead to local oxygen drawdown (due to decomposition) and accumulation of detritus that brachiopods cannot ingest. Heavy organic loading may clog their feeding apparatus and promote hypoxia, stressing or killing the brachiopods. Thus, normal background fluxes are tolerated and utilized, but unnaturally large or continuous inputs (eutrophication) cause stress through indirect oxygen depletion and fouling of their habitat.
Sedimentation & Turbidity	Highly sensitive. Brachiopods require hard substrates free of fine sediment and are intolerant of persistent turbidity or burial. They can endure short bursts of silt by snapping their shells shut and expelling particles (up to ~40 valve snaps/hour in experiments), indicating some behavioural tolerance to brief turbidity. But if sedimentation continues, their feeding/respiration is impeded. Even a thin smothering layer for weeks is likely fatal, as prolonged sediment cover prevents feeding and reduces oxygen. Brachiopods show low survival under chronic high sediment loads – growth and survival drop significantly at high turbidity over days to weeks. In sum, they thrive in clear, current-swept conditions and suffer in silty, sediment-laden environments.

Deep-sea brachiopods in New Zealand’s bathyal zone emerge from this report as resilient yet vulnerable components in the marine ecosystem. On one hand, their ancient lineage has endowed them with remarkable tolerance to certain natural stresses – they endure low food periods and low oxygen episodes by virtue of slow metabolism and efficient physiology. On the other hand, brachiopods are highly sensitive to disturbances that exceed their adaptive scope, with low resilience to rapid or persistent environmental deterioration – prolonged deoxygenation, heavy sediment influx, or mechanical damage. Brachiopod health index models based on the data that were available illustrate that brachiopod health was highest at moderate sedimentation rates with sufficient oxygen (Figure 4-1), and under moderate to high oxygen concentrations and intermediate POC flux (Figure 4-2).

Brachiopod beds around New Zealand enhance biodiversity and seafloor stability by adding structure, offering refuge for other species, and cycling nutrients via their filtration and shell production. Their ecological importance, while understated, includes serving as a foundation

for complex communities and as indicators of environmental health (their presence often signals a clear, well-oxygenated, undisturbed habitat).

4.4.2 Deep-sea corals (Bathyal 200-3000 m, New Zealand)

Legislation: Under New Zealand’s Exclusive Economic Zone & Continental Shelf (Environmental Effects) Act 2012, the EPA must, when deciding any marine-consent application, “take into account ... the importance of protecting the biological diversity and integrity of marine species, ecosystems and processes, and the importance of protecting rare and vulnerable ecosystems and the habitats of threatened species.” Deep-sea coral reefs and thickets are repeatedly cited by the courts and the EPA as textbook examples of such “rare and vulnerable ecosystems,” so the Act requires decision-makers to give them significant weight—often overriding purely economic arguments—when setting consent conditions or refusing an activity altogether. That duty is operationalised in subsidiary regulatory instruments. Schedule 6 of the EEZ Permitted-Activities Regulations 2013 lists “biogenic habitats (e.g. stony-coral thickets or reefs)” as “sensitive environments,” meaning even low-impact surveys must be relocated or adapted if they risk disturbance. Outside the EEZ Act, the Fisheries (Benthic Protection Areas) Regulations 2007 permanently closed 17 deep-sea zones—over 1.2 million km²—to bottom trawling and dredging to safeguard coral frameworks and other vulnerable benthic fauna. Together, these measures ensure that deep-sea corals are treated as high-value, with legally protected habitats across New Zealand’s entire maritime estate, shaping everything from mining plume limits and sediment-deposit caps to large-scale fishery closures.

Ecology: Deep-sea corals or cold-water corals (CWCs) are colonial or solitary cnidarians that live permanently below the reach of sunlight, from about 50 m to more than 6000 m depth. Unlike their tropical shallow-water relatives, they lack symbiotic, light-harvesting algae (zooxanthellae) and obtain energy by capturing plankton and organic particles sinking through the water column or delivered by deep sea currents. Deep-sea corals are often referred to as ecosystem engineers of the deep ocean, due to the three-dimensional habitat structures they create and the ecological functions they support. In New Zealand waters, the deep-sea stony coral *Goniocorella dumosa* is a major reef-forming species, building expansive thickets on seamounts and rocky banks (Bostock et al., 2015; Tracey & Hjørvarsdóttir, 2019). Other groups, such as *Solenosmilia variabilis* (another reef-building scleractinian), gorgonian “bubble gum” corals (*Paragorgia* spp.), black corals, and stylasterid hydrocorals, also contribute to structural habitats. By providing attachment surfaces and refugia, corals facilitate rich community assemblages; thus, areas with abundant corals tend to exhibit higher species richness and biomass than areas without structure (Clark & Rowden, 2009). This is why deep-sea coral habitats are often designated as Vulnerable Marine Ecosystems (VME) – their presence indicates a vulnerable, high-value ecosystem with many interdependent species. The habitat-forming qualities of these corals are key for biodiversity support, biogeochemical processes, and physical structure of the seafloor.

Deep-sea coral reefs dramatically boost local biodiversity by creating three-dimensional frameworks that provide refuge, attachment sites, and feeding grounds for a multitude of organisms (Clark & Rowden, 2009; Consalvey et al., 2006). In New Zealand, *Solenosmilia variabilis* thickets host sponges, bryozoans, crinoids, shrimps, and numerous fish species—many of which rarely occur outside coral matrixes. Coral branches and interstitial crevices serve as nurseries for juvenile crustaceans and fish, while both coral polyps and associated filter-feeders link pelagic OM to benthic food webs.

Beyond physical structure, cold-water coral assemblages act as hotspots of metabolic activity in low-food environments (Maier et al., 2020). Coral colonies and their symbiotic sponges and microbial consortia filter large volumes of seawater, capturing and remineralizing organic particulates (Liu et al., 2024). Within reef mounds—both in the Atlantic and analogous systems—rates of respiration, nutrient recycling, and secondary production far exceed those of adjacent sediment flats, effectively concentrating and regenerating carbon and nitrogen (Liu et al., 2024; Tracey & Hjørvarðsdóttir, 2019). Coral skeletons also sequester carbon as calcium carbonate, and trapped sediments enrich local organic stores.

Deep-sea corals construct complex, branching frameworks up to a metre or more above the seabed, transforming flat sediment plains into architecturally diverse “forests.” For example, *S. variabilis* can cover over 20% of unfished seamount substrates in New Zealand (Tracey & Hjørvarðsdóttir, 2019). These structures modify bottom currents, generate a mosaic of microhabitats (from open sands to vertical rock faces), and provide enduring hard substrate—even dead skeletons remain as habitat for decades. Over geological timescales repeated coral growth forms bioherms and mounds several metres high, which can influence internal wave dynamics and localized upwelling, further reinforcing food delivery and habitat persistence.

Sensitivity to oxygen availability and deoxygenation

Deep-sea corals generally require well-oxygenated waters, and many species are absent in regions of severe oxygen minimum zones. In New Zealand’s bathyal zone (200–3000 m), seawater is typically oxygenated, but even moderate declines in oxygen can stress these corals. Most deep-sea scleractinian and octocoral species are adapted to stable oxygen conditions; thus, a substantial drop in oxygen (hypoxia) can impair their respiration and metabolic functions (Liu et al., 2024). Some coral taxa do exhibit partial tolerance for low-oxygen environments – for example, stylasterid corals (hydrocorals, sometimes called “lace corals”) have been observed colonizing low-oxygen zones and can remain abundant within OMZs (Auscavitch, 2020). Nevertheless, such cases are exceptions, and overall, deep-sea corals thrive in well-oxygenated habitats. Climate-driven deoxygenation poses a significant emerging threat: as the ocean warms, oxygen supply to deep waters is projected to decrease (Liu et al., 2024). Because deep-sea communities evolved in relatively stable conditions, even small declines in oxygen may substantially lower coral fitness and resilience (Daufresne et al., 2009; Mora et al., 2013; Wijgerde et al., 2012). Corals living near the margins of their oxygen tolerances could face reduced growth or increased mortality if mid-water oxygen minima intensify or expand into their depth range. In summary, deep-sea corals are highly sensitive to oxygen reduction, with climate-driven deoxygenation and associated changes (warming, acidification) expected to shrink suitable habitat and stress coral populations in the New Zealand region and globally (Daufresne et al., 2009; Tracey & Hjørvarðsdóttir, 2019).

Sensitivity to organic matter supply (food pulses)

Although the deep sea is a food-limited environment, deep-sea corals have adapted to exploit episodic pulses of OM (Maier et al., 2023). In the New Zealand region, for instance, deep-sea coral assemblages on seamounts benefit from seasonal phytodetritus falls or sporadic zooplankton flux delivered by currents. These pulsed inputs of particulate organic matter (POM) are critical for their nutrition. Periodic OM pulses can thus sustain growth and reproduction, while prolonged famine (e.g. if surface productivity declines) would negatively impact the corals. On the other hand, an excessive or abrupt influx of organic material can also have

detrimental side effects. If a large pulse of organic detritus settles all at once, it may lead to a layer of flocculent material or marine snow blanketing the corals, potentially clogging their polyps. Such deposition can foster localized oxygen depletion (as microbes consume the material) and force corals to expend energy cleaning themselves (through mucus production and polyp movements) (Carreiro-Silva et al., 2022). In general, deep-sea corals are moderately sensitive to changes in OM supply: insufficient food limits their energy budget, whereas sudden heavy inputs can indirectly stress them through sedimentation or slight oxygen concentration decreases. A stable regime of intermittent, moderate food pulses appears optimal. Indeed, cold-water coral reefs are often found in habitats with strong currents or upwelling that regularly deliver food without allowing excessive accumulation of detritus (Maier et al., 2023; Maier et al., 2020). This specialization underscores the importance of maintaining natural productivity patterns, with the inference that climate-driven shifts in surface productivity or timing of phytoplankton blooms could disrupt the feeding behaviour of bathyal corals.

Sensitivity to sedimentation and turbidity

Deep-sea corals are highly sensitive to sedimentation. Most reef-forming corals in the deep sea prosper in areas with low sediment accumulation – typically on hard substrates like rock outcrops, seamount peaks, or canyon walls where currents keep the seabed clean. Fine sediments can be harmful: they clog the corals' feeding apparatus and smother their tissues (Larsson et al., 2013; Liu et al., 2024). Experimental and field observations consistently show that elevated sediment loads lead to stress or mortality in deep-sea corals (Larsson et al., 2013; Liu et al., 2024). Sediment particles settling on coral polyps cause tissue abrasion and can block food intake, forcing corals to expend energy on clearing sediment (e.g. by producing mucus) (Carreiro-Silva et al., 2022). If sedimentation is prolonged or heavy, corals experience reduced growth, lower reproductive output, and tissue necrosis, ultimately resulting in increased mortality (Carreiro-Silva et al., 2022). For instance, laboratory experiments on the New Zealand deep-sea stony coral *Goniocorella dumosa* (the dominant reef-builder in NZ bathyal waters) exposed to short-term sediment pulses found that while some polyps survived (indicating a degree of tolerance to brief high turbidity), the overall coral health declined over time under sustained sediment exposure (Mobilia et al., 2023). This suggests *G. dumosa* and similar corals can endure only short-lived, low-level sediment pulses, but chronic or intense sedimentation far exceeds their coping capacity. *In situ*, deep-sea corals rely on currents to periodically sweep away sediments; if those currents are altered or if sediment influx overwhelms the system (for example, due to resuspension from a nearby disturbance), corals can be buried or chronically coated in silt. Around New Zealand's slopes and seamounts, natural sedimentation rates are usually low. In summary, sedimentation is a critical stressor: high sediment loads cause smothering and tissue damage in deep corals, making them vulnerable to seafloor disturbance activities that increase sediment flux (e.g. trawling, mining) (Consalvey et al., 2006).

Visualization of deep-sea coral health and environmental thresholds

Rationale. Deep-sea coral reefs, particularly those formed by *Solenosmilia variabilis* and *Goniocorella dumosa*, are among the most ecologically significant habitats in New Zealand's bathyal zone. These corals support diverse assemblages of invertebrates and fishes, playing a critical role in benthic biodiversity (Clark et al., 2010; Tracey & Hjørvarsdóttir, 2019). Deep-sea corals are, however, highly vulnerable to anthropogenic stressors such as oxygen depletion, organic enrichment, and sedimentation (Mobilia et al., 2021; Mobilia et al., 2023; Putnam et al.,

2017; Tracey & Hjørvarðsdóttir, 2019). Defining thresholds for these environmental variables is essential for robust environmental impact assessment and effective management of deep-sea resources (Rowden et al., 2014; Rowden et al., 2013).

Methods. For this section we consulted scientific papers and reports that investigated deep-sea coral species in New Zealand waters, focusing on information that would be helpful to establish oxygen, OM and sedimentation or particle load thresholds. We focused on two dominant habitat-forming scleractinian corals – *Solenosmilia variabilis* and *Goniocorella dumosa* – based on their wide distribution, ecological function, and the availability of published threshold data for O₂, POC flux, and sedimentation (Mobilia et al., 2023; Tracey & Hjørvarðsdóttir, 2019). The “health index” (HI) quantifies coral response (range: 0–1) as a function of environmental variables. HI is calculated as the product of axis-specific response functions:

- **O₂:** Sigmoidal decline with a critical threshold (based on observed absence and mortality in the field and lab).
- **POC flux:** Gaussian optimum, with decline at both low and high flux (modelled and field evidence).
- **Sediment concentration:** Sigmoidal, with a steep drop in health above a critical threshold (lab and field evidence).

Equations for deep-sea coral health index

$$HI = \frac{1}{1+e^{-k(x-x_{50})}} \times \exp\left(-\frac{(y-\mu)^2}{2\sigma^2}\right) \quad \text{or} \quad HI = \frac{1}{1+e^{-k(x-x_{50})}} \times \frac{1}{1+e^{m(z-z_{50})}}$$

Whereby:

x: dissolved oxygen concentration

y: particulate organic carbon flux

z: sediment concentration

x₅₀: O₂ threshold (inflection point)

k: steepness parameter for O₂ response

μ: optimum POC flux

σ: standard deviation of Gaussian POC response

z₅₀: sediment concentration threshold

m: steepness parameter for sedimentation response

Threshold and optimum values were derived from published New Zealand field, laboratory, and habitat model studies. Where direct experimental thresholds for sedimentation were unavailable (e.g., for *S. variabilis*), a precautionary value was estimated based on international experimental studies with closely related deep-sea corals (*Lophelia pertusa*, *Desmophyllum dianthus*), as well as field evidence from New Zealand reefs (Larsson et al., 2013; Roberts et al., 2006). See Table 4-7. References used: (Graves et al., 2022b; Holland et al., 2020; Larsson et al.,

2013; Liu et al., 2024; Mobilia et al., 2021; Mobilia et al., 2023; Roberts et al., 2006; Thresher & Fallon, 2024; Tracey & Hjorvarsdottir, 2019)

Parameters used (see Table 4-7 for references)

Solenosmilia variabilis

- O₂ vs. POC Flux
 - O₂ = 5.76 & 6.57 mg L⁻¹ (field presence – non-limiting)
 - O₂ = 3.8 mg L⁻¹ (threshold)
 - POC flux = 12 mmol C m⁻² d⁻¹ (optimum)
- O₂ vs. Sediment concentration
 - Sediment concentration = 50 mg L⁻¹ (onset sub-lethal) and 100 mg L⁻¹ (probable acute) – inferred from *Lophelia* studies

Goniocorella dumosa

- **O₂ vs. Sediment concentration**
 - Sediment pulses at 45 mg L⁻¹: no immediate damage
 - Sediment pulses at 102 mg L⁻¹: tissue loss & mortality
 - Sediment pulses at 435 mg L⁻¹: severe effects
 - O₂ proxy: 3.8 mg L⁻¹
- **O₂ vs. POC Flux**
 - POC optimum = 12 mmol C m⁻² d⁻¹

Table 4-7: O₂, POC, and sedimentation threshold values and biological effects for deep-sea coral *Solenosmilia variabilis* and *Goniocorella dumosa*

Species	Variable	Threshold/Optimum	Response Curve	Source(s)	Biological Effects When Crossed
<i>Solenosmilia variabilis</i>	O ₂	3.8 mg L ⁻¹ (threshold)	Sigmoidal	Tracey and Hjørvarsdottir (2019)	Reef loss, high mortality below threshold
<i>Solenosmilia variabilis</i>	POC flux	12 mmol C m ⁻² d ⁻¹ (μ, σ=4)	Gaussian	Anderson et al. (2018)	Energetic stress, poor growth, smothering
<i>Solenosmilia variabilis</i>	Sediment concentration	50 mg L ⁻¹ (onset), 100 mg L ⁻¹ (likely acute)	Sigmoidal (assumed)	Larsson et al. (2013); Roberts et al. (2006)	Polyp retraction, tissue loss, mortality
<i>Goniocorella dumosa</i>	Sediment concentration	102 mg L ⁻¹ (acute)	Sigmoidal	Mobilia et al. (2023)	Coenosarc loss, polyp mortality
<i>Goniocorella dumosa</i>	O ₂	3.8 mg L ⁻¹ (proxy)	Sigmoidal	Tracey and Hjørvarsdottir (2019)	Loss of persistence
<i>Goniocorella dumosa</i>	POC flux	12 mmol C m ⁻² d ⁻¹ (μ, σ=4)	Gaussian	Anderson et al. (2018)	Energy limitation, smothering

Solenosmilia variabilis: O₂ vs Sedimentation (Thresholds Highlighted)

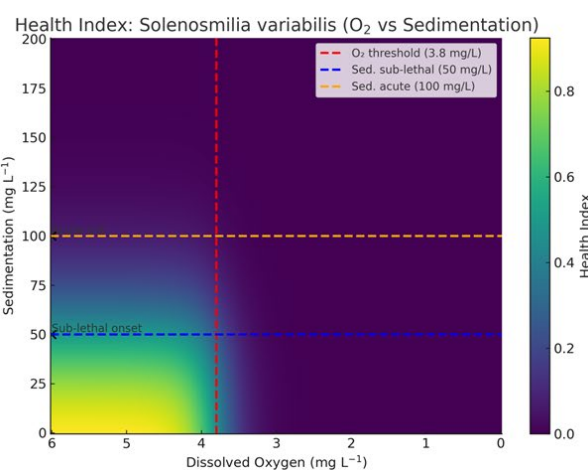
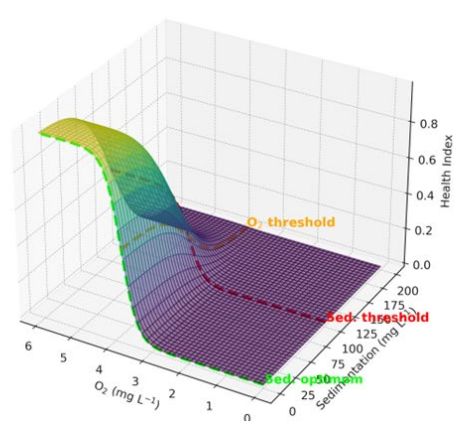
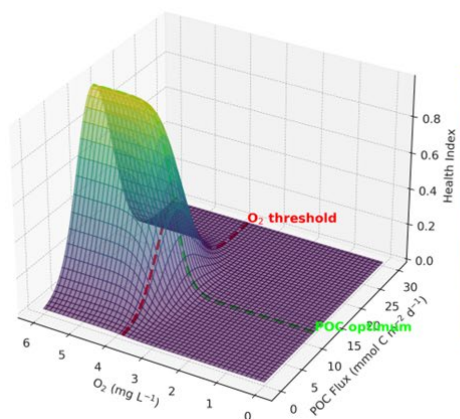


Figure 4-3: 3D (left) and 2D (right) surface plot for deep-sea coral *Solenosmilia variabilis* health index as a function of dissolved oxygen and suspended sediment concentration The 3D (left) and 2D (right) surface illustrate the predicted health index of *S. variabilis* across a gradient of O₂ (mg L⁻¹) and sediment concentration (mg L⁻¹), using a sigmoidal response based on international experimental studies and precautionary thresholds (Larsson et al., 2013; Roberts et al., 2006). Empirical points were used to indicate the onset of sub-lethal (50 mg L⁻¹) and probable acute (100 mg L⁻¹) sediment concentration effects and serve as provisional thresholds for *S. variabilis* in the absence of NZ-specific experimental data. O₂ threshold (orange (left), and red (right) dashed line) set at 3.8 mg L⁻¹. Exposure above these thresholds is predicted to result in polyp retraction, tissue loss, and increased mortality.

Solenosmilia variabilis: O₂ vs POC Flux (Thresholds Highlighted)



Health Index Surface: *Solenosmilia variabilis* (O₂ vs POC)

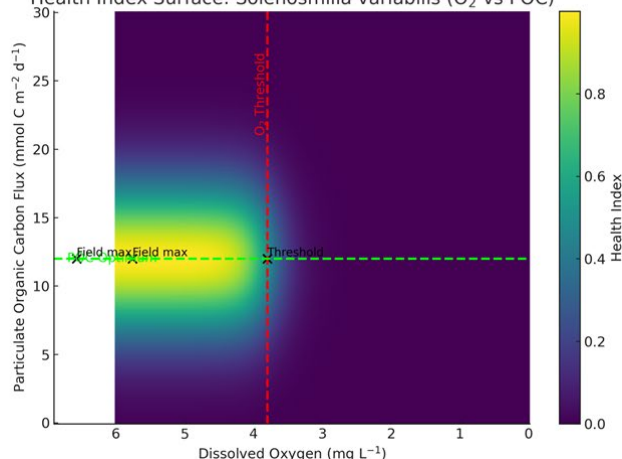
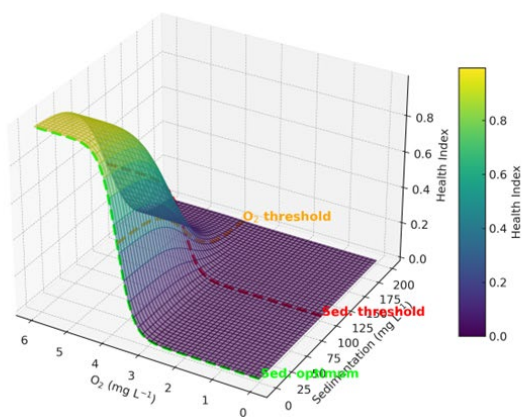


Figure 4-4: 3D (left) and 2D (right) surface plot for deep-sea coral *Solenosmilia variabilis* health index as a function of dissolved oxygen and POC flux. The 3D surface depicts the modelled health index of the reef-forming deep-sea coral *Solenosmilia variabilis* across gradients of O₂ concentration (mg L⁻¹) and POC flux (mmol C m⁻² d⁻¹). The health index is highest within an optimal POC flux (~12 mmol C m⁻² d⁻¹) and above the empirically defined oxygen threshold (~3.8 mg L⁻¹), with health declining at both lower and higher POC flux and under low-oxygen conditions. Dashed lines indicate the optimal POC flux (green) and the O₂ threshold (red), as determined from Earth Sciences New Zealand (formerly NIWA) habitat suitability models and field/lab studies (Anderson et al., 2018; Tracey & Hjørvarsdóttir, 2019). Crossing these thresholds is associated with energetic stress, polyp retraction, and loss of reef structure.

Goniocorella dumosa: O₂ vs Sedimentation (Thresholds Highlighted)



Health Index Surface: *Goniocorella dumosa* (O₂ vs Sedimentation)

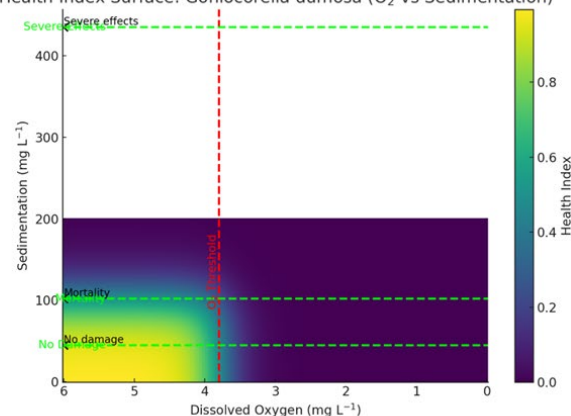


Figure 4-5: 3D (left) and 2D (right) surface plot for deep-sea coral *Goniocorella dumosa* health index as a function of dissolved oxygen and suspended sediment concentration. The modelled health index of *Goniocorella dumosa* is shown as a function of O₂ (mg L⁻¹) and sediment concentration (mg L⁻¹). Dashed lines highlight key empirical sedimentation thresholds: no acute damage (~45 mg L⁻¹), significant tissue loss and mortality (102 mg L⁻¹), determined from New Zealand laboratory exposure experiments (Mobilia et al., 2023). The O₂ threshold line (orange on left) marks the oxygen concentration below which no persistence in the field is observed. Health declines rapidly as sediment concentrations increase above 45 mg L⁻¹, with catastrophic loss above 102 mg L⁻¹.

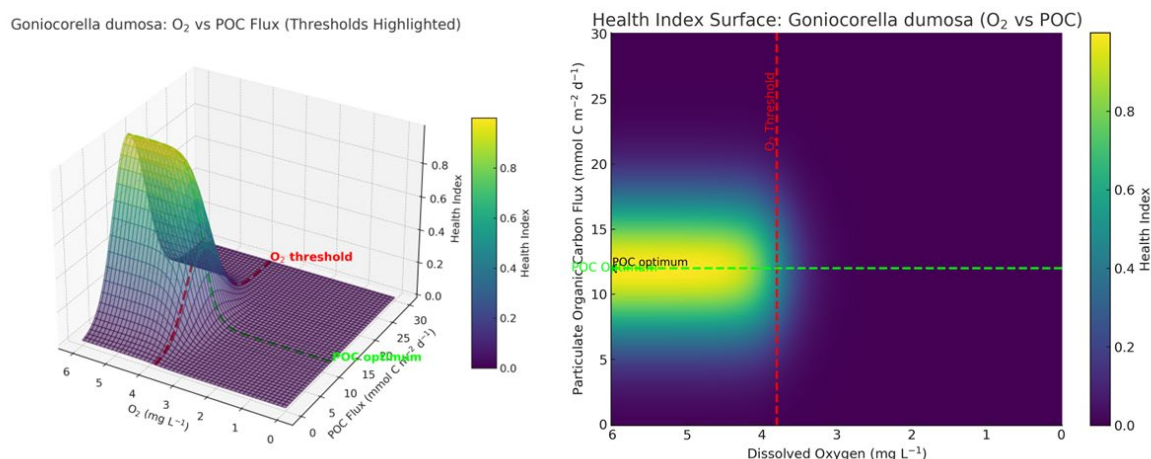


Figure 4-6: 3D (left) and 2D (right) surface plot for deep-sea coral *Goniocorella dumosa* health index as a function of dissolved oxygen and POC flux. The 3D (left) and 2D (right) surfaces represent the combined effects of O₂ and POC flux on the calculated health index of *G. dumosa* in New Zealand waters, modelled with the same response curves as for *S. variabilis*. Dashed lines indicate the O₂ threshold (red) and POC optimum (green). Values are inferred from Anderson et al. (2018) and Tracey & Hjørvarsdóttir (2019). Crossing the O₂ threshold or deviating from optimal POC flux results in decreased growth, energy limitation, and loss of persistence.

Summary and conclusions of deep-sea coral environmental sensitivities

Table 4-8: Summary of sensitivity of deep-sea corals to key environmental factors in New Zealand's bathyal zone. Citations indicate supporting research findings

Environmental Factor	Sensitivity of Deep-Sea Corals
Oxygen Availability	High sensitivity to oxygen depletion. Most deep-sea corals require well-oxygenated conditions and experience stress under hypoxia. Severe O ₂ declines can be lethal or force range shifts. Some taxa (e.g. stylasterids) tolerate mild hypoxia, but overall coral distribution is limited by oxygen levels (Auscavitch, 2020). Climate-driven deoxygenation is expected to reduce suitable habitat, as even small O ₂ drops can lower coral resilience (Mora et al., 2013).
Organic Matter Supply	Dependence on periodic food pulses. Deep corals thrive on episodic OM input; areas with regular POM flux (e.g. seasonal phytodetritus, zooplankton pulses) support healthy coral growth (Maier et al., 2023). Prolonged low food availability leads to energy deficit and slow growth (Maier et al., 2023). Conversely, excessive organic deposition can be harmful if it accumulates – decaying matter may cause localized oxygen reduction or smother coral surfaces (Maier et al., 2023). Overall, corals are adapted to moderate, intermittent food supply rather than constant or zero input (Maier et al., 2023).
Sedimentation	Extreme sensitivity to sedimentation. Fine sediments clog coral polyps and can smother colonies, causing tissue damage and mortality. Deep-sea corals favour habitats with low sediment accumulation; even short-term high turbidity can stress them (Mobilia et al., 2023). They can survive brief sediment pulses (some polyps may clear sediment via mucus) (Mobilia et al., 2023), but chronic sedimentation or burial is typically fatal (Mobilia et al., 2023). Sediment stress reduces feeding, growth, and reproduction, making this one of the most critical vulnerabilities for corals.

Deep-sea corals are among the most sensitive and ecologically important components of New Zealand's deep-sea ecosystems. Their life-history traits – slow growth, great longevity, and specific habitat requirements – make them vulnerable to environmental change and human impacts. Oxygen stress, increased sedimentation, and disruptions to food supply all pose challenges that these corals can only partially withstand. Despite these vulnerabilities, deep-sea corals play an important role in shaping benthic habitats: they form complex three-dimensional structures that support remarkable biodiversity and facilitate nutrient cycling and carbon storage in the deep ocean. Protecting deep-sea corals is therefore not only a matter of conserving individual species but also preserving the broader ecosystem functions and marine life that depend on the habitats they build.

The deep-sea coral health models in response to environmental thresholds and optima give insight into some of the sensitivity levels to oxygen, POC flux, and sediment concentrations, and indicate that these corals thrive under relatively narrow dissolved oxygen concentrations, while being somewhat resilient to enhanced sediment concentrations and requiring low to moderate organic matter fluxes to sustain them.

Deep-sea corals around New Zealand warrant strict management and further research, as their health is an indicator of deep ocean biodiversity and their loss would represent a decline in the region's natural heritage (Tracey & Hjørvarsdóttir, 2019).

4.4.3 Deep-sea sponges (Bathyal 200-3000 m, New Zealand)

Legislation: Sponge grounds are explicitly recognised in the EEZ Act 2012 as “ecologically significant benthic habitats” and are often included under Schedule 1 (Protected Species and Habitats) or equivalent listings in EPA marine consents to activities in deep-sea environments. Large deep-sea sponge aggregations are considered “habitat forming” that warrant particular management attention due to their biodiversity value and vulnerability. Consent documents typically list “deep-sea sponge grounds” as key benthic features requiring protection and monitoring.

Ecology: Deep-sea sponges (Porifera) are abundant and diverse in New Zealand's marine ecosystems, occurring from the shelf edge to abyssal depths. In the bathyal zone (200–3000 m), sponges from all three major classes – glass sponges (Hexactinellida), demosponges (Demospongiae), and calcareous sponges (Calcarea) – form important components of benthic communities. Many of these sponges are habitat-forming, creating biogenic structures on seafloor features such as seamounts, continental slopes, and submarine plateaux. New Zealand waters host rich sponge assemblages, including large reef-like sponge grounds (e.g. dominated by hexactinellids or astrophorid demosponges) as well as solitary encrusting forms on rock surfaces. These organisms are adapted to the stable yet food-limited deep-sea environment, but they face various natural and anthropogenic stressors.

Deep-sea sponges are recognized as crucial ecosystem engineers that significantly enhance biodiversity and shape benthic community structure in deep-sea habitats (Bell, 2008; Maldonado et al., 2015). Large sponge aggregations, known as sponge grounds or gardens, form complex three-dimensional habitats that provide refuge, nursery grounds, and feeding sites for a wide variety of invertebrates and fishes (Morrison et al., 2020). These structures serve as living reefs, with sponge bodies and their spicule networks creating shelter and attachment surfaces for sessile organisms such as corals and bryozoans (Maldonado et al., 2015). The presence of sponges increases local species richness and biomass, and commercially important fish

species often aggregate around sponge grounds due to the increased availability of prey and shelter (Maldonado et al., 2015).

Beyond their role as habitat formers, deep-sea sponges profoundly influence biogeochemical cycles through their extensive filtration activity. Sponges can filter thousands of cubic metres of seawater daily, removing particulate organic carbon (POC), bacteria, and dissolved organic matter, thereby linking pelagic and benthic ecosystems (Pham et al., 2019). Their microbial symbionts carry out important metabolic processes such as nitrification, denitrification, and carbon fixation, contributing to nitrogen and carbon cycling and acting as sinks for nitrogen compounds (Rooks et al., 2020). Sponges also contribute to the silicon cycle by incorporating dissolved silica into their siliceous spicules, which after sponge death slowly dissolve and release silica back to the environment (Maldonado et al., 2019).

Physically, sponges create structural complexity on the seafloor by producing spicule mats and reef-like frameworks. Glass sponges shed siliceous spicules that accumulate as dense mats, stabilizing sediments and providing hard substrates for colonization (Conway et al., 2019). Large demosponges form persistent skeletal mounds that increase habitat heterogeneity and influence local hydrodynamics, enhancing OM deposition and food availability for other benthic organisms (Bett & Rice, 1992; Eerkes-Medrano & Leys, 2006; Leys & Eerkes-Medrano, 2006). These structural contributions make sponge grounds ecologically comparable to cold-water coral reefs and justify their designation as Vulnerable Marine Ecosystems (Rogers et al., 2008).

Even smaller or encrusting sponge species play important ecological roles by stabilizing substrates, competing for space, and providing microhabitats for invertebrates within their canal systems (Barthel & Tendal, 1993). Collectively, all sponge forms contribute to maintaining deep-sea biodiversity, regulating nutrient fluxes, and physically shaping the benthic environment, making them foundational to deep-sea ecosystem functioning and resilience (Bell, 2008; Maldonado et al., 2015) (Maldonado et al., 2015; Bell, 2008).

Sensitivity to oxygen availability and deoxygenation

Bathyal sponges generally exhibit a good tolerance to low oxygen conditions (Micaroni et al., 2022). Experimental studies have shown that many sponge species can survive prolonged exposure to hypoxic water with minimal physiological impairment (Micaroni et al., 2022). For example, multiple sponge species (from temperate NE Atlantic and SW Pacific regions) maintained normal respiration rates even as dissolved oxygen was reduced to ca. $0.4 \text{ mg O}_2 \text{ L}^{-1}$ – a concentration far below typical deep-sea oxygen levels (Micaroni et al., 2022). Only under extreme deoxygenation (near-anoxic conditions, $\sim 0.13 \text{ mg O}_2 \text{ L}^{-1}$) did significant mortality occur in the most sensitive species (e.g. *Polymastia crocea*) (Micaroni et al., 2022). Sponges cope with low oxygen through a suite of adaptive strategies: they can uptake O_2 very efficiently at low concentrations and display phenotypic plasticity (physiological, morphological, and behavioural adjustments) to sustain metabolism under hypoxia. Unlike many metazoans, sponges lack complex oxygen-demanding organs and often host symbiotic microbes that may help modulate internal redox conditions, which together confer high hypoxia tolerance. Consequently, deep-sea sponges are less sensitive to declining oxygen than most other benthic invertebrates, including brachiopods which were discussed earlier. Moderate drops in oxygen (such as those projected with climate-driven deoxygenation) are unlikely to cause immediate sponge die-off; indeed, sponges might endure or even gain a relative advantage in low-oxygen zones as more sensitive fauna decline. However, severe or prolonged anoxia would eventually

exceed even sponges' tolerances. Overall, New Zealand's deep-sea sponges show low sensitivity to short-term oxygen fluctuations, though sustained ocean deoxygenation is a looming concern that could alter community structure over long timescales.

Sensitivity to organic matter supply

Deep-sea sponges rely on the downward flux of OM – primarily detrital particulate organic carbon (POC) and associated microbes – as their food source. Despite living in food-poor environments, sponges are highly efficient suspension feeders that can capture bacterioplankton, microplankton, and dissolved organic matter (DOM) from the water column (Pham et al., 2019). Sponges often host dense communities of symbiotic bacteria that process DOM, effectively enabling the sponge holobiont to utilize dissolved nutrients and recycle OM. The “sponge loop” process, known from shallow-water studies, may operate in the deep sea as well – sponges take up DOM and release particulate detritus (e.g. shed cells), thus transferring otherwise unavailable energy to higher trophic levels (Pham et al., 2019 and references therein). Because of their low metabolism and microbial associations, many deep-sea sponges can tolerate extended periods of low food input by reducing growth and reproduction rates. However, they are sensitive to long-term changes in OM supply in the sense that food availability strongly influences sponge population dynamics. Long time-series observations at an abyssal site (Station M off the coast of California, ~4100 m) revealed that deep sponge populations respond to pulses of organic flux from the surface: increases in POC flux were followed ~13 months later by marked increases in sponge density (through recruitment or regeneration) (Kahn et al., 2012). This suggests that episodic phytodetritus “blooms” reaching the seafloor can trigger sponge growth or reproductive events, while lean periods result in slower growth or dormant states. In New Zealand's bathyal zone, seasonal or interannual pulses of OM (e.g. from surface productivity cycles or mass phytoplankton export events) likely play a crucial role in sustaining sponge communities. Sponges are therefore moderately sensitive to variations in OM supply: they benefit from periodic food pulses and can withstand short-term famine, but significant reductions in particulate flux (for instance due to climate-driven shifts in primary production or stratification) could lead to sponge condition declines over time. In summary, a stable supply of organic carbon is important for deep-sea sponges' long-term persistence, and changes in food input can have pronounced effects on their population dynamics.

Sensitivity to sedimentation and turbidity

Sediments are a critical environmental stressor for filter-feeding sponges. Suspended sediment (fine particles in the water column) and settled sediment (seafloor deposits; sedimentation) can interfere with sponge feeding, respiration, and overall health (Bell et al., 2015). Sponges draw water through internal canals to filter food; excessive suspended sediments can clog these canals or cause sediment accumulation on tissues, impeding the flow of water and reducing feeding efficiency (Morrison et al., 2020). Laboratory and *in situ* studies indicate that even modest increases above background turbidity can induce sponge stress responses. For example, many sponges will slow or halt their pumping activity when high loads of silt are detected – an active behavioural response to avoid clogging (Morrison et al., 2020). Glass sponges *in situ* have been observed to arrest their feeding currents when exposed to turbid plumes (Grant et al., 2018; Tompkins-MacDonald & Leys, 2008). Some sponges produce mucus to trap and slough off sediments or can physically reorient or move slightly to shed accumulated particles (although mobility is very limited). These adaptations enable sponges to tolerate short-

term or low-level sedimentation. Indeed, a number of studies report that sponges are present and can even thrive in naturally sedimented environments (Kendrick et al.; Schönberg, 2016; Strehlow et al., 2017; Wurz et al., 2021), suggesting many species have some resilience to intermittent sediment influx, although effects are generally negative (Bell et al., 2015).

However, chronic or heavy sedimentation presents a high risk to sponges. When sediment concentrations remain elevated for long durations, sponges experience reduced respiration and filtration rates, decreased growth, and can suffer tissue smothering or necrosis (Morrison et al., 2020). Fine sediments can blanket sponge surfaces, blocking the ostia (intake pores) and preventing gas exchange. Over time this may cause hypoxia in sponge tissues despite adequate ambient oxygen. Sediment can also abrade or damage sponge choanocyte cells (responsible for feeding) and interfere with reproduction – for instance, sediment-coated substrates can prevent larval sponges from successfully settling (Wahab et al., 2019). Sponge larvae and juveniles are particularly sensitive: studies have found that increased turbidity and sediment deposition significantly lower the survival of sponge juveniles and impede larval settlement (Maldonado et al., 2008). In New Zealand, experimental exposures of the deep-sea sponge *Ecionemia novaezelandiae* to suspended silty sediment revealed that while the sponge endured short bursts of high sediment load with some reversible stress, longer-term exposure (several days to weeks) at even moderate sediment levels caused sustained respiration declines and partial tissue mortality (Mobilia et al., 2021). These findings align with international studies – sponges can often recover from acute, short sediment events (on the order of hours to days) once conditions improve, but continuous or repeated sedimentation leads to cumulative damage and protracted recovery times (weeks to months, if not longer) (Bell et al., 2015; Durden et al., 2023). Notably, sponge morphologies influence sediment tolerance: upright or cup-shaped sponges tend to trap more sediment and may be more quickly overwhelmed, whereas encrusting or massive forms can better resist burial by shedding sediment or growing around it (Pineda et al., 2017; Pineda et al., 2016).

In the bathyal habitats of New Zealand, sedimentation can result from natural processes (e.g. downslope transport, hemi-pelagic sedimentation, bioturbation) but is increasingly also associated with human activities (discussed below). Overall, deep-sea sponges have limited tolerance for sustained high sediment loads. They exhibit active and passive mechanisms to cope with mild increases in suspended sediment and can survive in moderately turbid settings (Bell et al., 2015), but heavy sedimentation is highly detrimental, causing reduced feeding, growth inhibition, and increased mortality (Morrison et al., 2020). Sedimentation is thus considered a significant sensitivity for deep-sea sponges, meaning that activities generating persistent sediment plumes pose a serious threat to sponge-dominated communities.

Visualization of deep-sea sponge health and environmental thresholds

Rationale

Deep-sea sponges are among the most important habitat-forming taxa in New Zealand's benthic ecosystems, providing structure, food-web support, and functional diversity across a range of depths and habitats. Their vulnerability to anthropogenic stressors, particularly oxygen depletion, increased sedimentation, and altered food supply (POC flux), makes them key indicators for environmental impact assessments and threshold modelling (Mobilia et al., 2021; Mobilia et al., 2023)

Methods

Two modelling approaches are warranted: Gaussian responses (for oxygen and POC) capture the concept of physiological optima, with health declining both above and below the ideal range (Stratmann et al., 2024); Sigmoidal responses (for sedimentation) reflect a threshold effect, where sponge health is stable below a tipping point but rapidly declines above it, as empirically observed for *Ecionemia novaezealandia* (Mobilia et al., 2021). We integrated these approaches in two dimensions (O₂-POC and O₂-sedimentation) for both individual species and functional clusters, informed by available literature. We projected both optima and threshold lines onto 2D and 3D health landscapes, enabling prediction of vulnerability and resilience under changing environmental conditions.

Equations for deep-sea sponge health index

Oxygen & POC (Gaussian-Gaussian)

$$HI_{O_2}(O_2) = \exp\left(-\frac{(O_2 - \mu_{O_2})^2}{2\sigma_{O_2}^2}\right)$$
$$HI_{POC}(POC) = \exp\left(-\frac{(POC - \mu_{POC})^2}{2\sigma_{POC}^2}\right)$$
$$H_{O_2,POC} = H_{O_2}(O_2) \times H_{POC}(POC)$$

Sedimentation (Gaussian – Sigmoidal)

$$HI_{sed}(Sed) = \frac{1}{1 + \exp\left(\frac{S_{sed} - T_{50}}{s}\right)}$$
$$H_{IO_2,sed} = H_{O_2}(O_2) \times H_{sed}(Sed)$$

Where:

- μ_{O_2}, μ_{POC} = optima for O₂ and POC
- $\sigma_{O_2}, \sigma_{POC}$ = standard deviation (threshold range)
- T_{50} = sediment concentration at which health is halved
- s = steepness of decline

Parameters

Table 4-9: Thresholds and optima are based on experimental and field data

Taxon or Cluster	Variable	Optimum	Threshold Range	Health Effect Beyond Threshold	Reference
Ecionemia novaezealandiae	O ₂	220 μmol/kg	175–265 μmol/kg	Health declines outside range	Stratmann et al. (2024)
	POC flux	1.2 g C/m ² /yr	0.6–1.8 g C/m ² /yr	Health declines outside range	Stratmann et al. (2024)
	Sediment concentration	—	55 ± 15 mg/L	Respiration and health decline, necrosis above	Mobilia et al. (2021)
Sponge cluster (NZ)	O ₂	220 μmol/kg	175–265 μmol/kg	Habitat suitability and metabolism decline	Stratmann et al. (2024)
	POC flux	1.2 g C/m ² /yr	0.6–1.8 g C/m ² /yr	Habitat suitability and health decline	Stratmann et al. (2024)
	Sediment concentration (SSC)	—	55 ± 15 mg/L*	(Proxy) Decline as for Ecionemia	Mobilia et al. (2021)

Ecionemia novaezealandiae
Health vs. O₂ & POC flux
with Projected Optimum and Threshold Lines

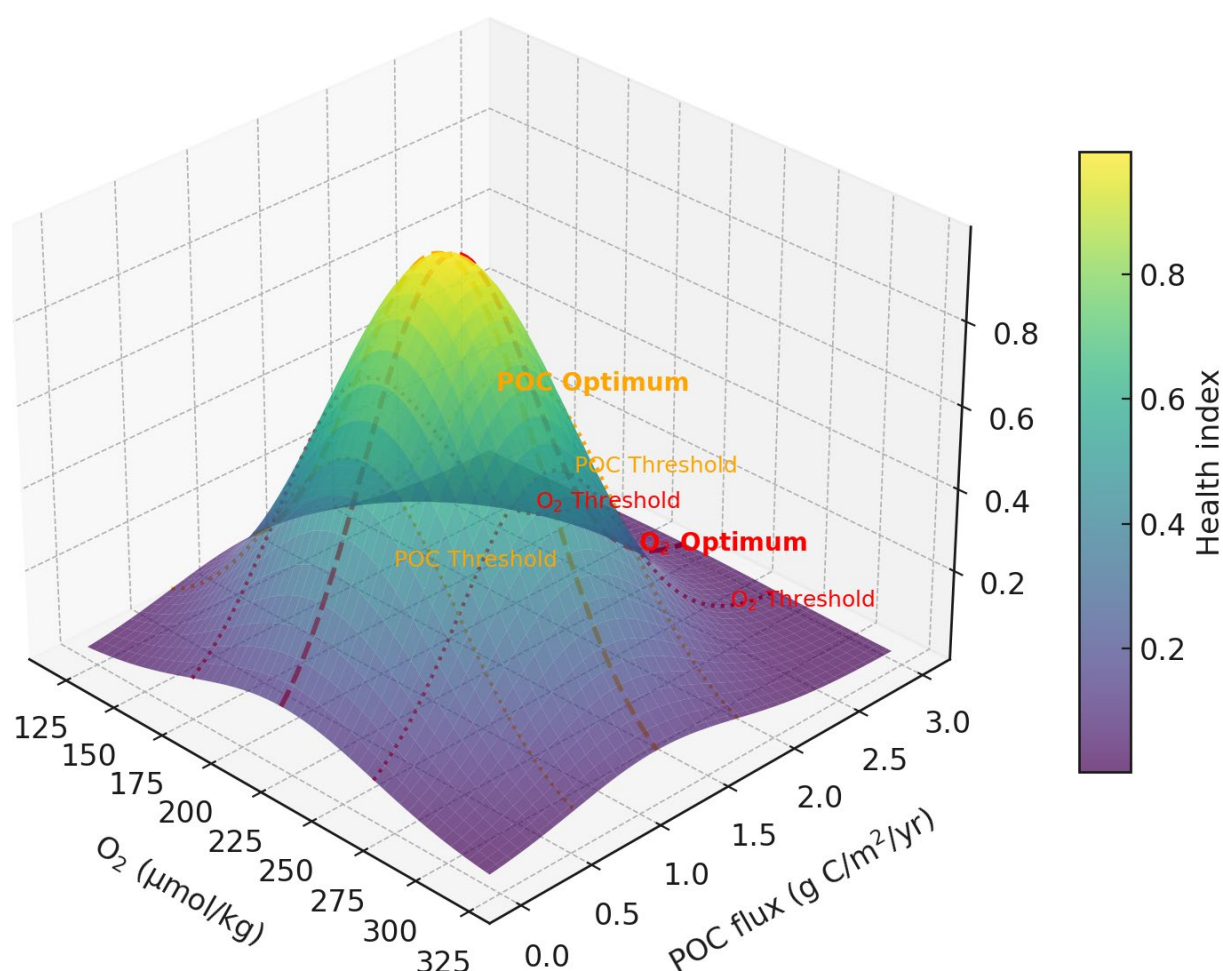


Figure 4-7: 3D surface plot of the health index of the sponge *Ecionemia novaezealandiae* as a function of oxygen concentration and POC flux. The health index is modelled as a Gaussian response to both O₂ (μmol kg⁻¹) and POC flux (g C m⁻² yr⁻¹), with an optimum at 220 μmol kg⁻¹ and 1.2 g C m⁻² yr⁻¹, respectively. Red and orange dashed lines indicate O₂ and POC optima, respectively, while red and orange dotted lines indicate O₂ and POC threshold zones, respectively (±1 standard deviation from optimum), beyond which health declines sharply. These thresholds are based on metabolic and distributional data for deep-sea sponges in New Zealand waters (Stratmann et al., 2024).

Ecionemia novaezealandiae
 Health vs. O₂ (inverted) & Sedimentation
 with Projected Optimum and Threshold Lines

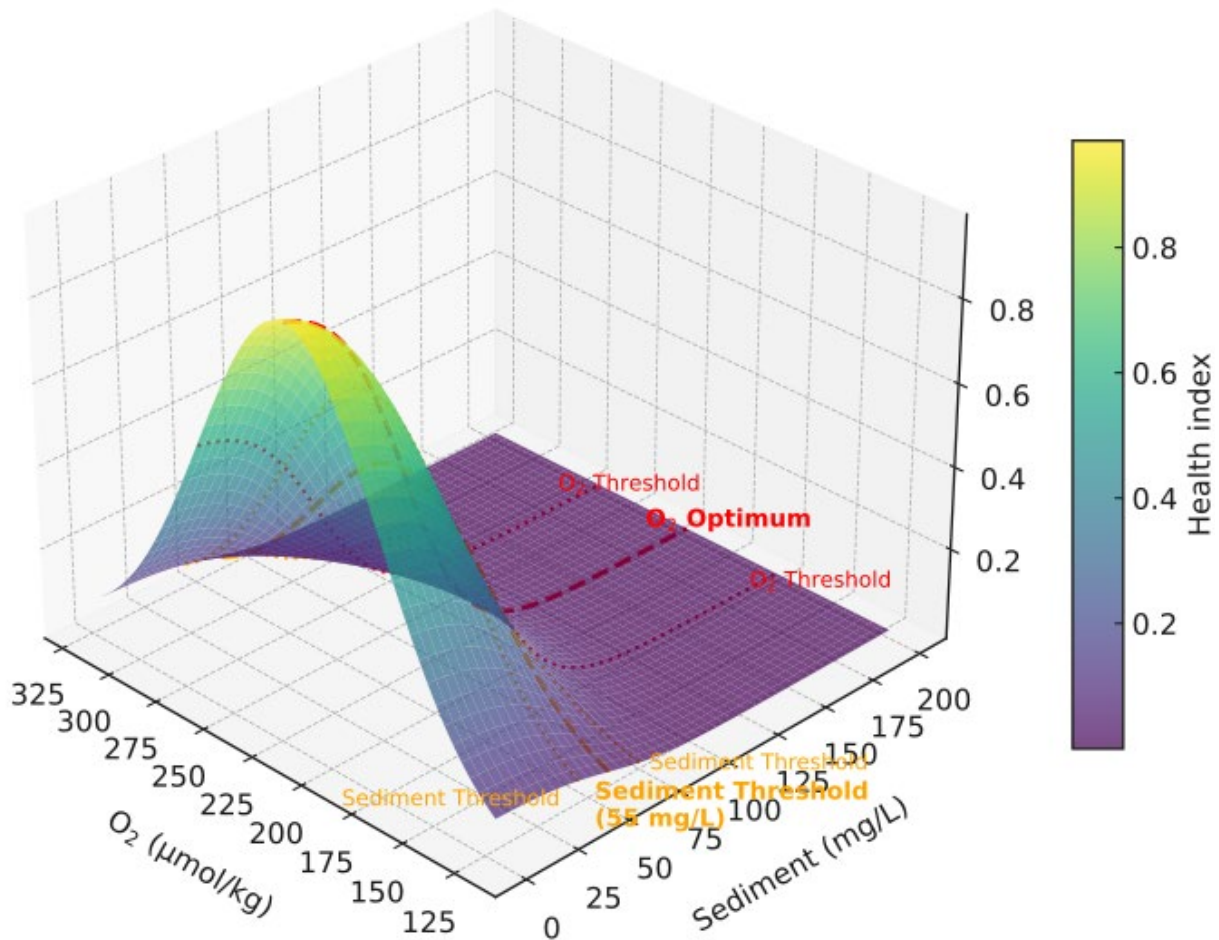


Figure 4-8: 3D surface plot of the health index of the sponge *Ecionemia novaezealandiae* as a function of oxygen concentration and suspended sediment concentration. *Ecionemia novaezealandiae* health index as a function of oxygen and suspended sediment concentration. The health index is plotted as a Gaussian response to O₂ and a sigmoidal response to sediment concentration (mg/L), with a steep decline above 55 mg L⁻¹ (T₅₀) and rapid health loss between 40–70 mg L⁻¹. Projected optimum and threshold lines highlight the range of environmental tolerance. Sediment thresholds are derived from direct experiments (Mobilia et al., 2021).

Deep-sea sponge cluster
Health vs. O₂ & POC flux
with Projected Optimum and Threshold Lines

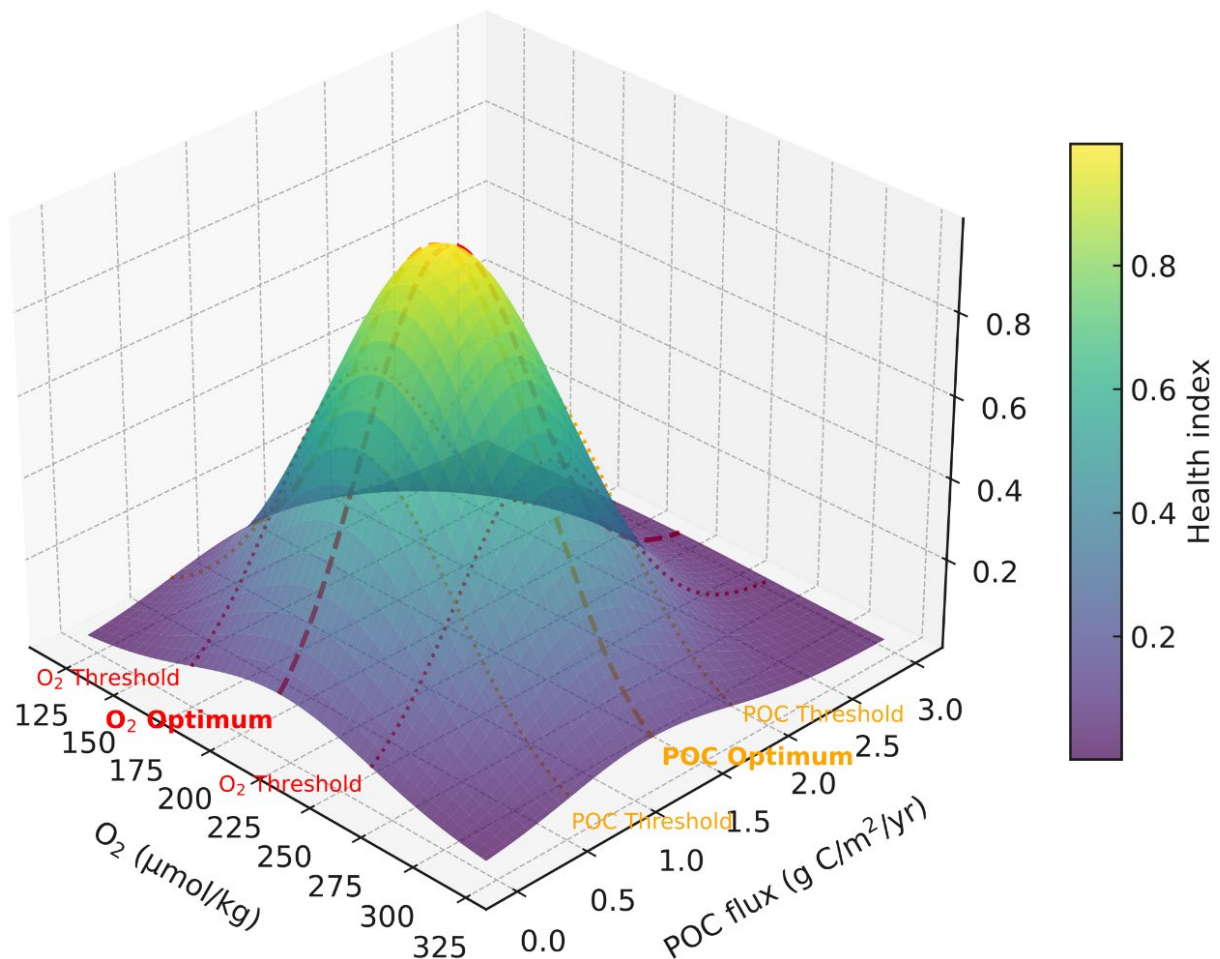


Figure 4-9: 3D surface plot of the health index of a deep-sea sponge cluster as a function of oxygen concentration and POC flux. Deep-sea sponge cluster health index as a function of oxygen and POC flux. A Gaussian–Gaussian response surface, parameterized as for *Ecionemia novaezealandiae* (220 μmol kg⁻¹ O₂, 1.2 g C m⁻² yr⁻¹ POC), projects both optima and thresholds onto the health surface plot. Thresholds delineate the range of environmental conditions associated with maximum habitat suitability, based on metabolic and habitat modelling for major New Zealand sponge taxa (Stratmann et al., 2024).

Deep-sea sponge cluster
Health vs. O₂ (inverted) & Sedimentation
with Projected Optimum and Threshold Lines

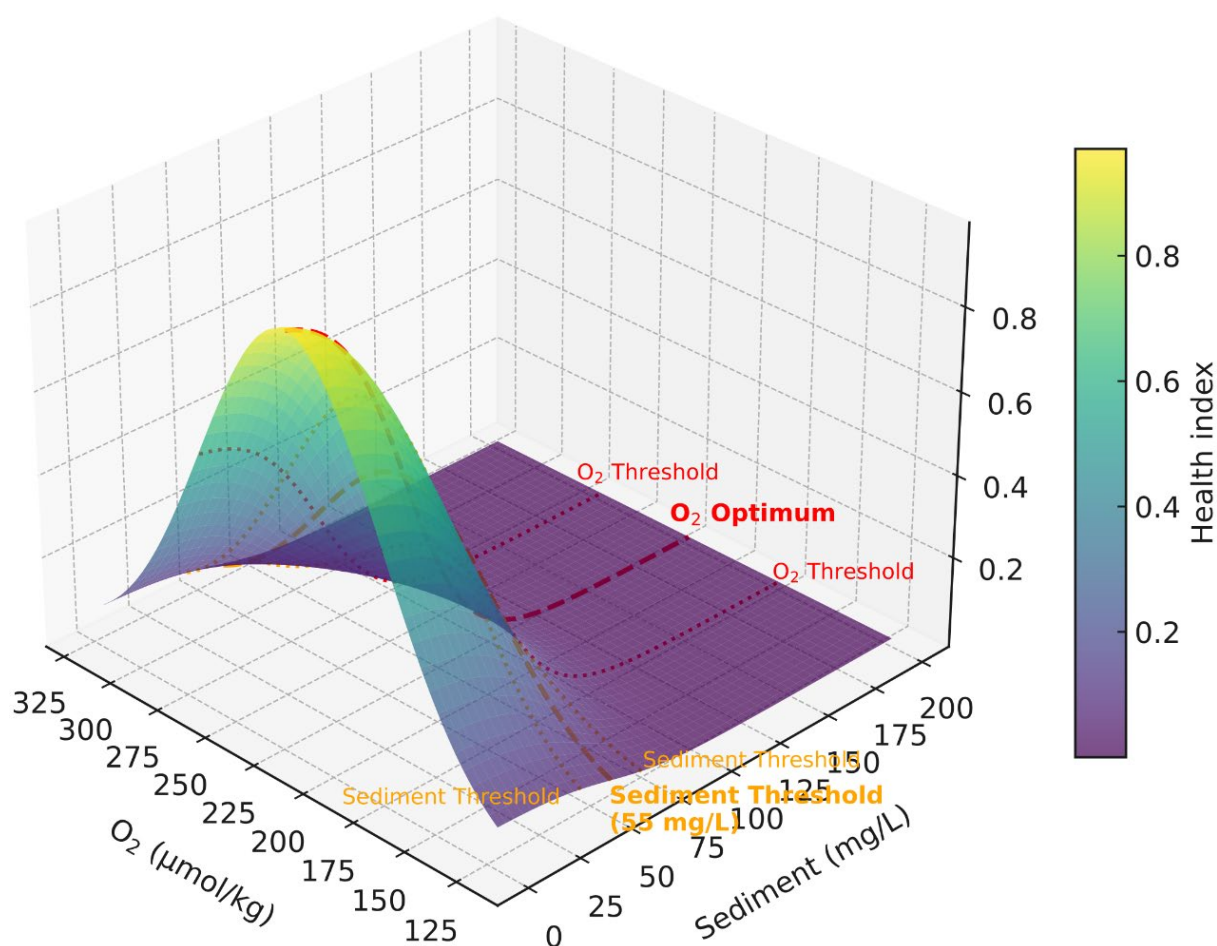


Figure 4-10: 3D surface plot of the health index of a deep-sea sponge cluster as a function of oxygen concentration and suspended sediment concentration. Deep-sea sponge cluster health index as a function of oxygen and sediment concentration. Gaussian (O₂) and sigmoidal (sediment concentration) responses combine to model the health of a representative sponge cluster. Threshold lines are projected at 55 mg L⁻¹ (± 15 mg L⁻¹) for sediment concentration and at ± 45 μmol kg⁻¹ from the O₂ optimum. Sediment concentration thresholds are conservatively assigned from *Ecionemia novaezealandiae* data (Mobilia et al., 2021).

Summary and conclusions on deep-sea sponge sensitivities

Table 4-10: Summary of sensitivities and responses of deep-sea sponges (Hexactinellidae, Demospongiae, Calcarea) to dissolved oxygen, organic matter supply, and sedimentation.

Environmental Factor	Sensitivity of Bathyal Sponges (200–3000 m)
Low Oxygen (Hypoxia)	Low sensitivity (high tolerance): Deep-sea sponges are generally very tolerant of low oxygen conditions. Most species tested survived severe hypoxia ($\sim 0.5\text{--}0.4\text{ mg O}_2\text{ L}^{-1}$) with little change in respiration and maintained oxygen uptake at concentrations where many animals would suffocate (Micaroni et al., 2022). Only extreme near-anoxic levels ($<0.2\text{ mg O}_2\text{ L}^{-1}$) caused significant sponge mortality in experiments (Micaroni et al., 2022). Sponges exhibit adaptive physiological and behavioural changes under hypoxia (e.g. reducing metabolism, changing morphology) that enable survival (Micaroni et al., 2022). Compared to other benthic fauna, sponges have higher tolerance to deoxygenation, suggesting they may persist in or even dominate low-oxygen habitats (Micaroni et al., 2022).
Organic Matter Supply (Food availability from detrital POC/DOM)	Moderate sensitivity (dependency on flux): Sponges rely on sinking OM for nutrition and show dynamic responses to changes in food supply. They can endure oligotrophic periods by slowing growth, but sponge populations thrive when organic flux increases. Long-term studies indicate that spikes in particulate organic carbon flux from the surface can lead to recruitment or growth pulses in deep sponges ~ 1 year later (Kahn & Leys, 2012; Kahn et al., 2012). Thus, sponges benefit from seasonal/intermittent “food falls” and are <i>food-limited</i> to some extent. Prolonged reduction in food (due to lower surface productivity or altered currents) may weaken sponges, reduce reproduction, and eventually cause declines in abundance. Conversely, sponges efficiently utilize even low concentrations of suspended bacteria/DOM, aided by symbiotic microbes, which buffers short-term food scarcity. Overall, sponge distribution and vitality are closely tied to OM availability, but they can tolerate short lean periods and capitalize on pulses.
Sedimentation (Suspended and settled sediments)	High sensitivity to heavy sedimentation (low tolerance): As sessile filter feeders, sponges are vulnerable to elevated sediment loads. Increased turbidity and sediment deposition can clog sponge filtering apparatus, leading to reduced pumping/feeding and oxygen stress (Morrison et al., 2020). Sponges employ some tolerance strategies – e.g. temporarily stopping filtration, shedding mucus to remove particles – and many species withstand <i>mild, short-term</i> sediment influx with full recovery (Bell et al., 2015). However, chronic or intense sedimentation is detrimental. Experiments show that sustained suspended sediment concentrations (even at $\sim 10\text{--}50\text{ mg L}^{-1}$) causes significant drops in sponge respiration and filtration rates and can smother tissue over days (Morrison et al., 2020). Fine silt covering sponges can compromise health and is often lethal to larvae and juveniles (Morrison et al., 2020). Sediment sensitivity varies by morphology (encrusting forms shed sediment more easily than cup-shaped forms). In sum, sponges tolerate only limited sedimentation; high sediment loads, or long-duration plumes result in stress, impaired feeding, and potential mortality, making this a major sensitivity for deep-sea sponges.

Deep-sea sponges in New Zealand’s bathyal ecosystems are both resilient and vulnerable: they have survived for millennia in the deep ocean by withstanding low food conditions and occasional environmental stress, yet they are very susceptible to physical disturbance and suffocation by sediments. In general, these sponges show robustness to natural fluctuations –

for example, they tolerate short-term severe hypoxia and can adjust to episodic changes in OM input – but have limited resilience to acute anthropogenic impacts. Climate change adds a new layer of challenge, with deoxygenation likely to test sponge endurance in some regions (although sponges may fare better than many animals in low-O₂ scenarios) and alterations in food supply potentially influencing sponge population health. Despite these threats, deep-sea sponges remain cornerstones of New Zealand’s deep benthic ecosystems. They form complex habitats that rival cold-water coral reefs in biodiversity value, provide refuge and nursery areas for fish and invertebrates, and drive crucial biogeochemical processes from filtering water to cycling nutrients. The overall sensitivity of deep-sea sponges can therefore be viewed as a trade-off: environmentally hardy in their ability to live in the cold, dark, low-oxygen deep sea, yet highly fragile in the face of mechanical damage and smothering. Protecting deep sponge habitats in the New Zealand region is critical for maintaining the health and functioning of the wider deep-sea ecosystem. Given their ecological importance and vulnerability, deep-sea sponges merit careful management attention.

4.4.4 Deep-sea infauna (bathyal 200-3000 m, New Zealand)

Legislation: The NZ EEZ Act does not list specific sediment infaunal species but covers all seabed and sub-seafloor fauna, including infaunal benthic macrofauna, under its jurisdiction, as it regulates activities that disturb or damage the seabed ([Regulatory Impact Statement: EEZ Act](#)). Technical expert testimonies such as those provided to the EPA have described macro-infaunal communities (animals >300 µm) dominated by polychaetes and peracarid crustaceans on the Chatham Rise, recognized as part of the deep-sea fauna in the NZ EEZ ([statement of evidence for Chatham Rock Phosphate Limited before the EPA](#))

Ecology: Deep-sea infaunal communities in New Zealand’s EEZ occur across bathyal depths (~200–3000 m) in diverse habitats, from soft sediment slopes and submarine canyons (Leduc et al., 2020b; Pilditch et al., 2015) to hard-substrate crevices and biogenic structures (e.g. sponge gardens, coral thickets) (Leduc et al., 2016). These infaunal organisms – including polychaete worms, and other macroinfauna (generally defined as organisms retained on 300 µm mesh sieve) such as small crustaceans and molluscs, and meiofauna (organisms retained on 32 µm mesh sieve, predominantly nematodes and harpacticoid copepods) – are key components of benthic ecosystems (Schratzberger & Ingels, 2018).

Deep-sea infaunal communities play vital and dynamic roles in ecosystem functioning and biogeochemical cycling well beyond being passive sediment dwellers. Their activities—particularly those of polychaetes, echinurans, and burrowing crustaceans—drive sediment mixing and bioturbation to depths of 10–20 cm in the bathyal zone (Schratzberger & Ingels, 2018; Sturdivant et al., 2024). This biogenic reworking disrupts stratified sediment layers, oxygenates deeper horizons, and facilitates the burial and remineralisation of OM. As a result, infaunal bioturbation enhances sediment permeability and establishes strong redox gradients, accelerating the decomposition of detritus and supporting the release and recycling of nutrients such as carbon, nitrogen, phosphorus, and silica (Snelgrove et al., 2014; Snelgrove et al., 2018; Sturdivant et al., 2024). The coupling between organic content and bioturbation intensity is especially evident in New Zealand slope sediments, where greater food supply supports larger, deeper-burrowing fauna and thus intensifies sediment mixing. Through these processes, infaunal animals provide a critical link between the pelagic and benthic realms, influencing long-term carbon burial and ecosystem productivity.

The nutrient cycling functions of infaunal communities are equally essential. By feeding, excreting, and ventilating burrows, infauna mediate transformations and fluxes of key nutrients across the sediment-water interface. Their bioturbation introduces oxygen into ammonium-rich sediments, promoting bacterial nitrification and subsequent denitrification, thereby facilitating the removal of biologically available nitrogen from the marine system (Meysman et al., 2006; Sturdivant et al., 2024). In addition, infaunal irrigation mobilizes phosphate and silica from porewaters to the overlying water, making them accessible to primary producers. Experimental and observational studies in deep habitats reveal that infauna-rich sediments exhibit higher rates of oxygen consumption and nutrient efflux. Notably, sediments beneath bamboo coral thickets with high infaunal densities can display nitrogen fluxes on par with shallower, more productive environments—likely due to enhanced trapping and processing of OM. Such processes ensure efficient recycling and rapid turnover of nutrients, maintaining the productivity of ocean ecosystems. In the absence of infauna, sediment biogeochemistry becomes more stagnant, and nutrient cycling slows, underscoring the regulatory influence of these organisms.

Trophically, infaunal animals are integral to deep-sea food webs. They exploit a range of food sources: polychaetes and holothurians consume bulk sediment, nematodes graze bacteria and microalgae, and amphipods and gastropods act as scavengers. By fragmenting detrital organic particles and converting them to microbial biomass, infauna channel energy and nutrients into forms usable by higher trophic levels. They are themselves prey for a variety of demersal fish (e.g., rattails, hakes, flounders) and megafaunal invertebrates (shrimps, crabs, sea stars), thus serving as a critical link between detrital inputs and top consumers. Some infaunal taxa (certain polychaetes, nematodes) are also active predators, structuring intra-benthic trophic relationships (Leduc et al., 2016). In sum, infaunal biodiversity—from meiofauna to large burrowers—underpins a complex network of interactions that sustains deep-sea productivity and resilience. Disruption or simplification of these communities may reverberate throughout the food web, ultimately affecting commercially and ecologically important species.

While soft-sediment slopes harbour most bathyal infauna, New Zealand's deep sea also features infaunal assemblages associated with hard substrates and biogenic structures (Clark & Rowden, 2009). Organisms inhabiting the interstices of rocky outcrops, carbonate ledges, or the matrices of coral and sponge gardens contribute further to benthic heterogeneity (Henry & Roberts, 2007). Biogenic habitats—such as those formed by scleractinian and bamboo corals or deep-sea sponges—create three-dimensional structures that enhance both infaunal biodiversity and density compared to bare sediments (Pierrejean et al., 2020). These structures baffle currents and trap organic particles, fostering microhabitats rich in deposit feeders and detritivores. For instance, sediments under bamboo coral canopies may support higher infaunal abundances (especially crustaceans and polychaetes) and show elevated rates of nutrient regeneration relative to adjacent open sediment (Pierrejean et al., 2020). Sponge grounds likewise stabilize sediments and provide refugia for a variety of small infauna. Community composition in these structured habitats can differ markedly from that in open soft sediments. The complexity of hard and biogenic substrates thus generates unique niches and contributes to regional biodiversity.

Together, both soft-sediment and hard-substrate habitats make essential contributions to the diversity and ecological function of bathyal infauna in New Zealand's deep sea. Effective

management and conservation must account for the vulnerability and ecological significance of infaunal communities across all substrate types.

Sensitivity to oxygen availability and deoxygenation

Oxygen is a critical limiting factor for deep-sea infauna, and even moderate hypoxia can alter community composition. Most bathyal New Zealand habitats are well-oxygenated; however, lessons from oxygen minimum zones (OMZs) elsewhere illustrate infaunal responses to low O_2 (Levin, 2003). Under severe hypoxia ($O_2 < 0.5 \text{ mL} \cdot \text{L}^{-1}$), larger macrofauna decline sharply, and communities become dominated by a few tolerant taxa (Neira et al., 2018). For example, on the Costa Rica margin OMZ, total meiofauna densities peaked at the low-oxygen core (~400 m, $O_2 \sim 0.05 \text{ mL} \cdot \text{L}^{-1}$) but were almost entirely dominated by nematodes (up to 99% of individuals) with very low diversity (Neira et al., 2018). Harpacticoid copepods and polychaete larvae were nearly eliminated in the OMZ core, only increasing in abundance at deeper, more oxygenated sites. This indicates nematodes have high tolerance for low O_2 , whereas many crustacean and polychaete infauna require higher oxygen levels (Ingels et al., 2023; Sapir, 2021). Overall taxonomic diversity is reduced under chronic low oxygen, and community functional complexity diminishes as sensitive groups drop out (Neira et al., 2018).

Climate-driven Ocean deoxygenation is a growing concern for bathyal ecosystems. Intermediate-water oxygen concentrations have been declining globally in recent decades, leading to OMZ expansion (Neira et al., 2018). Infaunal assemblages may shift toward smaller, hypoxia-tolerant forms (e.g. nematodes, certain polychaetes) at the expense of less tolerant taxa (Cook et al., 2000; Neira et al., 2018). For instance, some opportunistic polychaetes (e.g. *Linopherus*, *Prionospio*) and gutless worms have been observed to persist or even dominate in low-oxygen, high-organic settings (Leduc et al., 2016). Nonetheless, prolonged oxygen depletion beyond critical thresholds can cause mass mortality of infauna, reduced bioturbation, and impaired benthic nutrient cycling. Thus, while many deep-sea infauna tolerate the naturally low O_2 levels of deep water, they are sensitive to further O_2 declines. Continued climate-driven deoxygenation could lead to less diverse, functionally impoverished infaunal communities in New Zealand's bathyal zone, mirroring OMZ effects observed internationally (Neira et al., 2018).

Sensitivity to organic matter supply and pulsed food inputs

Food availability – primarily in the form of sinking OM (phytodetritus, marine snow, carcasses, etc.) – is a dominant driver of deep-sea infaunal distribution and abundance. New Zealand's productive waters provide episodic pulses of organic material to the bathyal seafloor, especially in regions like the Chatham Rise and submarine canyons. Infaunal communities are highly responsive to these pulses. When labile OM inputs increase, many deposit-feeding infauna show population and activity increases. For example, in Kaikōura Canyon (a relatively short, coast-connected, high-productivity canyon (De Leo et al., 2010) macrofaunal and meiofaunal biomass and density are significantly higher than in the less productive Hokitika Canyon, which receives mainly refractory land-derived detritus (Gibbs et al., 2020; Leduc et al., 2020b). (Leduc et al., 2020b). The Kaikōura Canyon's enriched, chlorophyll-rich sediments support abundant polychaetes and nematodes, whereas Hokitika's food-poor sediments (dominated by inert terrestrial plant material) sustain much lower infaunal biomass (Leduc et al., 2020b). This suggests that fresh marine OM is crucial for infaunal nutrition; vascular plant detritus alone is of low food value, though it can supplement diets when mixed with phytodetritus (Leduc et al., 2020b).

Many polychaetes and some crustacean infauna are opportunistic feeders that rapidly exploit new organic deposits. Spionid polychaetes, for instance, are known opportunists that can switch between surface deposit feeding and suspension feeding, allowing them to capitalize on phytodetrital falls (Leduc et al., 2016). Enhanced food supply often leads to increased reproduction and recruitment in such species. Meiofauna (nematodes, benthic copepods) also increase in abundance with greater organic carbon availability, although extremely high loads of OM can lead to oxygen consumption by microbes and create localized hypoxia that stresses infauna (Neira et al., 2018). Thus, there is a balance: moderate, frequent food inputs sustain diverse communities, whereas large, abrupt pulses can favour a few tolerant opportunists and reduce diversity (the classic “boom-and-bust” deep-sea dynamic). Overall, bathyal infaunal communities are food-limited and therefore highly sensitive to changes in OM flux. Any climate- or human-driven shifts in surface productivity that decrease the quantity or quality of sinking POC (particulate organic carbon) would likely reduce infaunal abundance and alter community composition in New Zealand’s deep sea (Leduc et al., 2020b).

Sensitivity to sedimentation and turbidity

Sedimentation rates and episodic depositional events strongly influence infaunal communities (Hewitt & Lohrer, 2013). Most bathyal infauna are adapted to a relatively low, chronic rain of fine sediment. However, abrupt burial by fast-deposited sediment (e.g. turbidites, slides, or sediment plumes) can smother infauna and physically alter habitat structure. A dramatic example was the 2016 Kaikōura earthquake, which triggered a submarine canyon flushing and turbidity flow that scoured and buried extensive seafloor area (Mountjoy et al., 2018). Immediately after this event, meiofaunal abundances in Kaikōura Canyon plummeted to a small fraction of pre-disturbance levels (Bigham et al., 2024). Core samples showed that virtually all small benthic metazoans were wiped out or significantly reduced by the mass deposition of sediments. Only after about four years did the meiofauna community recover to resemble its pre-event state, indicating the long-lasting impact of a single large sedimentation disturbance (Bigham et al., 2024). Even after 4 years, certain taxa (e.g. some nematodes) were still not fully back to prior composition, with full recovery for the nematode assemblage estimated at ~5 years (Bigham et al., 2024). This natural experiment underscores that deep-sea infauna have low resilience to sudden, major sedimentation events – recovery can take several years or more, even for meiofaunal organisms with fast life cycles.

Lesser sedimentation events, such as minor turbidity currents or high sedimentation from flood plumes, can also impact infauna. Burial by a few centimetres of sediment may kill sedentary suspension feeders and tube-dwelling species that cannot quickly relocate their feeding structures or move out of the deposits. More mobile burrowing fauna (e.g. some polychaetes and amphipods) might escape light burial by moving upward, depending on the fluidity of the deposit (Tillin & Ashley, 2020). Fine sediments can clog respiratory and feeding structures (gills and siphons) – a particular problem for taxa like bivalves and foraminifera (Brooks et al., 2004; Levinton & Bambach, 1975). Changes in grain-size and substrate compactness after deposition can further alter habitat suitability for infauna. For instance, a shift from coarser to very fine sediment may favour smaller deposit feeders (nematodes, small worms). Overall, while background sediment accumulation is part of the natural environment, significant increases in sedimentation rate or episodic deposition decrease infaunal densities and change community structure in bathyal habitats (Bigham et al., 2024). The Kaikōura Canyon study suggests that

physical habitat change (e.g. altered sediment texture, loss of organic materials) after disturbance correlates with the trajectory of community recovery (Bigham et al., 2024).

Visualization of deep-sea infaunal health and environmental thresholds

Rationale

Polychaetes are the dominant infaunal macrofaunal group at bathyal and abyssal depths (1000–3000 m) east of New Zealand, particularly on the Chatham Rise, Hikurangi Margin, and adjacent deep-sea habitats (Leduc et al., 2016; Pilditch et al., 2015; Probert et al., 2009; Probert et al., 1996; Probert et al., 2001). They play key roles in benthic ecosystem functioning as bioturbators, detritivores, and opportunistic colonizers. Their abundance, biomass, and community composition are sensitive to changes in environmental conditions, especially dissolved oxygen (O_2), particulate organic carbon (POC) flux, and sedimentation rate (Levin, 2003; Smith et al., 2008).

Methods

Thresholds and optima for polychaete health index modelling were primarily sourced from global reviews and experimental literature. For dissolved oxygen, we used the thresholds summarized by Levin (2003), who reports rapid macrofaunal declines below $60 \mu\text{mol } O_2/\text{kg}$ and acute stress below $45\text{--}50 \mu\text{mol } O_2/\text{kg}$. For POC flux, we relied on Smith et al. (2008), who define an optimum range for macrofaunal diversity (including polychaetes) as $5\text{--}10 \text{ mg C m}^{-2} \text{ d}^{-1}$, with declines at lower or higher values. Sedimentation thresholds are based on controlled experiments in shallow subtidal New Zealand habitats. Lohrer et al. (2004b) found that just 3–7 mm of terrigenous deposit ($\sim 3\text{--}7 \text{ g m}^{-2}$) significantly reduced polychaete density within 10 days, and Lohrer et al. (2006b) demonstrated that thicker layers ($\sim 10\text{--}20 \text{ mm}$; $\sim 10\text{--}20 \text{ g m}^{-2}$) led to further substantial declines, suggesting near-collapse at maximal deposition – limited further information is available in Hewitt & Lohrer (Hewitt & Lohrer, 2013) We applied these threshold values tentatively to deep-sea modelling, acknowledging the limited analogy. O_2 and POC flux values are based on global deep-sea polychaete/macrofaunal studies. Sedimentation thresholds are inferred from New Zealand shallow-water experiments, which are the best available proxies but may over- or underestimate deep-sea tolerance.

Equations for deep-sea polychaete health index

Oxygen response:

A sigmoidal function captures the sharp drop-off below $\sim 50 \mu\text{mol } O_2/\text{kg}$

$$H I_{O_2}(x) = \frac{1}{1 + \exp[-k_{O_2} \cdot (x - 55)]}$$

- $x = O_2 (\mu\text{mol}/\text{kg})$
- k_{O_2} = slope parameter (choose $k_{O_2} = 0.25\text{--}0.3$ for a steep drop near $50 \mu\text{mol}/\text{kg}$)

Interpretation:

- $HI \approx 1$ when $O_2 > 60 \mu\text{mol}/\text{kg}$
- HI drops rapidly below $50 \mu\text{mol}/\text{kg}$

POC flux response:

A Gaussian function fits the data, with optimum at $7.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ and σ (width) set to include most of the optimum range (5–10):

$$HI_{POC}(y) = \exp\left(-\frac{(y - 7.5)^2}{2 \cdot 2^2}\right)$$

- y = POC flux ($\text{mg C m}^{-2} \text{ d}^{-1}$)
- Centred at 7.5, $\sigma = 2$

Interpretation:

- $HI \approx 1$ at POC 5–10
- $HI < 0.5$ when POC < 2 or > 12

Sedimentation response:

A piecewise linear (or step) function:

$$HI_{Sed}(z) = \begin{cases} 1 & \text{if } z < 3 \\ 1 - \frac{z-3}{7} & \text{if } 3 \leq z \leq 10 \\ 0.5 - \frac{z-10}{10} & \text{if } 10 \leq z \leq 20 \\ 0.2 & \text{if } z \geq 20 \end{cases}$$

z = Sedimentation (g m^{-2} , single event)

Interpretation:

- $HI \approx 1$ if $< 3 \text{ g m}^{-2}$
- $HI \approx 0.5$ at 10 g m^{-2}
- $HI \approx 0.2$ for $\geq 20 \text{ g m}^{-2}$

Combined Health Index

$$HI(x, y) = HI_{O_2}(x) \times HI_{POC}(y)$$

$$HI(x, z) = HI_{O_2}(x) \times HI_{Sed}(z)$$

Parameters used:

Table 4-11: Environmental thresholds and health index response for deep-sea polychaetes (1000-3000 m, New Zealand Region)

Parameter	Optimum / Threshold Range	Health Index Response	Source(s)
O₂	Optimum: >60 µmol/kg	HI ≈ 1 (no oxygen stress)	(Levin, 2003)
	Threshold: 45–50 µmol/kg	Rapid decline in health	(Levin, 2003)
POC Flux	Optimum: 5–10 mg C m ⁻² d ⁻¹	HI ≈ 1 (max. biomass/diversity)	(Ruhl & Smith, 2004; Smith et al., 2008) and references therein
	Thresholds: <2 or >12 mg C m ⁻² d ⁻¹	HI < 0.5 (food limitation or opportunists dominate)	(Ruhl & Smith, 2004; Smith et al., 2008) and references therein
Sedimentation	Optimum: <3–7 g m ⁻²	HI ≈ 1 (minimal stress)	(Lohrer et al., 2004b; Lohrer et al., 2006b; Smith et al., 2008)
	Threshold: 10–20 g m ⁻²	HI declines significantly (<0.5), large losses	(Lohrer et al., 2004b; Lohrer et al., 2006b)
	>20 g m ⁻²	HI < 0.2 (substantial collapse of polychaete taxa)	(Lohrer et al., 2004b; Lohrer et al., 2006b)

Polychaete Health Index: O₂ vs POC flux (thresholds on surface)

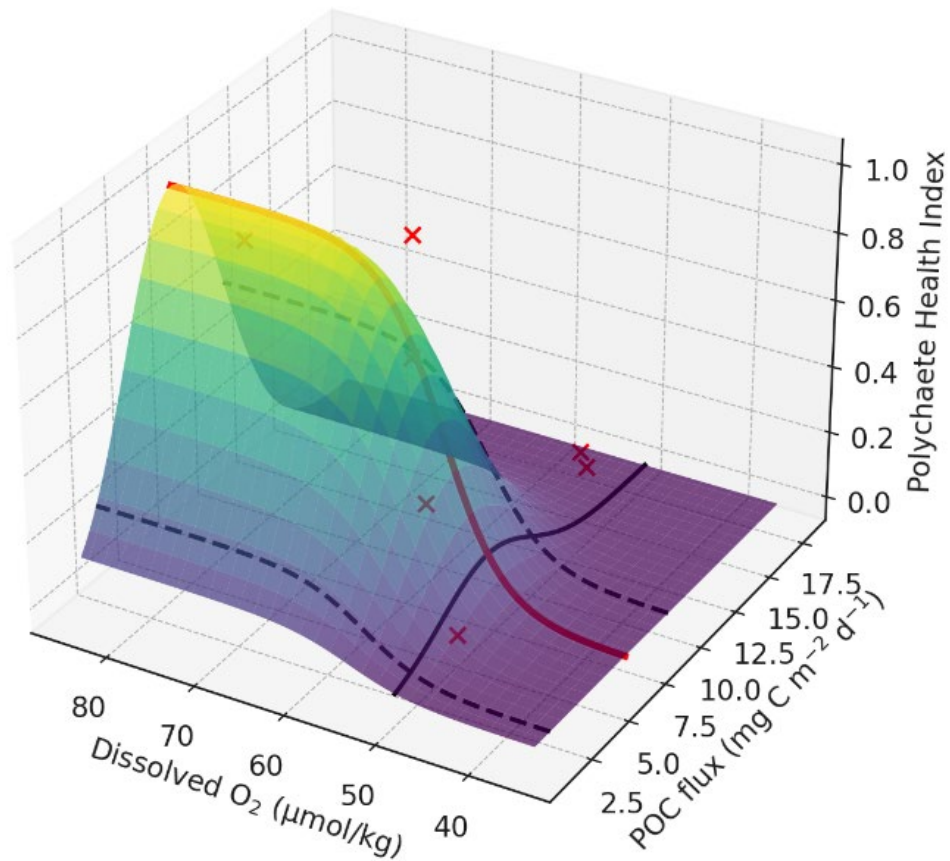


Figure 4-11: 3D surface plot of the polychaete health index as a function of bottom-water dissolved oxygen and POC flux. 3D surface plot of the calculated health index for deep-sea polychaetes (1000 – 3000 m) as a function of bottom-water dissolved oxygen O₂, (μmol kg⁻¹) and POC flux to the seafloor (mg C m⁻² d⁻¹). Health Index values range from 0 (low health) to 1 (optimal health). The model uses a sigmoidal decline for O₂ (threshold at 50 μmol kg⁻¹) based on Levin (2003), and a Gaussian peak for POC flux (optimum 5–10 mg C m⁻² d⁻¹, threshold <2 or >12), as synthesized by Smith et al. (2008). The dashed black horizontal lines indicate POC thresholds at 2 and 10 mg C m⁻² d⁻¹, beyond which health deteriorates due to food limitation or dominance of opportunistic species. The bold red line highlights the optimum POC flux (~7 mg C m⁻² d⁻¹) for sustaining healthy polychaete communities. Red dots represent empirical data points from field studies (Leduc et al., 2012; Smith et al., 2008).

Polychaete Health Index: O₂ vs Sedimentation (thresholds on surface)

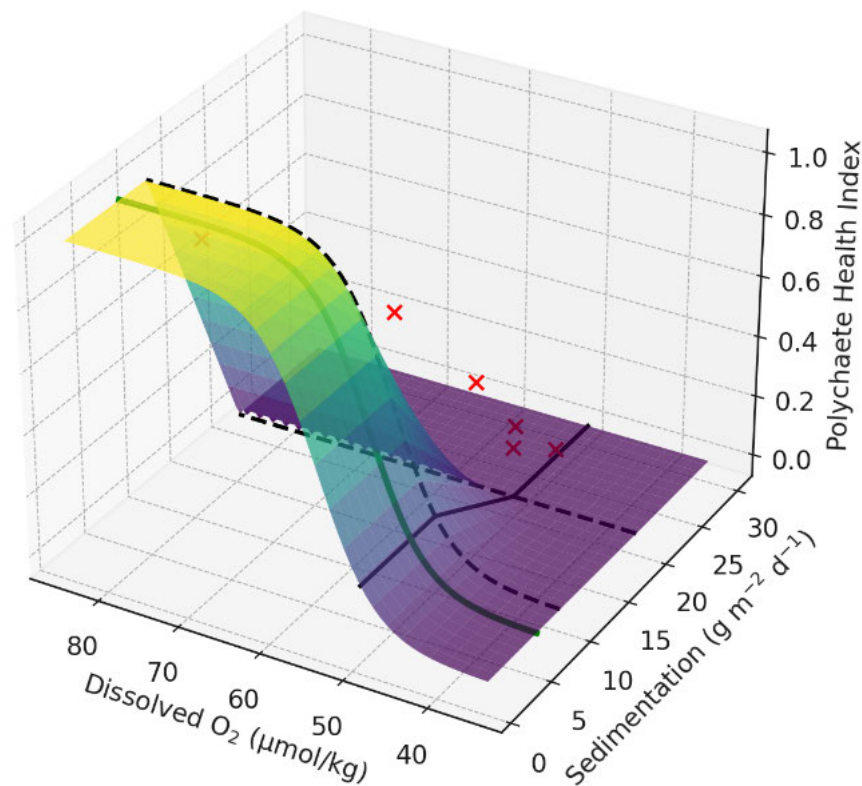


Figure 4-12: 3D surface plot of the polychaete health index as a function of bottom-water dissolved oxygen and sedimentation. 3D surface plot of the calculated health index for deep-sea polychaetes (1000 – 3000 m) as a function of bottom-water dissolved oxygen (O₂, μmol kg⁻¹) and single-event sedimentation rate (g m⁻² d⁻¹). The health index values range from 0 (low health) to 1 (optimal health). The health index sharply declines at O₂ concentrations below 50 μmol kg⁻¹, consistent with macrofaunal and polychaete response thresholds as reported by Levin (2003). Sedimentation thresholds are based on controlled shallow-water experiments (Lohrer et al., 2006a; Lohrer et al., 2004a). The health index remains high (< 3 – 7 g m⁻²), declines steeply from 10–20 g m⁻², and collapses at ≥ 20 g m⁻² d⁻¹. All threshold and optimum lines are drawn on the plot surface for visual clarity. Empirical points represent published experimental or observed values where available in accordance with Table 4-11. These sedimentation thresholds are proxies, not direct deep-sea measurements – interpretation should not this limitation. The health index surface thus represents current best estimates for polychaete sensitivity to combined oxygen depletion and sediment events.

Summary and conclusion on deep-sea infaunal sensitivities

Summarizes the relative sensitivity of major bathyal infaunal groups to three key environmental factors: low oxygen, OM availability, and sedimentation/burial. “Sensitivity” is defined here as vulnerability or responsiveness (high sensitivity = strongly negatively affected by stress or requiring that factor; low sensitivity = tolerant of stress/variable conditions). These general trends apply to most deep-sea slope communities, although individual species may vary.

Table 4-12: Qualitative sensitivity of major deep-sea infaunal groups to low oxygen, organic matter supply, and sedimentation disturbances. “High sensitivity” = *strongly negatively affected by stress (or narrow requirement for high levels)*; “Low sensitivity” = *relatively tolerant/resilient*. Oxygen values are given in mL·L⁻¹ for context. Sources (including shallow-water proxies and non-NZ studies): (Donald, 1996; Gadeken & Dorgan, 2024; Luigi et al., 2003; Marc et al., 2007; Steyaert et al., 2005).

Infaunal Group	Sensitivity to Low Oxygen	Response to Organic Matter Supply	Sensitivity to Sedimentation
Polychaete worms (macrofauna)	Moderate. Many polychaetes tolerate mild hypoxia, but diversity declines below ~0.5 mL·L ⁻¹ O ₂ ; a few opportunistic species (e.g. <i>Dorvilleidae</i> , <i>Spionidae</i>) survive in OMZ edges. Most require some O ₂ for aerobic metabolism and are absent in anoxic zones.	Strongly food responsive. Abundance and recruitment surge with phytodetritus pulses; opportunists can quickly exploit fresh organic deposits. Sustained marine organic input supports higher biomass and diversity. Under low food, many polychaetes shrink in size or reproduce less.	Moderate. Many burrowers can migrate upward or rebuild tubes after light sedimentation. However, heavy or rapid burial (>a few cm) smothers tubes and burrows, causing mortality. Sediment infill clogs feeding structures for suspension-feeding polychaetes. Recovery from major deposition can take years.
Nematodes (meiofauna)	Low sensitivity (high tolerance). Nematodes are among the most hypoxia-tolerant metazoans, remaining abundant even at O ₂ <0.1 mL·L ⁻¹ . Many can employ anaerobic metabolism; diversity is lower in anoxic conditions, but a few species thrive in OMZ cores.	Flexible but food limited. Ubiquitous even in low-food sediments, feeding on bacteria and detritus. Their densities increase with higher organic carbon availability, but extremely high enrichment may favour fast-growing species and reduce overall diversity. Generally resilient to sporadic feast-and-famine cycles.	Moderate. Owing to their small size, nematodes can persist within interstices even if a sediment layer is deposited. They can slowly migrate through pore spaces. Yet significant burial can reduce nematode abundance – deep deposits isolate them from the oxic sediment-water interface and food source.
Harpacticoid Copepods (meiofauna)	High sensitivity (low tolerance). Benthic copepods require well-oxygenated sediments; they sharply decline in persistent hypoxia. They are largely absent in OMZ core areas and flourish in oxygen-rich environments.	Dependent on detritus and biofilms. Copepods graze on meiobenthos (bacteria, microalgae) and detrital matter. Adequate OM sustains their populations. Under poor food supply, copepod abundance and reproduction drop. They benefit from moderate, continuous detrital rain; however, severe organic enrichment (leading to anoxia) will eliminate them.	High sensitivity. Copepods have limited mobility and cannot escape sediment burial. Even thin sediment layers can smother interstitial habitats and disrupt their grazing. They are easily depleted by sediment disturbances and take time to recolonize from surrounding areas.

Infaunal Group	Sensitivity to Low Oxygen	Response to Organic Matter Supply	Sensitivity to Sedimentation
Bivalve & Gastropod Molluscs (macrofauna)	High sensitivity. Most deep-sea bivalves and gastropods need oxic conditions. They are not found in anoxic sediments except for specialized chemosymbiotic bivalves. Shellfish lack adaptive mechanisms for sustained hypoxia (aside from short-term valve closure in some bivalves).	Food-coupled. Many are suspension or deposit feeders relying on settling POM (Particulate Organic Matter). Sufficient organic flux is required for growth (e.g. filter-feeding bivalves depend on phytodetritus). In low-food settings, growth is slow and recruitment sporadic. They can utilize pulses of food but can also starve during long oligotrophic periods.	High sensitivity. Sessile or sedentary burrowers can be easily smothered. Bivalves can only burrow a limited distance; if sediment deposition exceeds their siphon length, they cannot respire or feed and will perish if they are unable to move upwards in the sediment column. Fine sediment also clogs gills. Gastropods can also crawl, but thick silt layers hinder their mobility and bury food sources.
Crustaceans (macrofaunal; e.g. amphipods, isopods)	Moderate to high sensitivity. Many crustacean infauna have relatively high oxygen demands and avoid low-O ₂ areas. Amphipods and isopods are scarce in OMZ core habitats. Some facultative scavenger amphipods tolerate short-term hypoxia, but sustained low O ₂ leads to mortality or emigration.	Reliant on organic matter via food web. Many amphipods are scavengers, feeding on carrion or detritus, and isopods often are predators or detritivores. Their populations indirectly reflect surface productivity – more sinking OM means more prey/carrion. They are often quick to colonize food falls (e.g. dead fish, marine snow accumulations). Poor food supply leads to low densities, while enriched conditions attract them until O ₂ becomes limiting.	High sensitivity. Most crustacean infauna are mobile burrowers or surface dwellers that cannot withstand sudden burial. They require access to the sediment surface for feeding and oxygen. Even a few centimetres of deposited sediment can trap them or force them to flee. In sediment plume impacts, crustaceans are often among the first to disappear.

Bathyal infaunal communities in New Zealand’s deep-sea ecosystems display a delicate balance of resilience and sensitivity. They are adapted to the generally stable conditions of the deep ocean, yet modest environmental perturbations can significantly alter their structure. Low oxygen conditions favour only the hardiest of small metazoans (e.g. nematodes), leading to simplified communities under hypoxic stress. Variations in OM input – the fuel for these benthic systems – strongly regulate infaunal abundance and diversity, with food-rich areas (such as productive canyons) supporting rich communities that dwindle in food-poor regions (Leduc et al., 2020a). Infauna are vulnerable to physical disturbances and sedimentation (Bigham et al., 2024; Leduc et al., 2016). Despite their small size, these infaunal organisms play important ecological roles in sediment mixing, nutrient recycling, and supporting food webs, essentially keeping the deep-sea ecosystem functioning (Pierrejean et al., 2020; Sturdivant et al., 2024). In New Zealand’s deep-sea habitats, infaunal communities facilitate the remineralisation of organic carbon and linking of surface production to benthic consumers, acting as a living bridge in the ocean’s biological pump. Their overall sensitivity and slow turnover mean that continued

stress could impair these functions, with system-wide consequences. It is important to note that within the infauna, there are many different taxa that may exhibit different responses to different stressors, and the outcome of the community as whole will be dependent on the interactions between different components resulting in potential shifts and trade-offs. In summary, New Zealand's deep-sea infauna are both sentinels and stewards of benthic ecosystem health: sensitive to disturbance yet essential for the resilience and biogeochemical functioning of the deep ocean (Pierrejean et al., 2020; Sturdivant et al., 2024).

4.4.5 Deep-sea xenophyophores (Bathyal 200-3000 m, New Zealand)

Legislation: In New Zealand, xenophyophore beds – areas where these large deep-sea protists occur at densities of at least ~1 individual per m² – are explicitly defined as “sensitive marine benthic habitats” in the regulatory definitions used across environmental impact assessments in New Zealand's EEZ, reflecting their recognized ecological importance and vulnerability. These beds are treated similarly to other habitat-forming systems such as coral reefs or bryozoan thickets because they: 1) Provide structurally complex habitat that supports elevated infaunal and epifaunal diversity; 2) host fragile assemblages that are slow to recover from physical disturbance, 3) occur in discrete, spatially bounded patches that qualify as sensitive under regulatory sampling criteria, including imagery and sediment-core-based density thresholds (Anderson et al.; MacDiarmid et al., 2013).

Ecology: Deep-sea xenophyophores are giant single-celled protozoans (foraminiferans) that inhabit the bathyal zone (~200–3000 m) of oceans worldwide. Xenophyophores form elaborate sediment-agglutinated tests (shells) that can reach 25 cm in diameter. These tests are composed of mineral grains, sponge spicules, and organic debris bound by the organism's secretions. Remarkably, <5% of the test volume contains living protoplasm – the rest is a matrix of non-living material.

Their presence adds three-dimensional structure and heterogeneity to otherwise monotonous seabed (Levin et al., 1986; Levin & Gooday, 1992). Each xenophyophore test, with its crevices and surfaces, provides living space and refuge for a variety of organisms. Small metazoans such as polychaete worms, nematodes, crustaceans, and brittle stars commonly inhabit or cling to the tests. Bacteria and other microbes colonize the organic-rich interiors of the tests, sometimes forming symbiotic relationships or serving as an additional food source for the xenophyophore. Environments with abundant xenophyophores have been called “hotspots” of diversity: studies have documented higher densities and diversity of meiofauna and macrofauna in areas where xenophyophores are present compared to adjacent areas without them (Levin et al., 1986; Levin & Gooday, 1992). Xenophyophores also engage in unique interactions; a recent discovery showed that deep-sea snailfish (*Liparidae*) deposit their eggs within xenophyophore tests, using them as nurseries for developing embryos (Levin & Rouse, 2020). This is the first known case of fish utilizing a protist's structure for reproduction, underscoring the ecological facilitation these giant protozoans provide. Because of their role in enhancing local biodiversity, xenophyophores are regarded as important contributors to vulnerable marine ecosystems. If xenophyophore beds are removed (by disturbance or environmental change), many dependent species likely lose habitat and shelter.

Beyond structural habitat, xenophyophores influence deep-sea biogeochemical processes. By trapping fine particles and OM, xenophyophore tests create localized “depocenters” of organic carbon on the seafloor, with enhanced deposition of fine detritus in and around the tests (Levin

& Gooday, 1992). The micro-environment inside a test often contains copious stercomata (pellets of waste material) sequestered by the xenophyophore. These organic-rich waste deposits can foster high microbial activity (as first suggested by Tendal (1975)). In essence, each xenophyophore acts as a small biogeochemical reactor: OM is collected and partially broken down, supporting bacteria and fungi, which in turn mineralize nutrients. This can create hotspots of carbon mineralization and nutrient regeneration in what would otherwise be low-activity abyssal sediments. The concentration of labile material might also attract other deposit feeders that graze near xenophyophores, thus transferring energy to higher trophic levels. There is also evidence that xenophyophores take up dissolved organic compounds directly from seawater (perhaps through their extensive surface area), contributing to carbon cycling in a way that bypasses typical trophic links. Additionally, xenophyophores play a role in the cycling of elements: they selectively accumulate certain metals in their tests and cytoplasm. Studies have found unusually high concentrations of barite (barium sulphate) crystals and metals like lead, uranium, and mercury inside xenophyophores, indicating they may act as sinks for these elements over time (Hopwood et al., 1997; Rothe et al., 2011). Upon the death and disintegration of a xenophyophore, those sequestered metals and nutrients are released to the sediment, potentially affecting local geochemistry. In summary, xenophyophores are more than passive inhabitants – they actively modify their environment by concentrating OM and elements, thus influencing carbon burial and nutrient landscapes on the deep seafloor.

The physical structures created by xenophyophores can be likened to small “reefs” in the deep sea. Individually, a single test (often 5–10 cm across, but up to 25 cm) adds rugosity to a soft-sediment habitat, providing attachment surfaces and flow refuges. Collectively, aggregations of xenophyophores form patch-scale habitats that can cover kilometres. Surveys have reported xenophyophore patch densities that qualify as beds (e.g., ≥ 1 individual per m^2 on average) over sizable areas (Tendal & Lewis, 1978). Brittle stars coil around the lattice, shrimps and squat lobsters may shelter beside them, and sessile organisms can settle on the hard substrate of the test (e.g. small hydroids or foraminifera attaching to the grainy surface). At the landscape scale, xenophyophore fields contribute to habitat heterogeneity by introducing complex biogenic structures into largely unstructured sediment plains. This increases the spatial complexity of the benthic environment, which is linked to higher faunal diversity and abundance. Notably, xenophyophore structures occur in sedimented habitats that otherwise may lack large physical complexity, making their role even more pronounced. The presence of many xenophyophores can also alter local physical processes: their tests protrude into the benthic boundary layer flow, causing small-scale eddies that may enhance the deposition of particles immediately downstream (Levin & Gooday, 1992). In New Zealand’s case, xenophyophore beds on the Chatham Rise and slopes likely work in concert with other structure-forming taxa (e.g. sponges, corals) to create a richer physical habitat for deep-sea life. Their contribution is unique in that they do not require hard rock – they build on and reinforce soft sediments. The loss of these structures (through disturbance or environmental change) would thus decrease the habitat complexity and potentially reduce the carrying capacity for various organisms.

Sensitivity to oxygen availability and deoxygenation

Xenophyophores are generally found in areas with at least moderate oxygen levels, though they exhibit some tolerance to low-oxygen (hypoxic) conditions. They have been observed on eastern Pacific seamounts below ~1200 m, indicating tolerance of the oxygen minima in those regions (Levin, 1994). In fact, evidence suggests certain xenophyophores can survive at oxygen

concentrations as low as ~0.4 mL/L (about 18 μ M) (Ashford et al., 2014). This is a remarkable adaptation, allowing them to persist near oxygen minimum zones. However, they are absent from severely hypoxic or anoxic zones (Levin & Gooday, 1992). Thus, while xenophyophores can endure low oxygen better than many metazoans, they still require a baseline oxygen supply. Climate-driven deoxygenation poses a concern: as mid-depth oxygen minimum zones expand or intensify, the suitable habitat for xenophyophores may shrink. Regions of the Southwest Pacific with well-oxygenated deep waters (such as around New Zealand currently) support xenophyophore populations (Tendall and Lewis, 1978), but future deoxygenation could force these organisms to migrate, decline, or face local extinction if oxygen drops below their tolerance. In summary, xenophyophores have a moderate tolerance to low oxygen – they can live in oxygen-poor settings to a point (Ashford et al., 2014), but further oxygen depletion beyond ~0.4 mL/L will likely inhibit their survival and distribution.

Sensitivity to organic matter supply

Food availability (in the form of sinking OM) is a key driver of xenophyophore distribution and vitality. These protists are detritivores and occur most abundantly beneath areas of high surface productivity where particle flux to the seafloor is elevated (MacDiarmid et al., 2013). They are especially common under productive waters and in submarine canyons that funnel organic detritus to depth (Gooday et al., 2011; Levin & Gooday, 1992). They are highly responsive to food pulses: experiments have shown xenophyophores rapidly ingest fresh organic material (both particulate and dissolved) delivered to them, indicating an ability to quickly capitalize on episodic food falls (Tsuchiya & Nomaki, 2021), finding that xenophyophores efficiently collected phytodetritus within days of its arrival, likely supporting their surprisingly fast growth rates. Field observations confirm that increased organic flux triggers bursts of growth and reproduction in xenophyophore populations. For example, the giant species *Syringammina fragilissima* can double in size within months during periods of enhanced food supply (Gooday, 1993). Overall, xenophyophores are sensitive to changes in OM supply: they thrive and grow rapidly when food is plentiful, but a sustained reduction in particulate organic carbon (e.g. due to climate-driven shifts in surface productivity) could limit their growth, reproduction, and abundance.

Sensitivity to sedimentation and turbidity

Sedimentation plays a complex role in xenophyophore ecology. These organisms live mostly epifaunally on soft seabed, sometimes extending slightly into the sediment. They construct their tests by cementing ambient sediment grains, and one New Zealand species (*Syringammina tasmanensis*) was noted to use whatever sediment type it lives on (showing little selectivity) (Bull & Tyler-Walters, 2024). In general, xenophyophores prosper in areas with *steady, moderate sediment accumulation* that provides building material and associated microbes. Their reticulated tests even act as passive particle traps, accumulating fine sediments and OM which in turn support microbes and meiofauna (Levin & Gooday, 1992). However, xenophyophores are fragile and not well-adapted to dynamic sedimentary disturbance. Strong bottom currents or sediment resuspension events can scour or smother them. Levin & Thomas (1988) reported that xenophyophore abundance declined in areas where flow was energetic enough to mobilize sediment into ripples. Heavy sedimentation bursts (e.g. turbidity flows or sediment plumes) may bury xenophyophores faster than they can reposition or grow. Most species are unable to withstand being completely covered by sediment for extended periods. Although one infaunal xenophyophore (*Occultammia profunda*) can bury itself up to 6 cm deep, the vast majority live on or just below the surface (Tendall et al., 1982). Thus, an increased sedimentation rate –

especially of inorganic particles – could clog their feeding structures and oxygen exchange or bury them. We infer that xenophyophores have low tolerance for abrupt or excessive sedimentation. Stable seabed conditions with fine particles gently raining down are ideal, whereas environments with high sediment instability (turbulence, frequent depositional events) are less suitable for xenophyophore beds. In summary, moderate sediment supply is beneficial (they incorporate sediment into tests), but high-energy sediment disturbance or burial poses a significant stress.

Visualization for deep-sea xenophyophore health and environmental thresholds

Rationale and methods

Xenophyophores are large deep-sea foraminifera prominent in the Clarion–Clipperton Zone (CCZ) and elsewhere, including New Zealand (Tendall and Lewis, 1978). Robust numeric environmental thresholds (e.g., for dissolved oxygen, POC flux, or sedimentation) are not established in literature. Instead, broad observational studies report that xenophyophores reach the highest abundance in areas with moderate oxygen and food supply, and stable, low sedimentation rates. Below, we synthesize available data using only qualitative statements and observed environmental ranges.

Table 4-13: Qualitative environmental information for deep-sea xenophyophores

Parameter	Observed Environmental Range	Ecological Response	Reference
Oxygen	Moderate (e.g., >90 $\mu\text{mol/kg}$)	Abundant in moderate O_2 ; rare in hypoxic zones	Gooday et al. (2011; 2020; 2017a; 2017b; 2017c; 1992), Kamenskaya et al. (2015; 2013), Simon-Lledo et al. (2019).
POC flux	Moderate (typical CCZ range)	Highest abundance in moderate food supply areas	Gooday et al. (2020)
Sedimentation	Low–moderate, stable	More common on stable/undisturbed sediments	Jones et al. (2017)

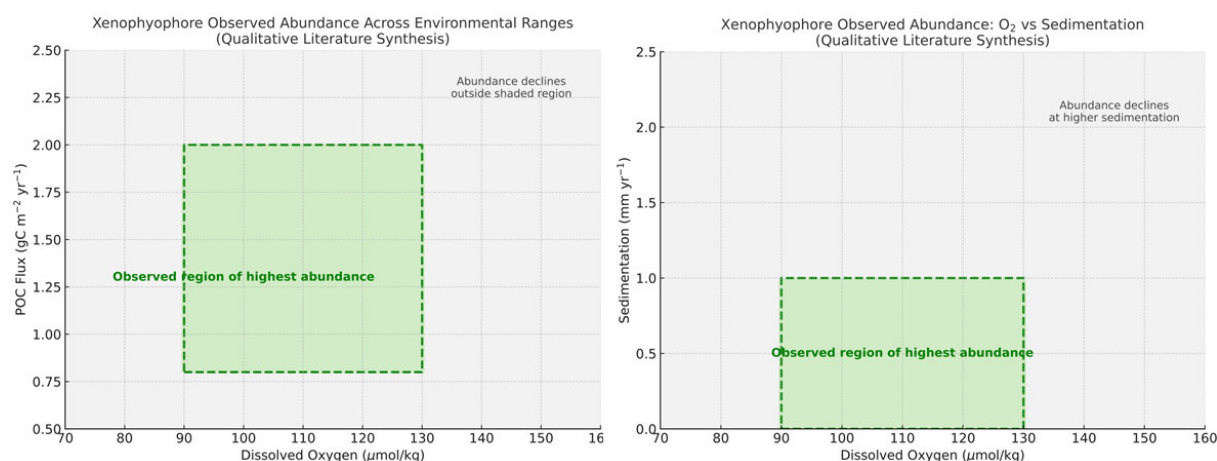


Figure 4-13: Xenophyophore observed abundance across O₂ and POC flux ranges. The green shaded regions indicate environmental conditions where highest abundance is reported in the literature; no sharp thresholds are implied. Abundance declines outside this region; xenophyophore observed abundance across O₂ and sedimentation. The shaded region reflects low to moderate, stable sedimentation where xenophyophores are most common. No numeric cutoffs are established. Abundance declines at higher sedimentation. Sources: Gooday et al. (2011; 2020; 2017a; 2017b; 2017c; 1992), Kamenskaya et al. (2015; 2013), Simon-Lledo et al. (2019), Jone et al. (2017).

Summary and conclusions on deep-sea xenophyophore sensitivities

Table 4-14: Summary of xenophyophores' sensitivity to oxygen availability, organic matter supply, and sedimentation. In addition to the here-mentioned sensitivity and response to oxygen availability, OM supply, and sedimentation, xenophyophores are fragile when facing physical disturbances. Recovery from such disturbances is slow and incomplete

Factor	Sensitivity and Response of Xenophyophores
Oxygen availability	Tolerate moderately low oxygen levels (down to ~0.4 mL L ⁻¹ O ₂) (Levin, 1994), allowing survival near OMZs. Absent if waters become severely hypoxic/anoxic. Further deoxygenation beyond tolerance leads to range contraction and stress. Overall: Moderate tolerance, but vulnerable to expanding low-oxygen zones.
Organic matter supply	Thrive on consistent detrital rain; highest densities occur beneath productive surface waters. Rapidly ingest and grow/reproduce after organic pulses (Tsuchiya & Nomaki, 2021). A decline in food flux reduces growth and may cause dormancy or population decline. Overall: Highly sensitive to food availability – positive response to pulses, negative impact from chronic food scarcity.
Sedimentation	Require stable sediment conditions with fine particles for test-building. Tests act as passive traps for particles (Levin & Gooday, 1992). High sediment resuspension or heavy deposition lowers survival: strong currents or turbid plumes can scour, smother, or bury them. Overall: Low tolerance to abrupt or excessive sedimentation; prefer steady, low-energy sedimentation regimes.

Deep-sea xenophyophores in New Zealand's bathyal ecosystems are both remarkably resilient in some respects and highly vulnerable in others. They show adaptive tolerance to low-oxygen and low-food conditions that prevail in the deep ocean – even thriving beneath productive waters and quickly exploiting episodic food pulses. Yet, their delicate tests and specialized habitat requirements make them sensitive to environmental perturbations. Declining oxygen or major shifts in organic flux due to climate change could substantially shrink their viable habitat.

Physical disturbances like bottom trawling and seabed mining could be particularly destructive. Despite these vulnerabilities, xenophyophores play an outsized ecological role: they are important habitat-formers that boost local biodiversity and foster micro-environments of intense biogeochemical activity. In New Zealand's deep-sea communities, xenophyophores likely function as keystone protists – providing food, shelter, and structural complexity in soft-sediment realms. Their overall sensitivity and ecological importance have led to their recognition as indicators for vulnerable marine ecosystems in need of protection. In summary, xenophyophores are fragile giants of the deep: highly susceptible to disturbance, but indispensable for the richness and functioning of New Zealand's deep-sea habitats. Protecting these unique organisms and the conditions they require will be crucial for maintaining deep benthic ecosystem health in the face of growing anthropogenic pressures.

4.4.6 Deep-sea bryozoans (Bathyal <1000 m, New Zealand)

Ecology: Deep-sea bryozoans (sessile colonial filter-feeders) in the NZ EEZ include encrusting, erect-branching, and massive (reef-forming) forms. These long-lived, calcified colonies (>5 cm) occur on stable hard substrates with good water flow (Wood et al., 2013), but are mainly limited to shelf regions. They build three-dimensional biogenic reefs and support diverse invertebrate assemblages (e.g. sponges, worms, molluscs, etc.) and even juvenile fish (Wood et al., 2013). Many commercially important fish and invertebrates (e.g. scallops, snapper, tarakihi, oysters) use bryozoan thickets as nursery or feeding grounds (Wood et al., 2013). In effect, bryozoan reefs act as biodiversity “hotspots” and nursery habitats, seeding adjacent communities.

Functionally, bryozoans are filter-feeders that cycle OM and help clarify water. They capture particles and incorporate carbon into their CaCO₃ skeletons, contributing to deep-sea carbonate budgets and potential long-term carbon storage (analogous to deep coral frameworks). By trapping organic detritus and nutrients, bryozoan colonies can enhance local productivity and biogeochemical turnover on the seafloor.

However, they are physiologically and ecologically sensitive: they require well-oxygenated water, a steady supply of planktonic food, and low levels of fine sediment (Wood et al., 2013). Below we review their sensitivity to key environmental factors.

Sensitivity to oxygen availability and deoxygenation

Bryozoans depend on aerobic metabolism; low dissolved O₂ limits their survival (Barnes & Peck, 2005; Peck & Barnes, 2004). Data on deep-sea bryozoans is extremely limited, but, like other sessile filter-feeders, are expected to be highly intolerant of sustained hypoxia. They occupy well-ventilated currents and have little capacity to avoid O₂ drops, so climate-driven deoxygenation is a major threat (i.e. high sensitivity).

Sensitivity to organic matter pulses

As filter-feeders, bryozoans require planktonic food. Periodic influxes of organic particles (e.g. phytodetritus from surface blooms) generally benefit them. Areas of high surface productivity (upwelling, fronts) tend to harbour richer bryozoan communities (Wood et al., 2013). Thus, moderate increases in organic supply usually enhance growth and reproduction of deep-sea bryozoans (i.e. low sensitivity or positive response). There is little evidence that organic pulses themselves damage bryozoans, but this would depend on the magnitude and frequencies of the pulses – in fact, reduced food (through eutrophication-driven declines in primary production)

could stress them. However, note that high organic fluxes often accompany high sediment loads, and likely coincide with increased oxygen stress.

Sensitivity to sedimentation and turbidity

Bryozoans are vulnerable to burial by sediment a few centimetres of settling silt can smother colonies, clog feeding structures, and block respiration. For example, sensitivity assessments note that smothering by ~5 cm of sediment “prevents feeding, growth, reproduction, as well as respiration” and can physically remove colonies (Readman et al., 2023). Most deep bryozoans therefore thrive in high-flow areas where currents sweep sediments away (Wood et al., 2013). Increases in suspended particles (turbidity) also reduce their abundance due to constant clogging. In summary, heavy sedimentation (e.g., from turbid plumes) causes high mortality of bryozoans (i.e., high sensitivity). Only small reductions in sediment (and increases in food) favour colonization by these organisms.

Table 4-15. Sensitivity of deep-sea bryozoans to oxygen availability, organic matter pulses, and sedimentation

Environmental Factor	Sensitivity of Deep Bryozoans
Oxygen availability	High: require well-oxygenated flow; hypoxia halts metabolism (mortality under low O ₂).
Organic-matter pulses	Low (beneficial): additional food enhances growth; high productivity zones support richer bryozoan assemblages.
Sedimentation	High: a few cm of silt smothers colonies, blocking feeding/respiration; chronic turbidity clogs lophophores.

Visualization of deep-sea bryozoan health and environmental thresholds

Rationale

Bryozoans are key habitat-forming suspension feeders in New Zealand’s deep-sea environments, especially in thicket-forming assemblages (Wood et al., 2013). Their health, abundance, and habitat-structuring capacity are strongly controlled by environmental factors, primarily dissolved oxygen, particulate organic carbon (POC) flux, and sedimentation rate. Dissolved oxygen limits are crucial for deep-sea bryozoans, as sublethal hypoxia (O₂ < 60 µmol/kg) can cause physiological stress, reduced feeding, and ultimately collapse of thicket structure (Levin, 2003). POC flux provides food to suspension feeders, and bryozoan abundance peaks at moderate, continuous fluxes (Wood et al., 2013). Sedimentation rate can enhance food supply at low rates but causes smothering or hypoxia above chronic thresholds. Quantifying these environmental optima and thresholds is essential for assessing the vulnerability of bryozoan thickets to anthropogenic impacts (e.g., mining, climate-driven deoxygenation, organic matter pulses), and for setting regulatory boundaries.

Methods

A literature search was performed targeting deep-sea bryozoan studies from New Zealand, which yielded little specific information. Instead, we relied on two sources that provided oxygen thresholds (Levin, 2003), and POC flux data (2007) for areas where bryozoans have been found (Wood et al., 2013). No reliable information on sedimentation thresholds could be found specific for deep-sea bryozoans. There are two papers describing the role of environmental variables in shaping bryozoan distributions. Little et al (2018) dealt with intertidal epibiotic

bryozoans tracking decadal changes in bryozoan abundance in response to very shallow-water oxygen fluctuations ($< 4 \text{ mg L}^{-1}$) and water flow. This paper did not report any of the deep-sea parameters we need (POC flux, sedimentation rates, deep-sea O_2 profiles) and since it pertains to warm, shallow, highly variable coastal waters it deemed not usable for our New Zealand deep-sea bryozoan health index models. Wood et al (2013) does not report any quantitative sedimentation or particulate sedimentation rates; and we could therefore not deduce sedimentation thresholds from that source. Based on the data we were able to retrieve, we limited ourselves to the calculation of deep-sea bryozoan health in response to oxygen (Sigmoid response) and POC flux values (Gaussian response).

Table 4-16: Optimum and threshold values for O_2 and POC flux applied to deep-sea bryozoans

Parameter	Optimum	Lower Threshold	Upper Threshold	Literature
Dissolved Oxygen ($\mu\text{mol/kg}$)	$> 80 \mu\text{mol/kg}$	$60 \mu\text{mol/kg}$	—	(Levin, 2003)
POC Flux ($\text{mg C m}^{-2} \text{d}^{-1}$)	$10 \text{ mg C m}^{-2} \text{d}^{-1}$	$4 \text{ mg C m}^{-2} \text{d}^{-1}$	$15 \text{ mg C m}^{-2} \text{d}^{-1}$	(Nodder et al., 2007)

Equations

Oxygen & POC (Gaussian-Gaussian)

$$HI_{O_2}(x) = \exp\left(\frac{1}{1 + e^{-0.2(x-60)}}\right)$$

$$HI_{POC}(y) = \exp\left(-\frac{(y-10)^2}{23.5^2}\right)$$

$$HI(x,y) = HI_{O_2}(x) \times HI_{POC}(y)$$

Whereby

x = dissolved O_2 ($\mu\text{mol/kg}$)

y = POC flux ($\text{mg C m}^{-2} \text{d}^{-1}$)

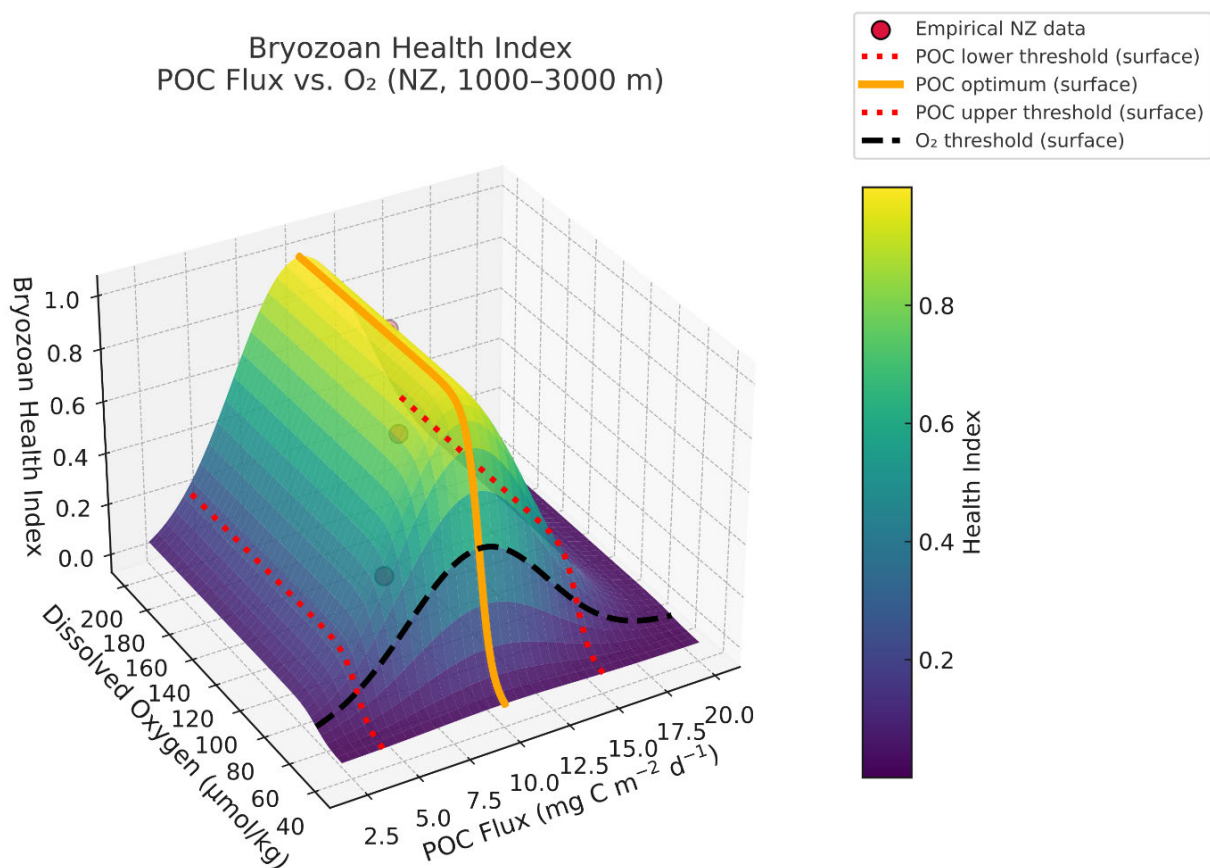


Figure 4-14: 3D surface plot showing modelled bryozoan health index as a function of POC flux and dissolved oxygen. The health index combines a sigmoid oxygen effect (steep decline below 60 μmol kg⁻¹) and a Gaussian POC flux response (optimum at 10 mg C m⁻² d⁻¹, decline below 4 mg C m⁻² d⁻¹ and above 15 mg C m⁻² d⁻¹). Curves overlaid on the surface represent POC lower threshold (4, red dotted), POC optimum (10, orange solid), and POC upper threshold (15, red dotted), as well as the oxygen threshold (60 μmol/kg, black dashed) across all POC fluxes. Empirical data points were informed by Chatham Rise measurements (Nodder et al., 2007) showing an inferred linear range of conditions under which bryozoan thickets exist (6–12 mg C m⁻² d⁻¹) where food supply is neither too low nor too high, although the presence of thickets seems water depth-limited (Wood et al., 2013). Note that (Nodder et al., 2007) did not assess bryozoan presence.

Summary and conclusion on deep-sea bryozoan sensitivity

Bathyal bryozoans in New Zealand are ecologically important yet sensitive ecosystem engineers. They are especially vulnerable to low oxygen and high sedimentation. By contrast, they thrive on ample food supply, making natural organic pulses relatively benign or beneficial. Conserving this structural benthic fauna will help protect NZ's deep-sea biodiversity and maintain essential biogeochemical functions. As Wood et al. (2013) note, bryozoan reefs span hundreds of square kilometres in NZ and are “prone to damage by anthropogenic impacts”, underscoring the need for targeted management and conservation.

5 Summary and conclusions

- **Brief and Scope:** This report, commissioned by Gigablue, reviews the scientific literature to inform threshold values for benthic dissolved oxygen (DO) perturbations and particulate deposition arising from Gigablue's Microalgae Carbon Fixation and Sinking (MCFS) activities in New Zealand's EEZ, relative to the AOI as communicated to us by Gigablue prior to producing this report.
- **Objectives:**
 - Quantify natural variability in bottom-water DO and particulate organic carbon (POC)/sediment flux in the study area.
 - Identify DO reduction levels and particle accumulation rates at which adverse impacts (hypoxia, smothering) occur for key deep-sea taxa.
 - Situate proposed thresholds within New Zealand's legal framework (EEZ Act 2012, Continental Shelf Act 1964, Wildlife Act 1953).
- **Methods:**
 - Comprehensive desktop review of relevant peer-reviewed studies
 - Focus on taxa protected or indicative of sensitive environments (e.g., stony corals, xenophyophores, bryozoans, sponges, brachiopods) as specified in national legislation.
 - Synthesis of global and regional observations to derive DO and POC/sedimentation baselines and thresholds.
- **Key Findings – Environmental Baselines:**
 - Bottom-water DO in the AOI ranges $\sim 150\text{--}200\ \mu\text{mol kg}^{-1}$, with a seasonal-stable minimum near $1200\text{--}1500\ \text{m}$ ($\sim 130\text{--}160\ \mu\text{mol kg}^{-1}$).
 - Natural POC flux to the seabed typically $1\text{--}5\ \text{mg C m}^{-2}\ \text{d}^{-1}$ (mean $\sim 3\text{--}4\ \text{mg C m}^{-2}\ \text{d}^{-1}$ in HNLC waters), episodically peaking to $\sim 8\text{--}10\ \text{mg C m}^{-2}\ \text{d}^{-1}$ during blooms. Sedimentation rates similarly variable but generally low ($<1\ \text{mm yr}^{-1}$).
- **Tentative Taxon-Specific Thresholds based on available data:**
 - Thresholds of impacts on organisms and/or ecosystems specific to MCFS activities and AOI are largely unknown and likely to be species and life-stage specific.
 - **Corals:** Critical DO threshold $\sim 40\text{--}50\ \mu\text{mol kg}^{-1}$ ($\sim 3.8\ \text{mg L}^{-1}$); sediment pulses above $50\text{--}100\ \text{mg L}^{-1}$ cause tissue loss and mortality.
 - **Sponges:** DO optimum $\sim 200\text{--}220\ \mu\text{mol kg}^{-1}$; health declines below $\sim 150\ \mu\text{mol kg}^{-1}$; sediment tolerances up to $\sim 55\ \text{mg L}^{-1}$ before sub-lethal effects.
 - **Brachiopods & Infauna:** DO limitations $\sim 40\text{--}50\ \mu\text{mol kg}^{-1}$; POC flux optima $\sim 3\text{--}10\ \text{mg C m}^{-2}\ \text{d}^{-1}$, with thresholds <2 or $>12\ \text{mg C m}^{-2}\ \text{d}^{-1}$.

- **Xenophyophores:** Broad tolerance region ($O_2 > 100 \mu\text{mol kg}^{-1}$; low-moderate sedimentation); no sharp numeric cut-offs but abundance declines outside these ranges.
- **Legal and Management Context:**
 - Proposed DO reduction limit: $<20 - 30\%$ decrease from background (i.e., avoid DO falling below $\sim 100\text{--}120 \mu\text{mol kg}^{-1}$) aligns with ecological sensitivities identified but exceeds “hypoxia” definition ($60 \mu\text{mol kg}^{-1}$).
 - Potential particulate deposition limit of $25 \text{ g m}^{-2} \text{ event}^{-1}$ should be assessed against taxon-specific sediment/particulate levels; but is likely to cause significant DO drawdown based on currently available scientific information.
- **Caveats:**
 - Although based on the preliminary findings of currently available data, MCFS operations should be constrained to limit DO drawdown to $<20\%$ from baseline (to maintain $>120 \mu\text{mol kg}^{-1}$) and particulate deposition below identified taxon-specific sedimentation concentrations.
 - It is important to note that negative taxon-specific and benthic community responses may still occur at DO reductions and particulate deposition levels less than stated here, since further research is needed to assess true empirical thresholds that are relevant to ‘confirmed’ sensitive environments in the AOI, and the specific characteristics of the particles and their behaviour *in situ*.
 - Thresholds of impacts on organisms and/or ecosystem specific to MCFS activities and the AOI are largely unknown and likely to species- and life stage-specific.
 - Due to the paucity of information, the here reported values have in many cases been inferred using proxies of similar taxa from international studies; available studies so far have not adequately assessed the taxa, community, and ecosystem responses to oxygen changes in specific relation to the proposed MCFS activities and within the declared AOI.
 - Further survey and experimental work need to be conducted to confirm taxa presence in the AOI, establish and refine thresholds, including *in situ* experiments on substrate-specific OM remineralisation and *in situ* and/or laboratory-based studies, so that uncertainties can be reduced and thresholds can be refined.

6 References

- Anderson, O., Stephenson, F., Behrens, E. (2018) Updated habitat suitability modelling for protected corals in New Zealand waters (Draft report; prepared for the Department of Conservation).
<https://www.doc.govt.nz/globalassets/documents/conservation/marine-and-coastal/marine-conservation-services/reports/pre-2019-annual-plans/pop-2018-01-coral-habitat-suitability-draft-report.pdf>
- Anderson, O., Stephenson, F., Behrens, E. (2020) Updated habitat suitability modelling for protected corals in New Zealand waters (Prepared for Department of Conservation) *NIWA Client Report* 2020174WN.
<https://www.doc.govt.nz/globalassets/documents/conservation/marine-and-coastal/marine-conservation-services/reports/pre-2019-annual-plans/pop2018-01-coral-habitat-suitability-final-report.pdf>
- Anderson, O., Tracey, D., Bostock, H., Williams, M., Clark, M. (2014) Refined habitat suitability modelling for protected coral species in the New Zealand EEZ (prepared for Marine Species and Threats, Department of Conservation) (WLG2014-69).
<https://www.doc.govt.nz/globalassets/documents/conservation/marine-and-coastal/marine-conservation-services/meetings/pre-2020-meetings/protected-coral-distribution-modelling.pdf>
- Anderson, T.J., Morrison, M., MacDiarmid, A., Clark, M., D'Archino, R., Nelson, W., Tracey, D., Gordon, D., Read, G., Kettles, H., Morrissey, D., Wood, A., Anderson, O., Smith, A.M., Page, M., Paul-Burke, K., Schnabel, K., Wadhwa, S. (2018) Review of New Zealand's key biogenic habitats. *NIWA Client Report* 2018139WN.
<https://research.ebsco.com/linkprocessor/plink?id=aa765460-495f-3cc1-8f67-230a90fafd5f>
- Angeletti, L., Canese, S., Cardone, F., Castellan, G., Foglini, F., & Taviani, M. (2020) A brachiopod biotope associated with rocky bottoms at the shelf break in the central Mediterranean Sea: Geobiological traits and conservation aspects. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(2), 402-411.
<https://doi.org/https://doi.org/10.1002/aqc.3255>
- Archer, D. (2011) *The global carbon cycle*. Princeton University Press.
- Armstrong, R.A., Lee, C., Hedges, J.I., Honjo, S., Wakeham, S.G. (2002a) A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep Sea Research Part II: Topical Studies in Oceanography*, 49(1-3), 219-236. [https://doi.org/10.1016/S0967-0645\(01\)00101-1](https://doi.org/10.1016/S0967-0645(01)00101-1)
- Armstrong, R.A., Lee, C., Hedges, J.I., Honjo, S., Wakeham, S.G. (2002b) A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals. *Deep Sea Research Part II*, 49(1-3), 219-236. [https://doi.org/10.1016/S0967-0645\(01\)00101-1](https://doi.org/10.1016/S0967-0645(01)00101-1)

- Armstrong, R.A., Peterson, M.L., Lee, C., Wakeham, S.G. (2009) Settling velocity spectra and the ballast ratio hypothesis. *Deep Sea Research Part II: Topical Studies in Oceanography*, 56(18), 1470-1478. <https://doi.org/10.1016/j.dsr2.2008.11.032>
- Arndt, S., Jørgensen, B. B., LaRowe, D. E., Middelburg, J. J., Pancost, R. D., & Regnier, P. (2013). Quantifying the degradation of organic matter in marine sediments: A review and synthesis. *Earth-Science Reviews*, 123, 53-86. <https://doi.org/http://dx.doi.org/10.1016/j.earscirev.2013.02.008>
- Ashford, O.S., Davies, A.J., Jones, D.O.B. (2014) Deep-sea benthic megafaunal habitat suitability modelling: A global-scale maximum entropy model for xenophyophores. *Deep Sea Research Part I: Oceanographic Research Papers*, 94, 31-44. <https://doi.org/https://doi.org/10.1016/j.dsr.2014.07.012>
- Auscavitch, S.R. (2020) Deep-Sea Coral Biogeography and Community Structure in Tropical Seamount Environments. Temple University.
- Baetge, N., Graff, J.R., Behrenfeld, M.J., Carlson, C.A. (2020) Net community production, dissolved organic carbon accumulation, and vertical export in the Western North Atlantic. *Frontiers in Marine Science*, 7, 227.
- Ballanti, L.A., Tullis, A., Ward, P.D. (2012) Comparison of oxygen consumption by *Terebratalia transversa* (Brachiopoda) and two species of pteriomorph bivalve molluscs: implications for surviving mass extinctions. *Paleobiology*, 38(4), 525-537.
- Banse, K., English, D.C. (1997) Near-surface phytoplankton pigment from the Coastal Zone Color Scanner in the Subantarctic region southeast of New Zealand. *Marine Ecology Progress Series*, 156, 51-66. <https://www.int-res.com/abstracts/meps/v156/meps156051>
- Barnes, D.K.A., Peck, L.S. (2005) Extremes of metabolic strategy in Antarctic Bryozoa. *Marine Biology*, 147(4), 979-988. <https://doi.org/10.1007/s00227-005-1628-3>
- Barthel, D., Tendal, O.S. (1993) The sponge association of the abyssal Norwegian Greenland Sea: Species composition, substrate relationships and distribution. *Sarsia*, 78(2), 83-96. <https://doi.org/10.1080/00364827.1993.10413524>
- Beaumont, J., Anderson, O., Davidson, S., Miller, A., & Peart, R. (2025). Benthic data summary for Gigablue's area of interest with respect to marine carbon dioxide removal.
- Bell, J.J. (2008) The functional roles of marine sponges. *Estuarine Coastal and Shelf Science*, 79(3), 341-353. <https://doi.org/10.1016/j.ecss.2008.05.002>
- Bell, J.J., McGrath, E., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J., Shaffer, M. (2015) Sediment impacts on marine sponges. *Mar Pollut Bull*, 94(1-2), 5-13. <https://doi.org/10.1016/j.marpolbul.2015.03.030>

- Bett, B.J., Malzone, M.G., Narayanaswamy, B.E., Wigham, B.D. (2001) Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. *Progress in Oceanography*, 50(1-4), 349-368.
<http://www.sciencedirect.com/science/article/B6V7B-445GJ8T-K/2/af623c39e0f91fbe465609ec54fc3f74>
- Bett, B.J., Rice, A.L. (1992) The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the porcupine seabight (bathyal NE Atlantic). *Ophelia*, 36(3), 217-226.
<https://doi.org/10.1080/00785326.1992.10430372>
- Bigham, K.T., Leduc, D., Rowden, A.A. (2024) Recovery of deep-sea meiofauna community in Kaikōura Canyon following an earthquake-triggered turbidity flow. *PeerJ*, 12, e17367. <https://doi.org/10.7717/peerj.17367>
- Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B., Priede, I.G. (2010) Long-term change in the abyssal NE Atlantic: The 'Amperima Event' revisited. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 57(15), 1406-1417.
<http://www.sciencedirect.com/science/article/B6VGC-4VNH3SH-2/2/2a1ddbe141e9f58c5dd57bac7860ff08>
- Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C. (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature*, 302(5908), 520-522. <http://dx.doi.org/10.1038/302520a0>
- Bitner, M.A. (2011) Recent brachiopods from New Zealand and surrounding waters. *Polish Journal of Geology*, 59(3), 213-226.
<https://geojournals.pgi.gov.pl/agp/article/view/10233>
- Bitner, M.A., Logan, A., James, N.P. (2008) Recent brachiopods from the deep shelf and slope of New Zealand and Australia. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 55(22-23), 2545-2555. <https://doi.org/10.1016/j.dsr2.2008.07.007>
- Bostock, H.C., Opdyke, B.N., Williams, M.J.M. (2010) Characterising the intermediate depth waters of the Pacific Ocean using $\delta^{13}\text{C}$ and other geochemical tracers. *Deep Sea Research Part I: Oceanographic Research Papers*, 57(7), 847-859.
<https://doi.org/https://doi.org/10.1016/j.dsr.2010.04.005>
- Bostock, H.C., Tracey, D.M., Currie, K.I., Dunbar, G.B., Handler, M.R., Mikaloff Fletcher, S.E., Smith, A.M., Williams, M.J.M. (2015) The carbonate mineralogy and distribution of habitat-forming deep-sea corals in the southwest Pacific region. *Deep Sea Research Part I: Oceanographic Research Papers*, 100, 88-104.
<https://doi.org/https://doi.org/10.1016/j.dsr.2015.02.008>
- Boudreau, B.P. (1997) Diagenetic models and their implementation (Vol. 505). Springer Berlin.
- Boyd, P., LaRoche, J., Gall, M., Frew, R., McKay, R.M.L. (1999) Role of iron, light, and silicate in controlling algal biomass in subantarctic waters SE of New Zealand. *Journal of Geophysical Research: Oceans*, 104(C6), 13395-13408.
<https://doi.org/https://doi.org/10.1029/1999JC900009>

- Boyd, P.W., Claustre, H., Levy, M., Siegel, D.A., Weber, T. (2019) Multi-faceted particle pumps drive carbon sequestration in the ocean. *Nature*, 568(7752), 327-335.
- Bradford-Grieve, J., Boyd, P., Chang, F., Chiswell, S., Hadfield, M., Hall, J., James, M., Nodder, S., Shushkina, E. (1999) Pelagic ecosystem structure and functioning in the Subtropical Front region east of New Zealand in austral winter and spring 1993. *Journal of Plankton Research*, 21(3).
- Bradford-Grieve, J.M., Chang, F.H., Gall, M., Pickmere, S., Richards, F. (1997) Size-fractionated phytoplankton standing stocks and primary production during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 31(2), 201-224.
<https://doi.org/10.1080/00288330.1997.9516759>
- Brooks, R.A., Bell, S.S., Purdy, C.N., Sulak, K.J. (2004) The benthic community of offshore sand banks: a literature synopsis of the benthic fauna resources in potential sand mining areas. USGS Outer Continental Shelf Studies Ecosystem Program Report USGSSIR-2004-5198 (CEC NEGOM Program Investigation Report No. 2004-01, February 2004); Minerals Management Service, OCS Study MMS-2004. (OCS Study MMS-2004). <https://www.boem.gov/sites/default/files/mm-research/2022-03/2004-USGS-BenthicCommunitySandBanks.pdf>
- Buesseler, K.O., Boyd, P.W., Black, E.E., Siegel, D.A. (2020) Metrics that matter for assessing the ocean biological carbon pump. *Proceedings of the National Academy of Sciences*, 117(18), 9679-9687.
- Bull, G., Tyler-Walters, H. (2024) Syringammina fragilissima field on Atlantic mid bathyal coarse sediment. In H. Tyler-Walters (Ed.), Marine Life Information Network: Biology and Sensitivity Key Information Reviews online. Plymouth: Marine Biological Association of the United Kingdom. Available from: .
<https://www.marlin.ac.uk/habitat/detail/1276>
- Burd, A.B., Hansell, D.A., Steinberg, D.K., Anderson, T.R., Arístegui, J., Baltar, F., Beupré, S.R., Buesseler, K.O., DeHairs, F., Jackson, G.A., Kadko, D.C., Koppelman, R., Lampitt, R.S., Nagata, T., Reinthaler, T., Robinson, C., Robison, B. H., Tamburini, C., Tanaka, T. (2010) Assessing the apparent imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological activity: What the @\$#! is wrong with present calculations of carbon budgets? *Deep Sea Research Part II: Topical Studies in Oceanography*, 57(16), 1557-1571.
<https://doi.org/https://doi.org/10.1016/j.dsr2.2010.02.022>
- Caromel, A.G., Schmidt, D.N., Phillips, J.C., Rayfield, E.J. (2014) Hydrodynamic constraints on the evolution and ecology of planktic foraminifera. *Marine Micropaleontology*, 106, 69-78.
- Carreiro-Silva, M., Martins, I., Riou, V., Raimundo, J., Caetano, M., Bettencourt, R., Rakka, M., Cerqueira, T., Godinho, A., Morato, T., Colaço, A. (2022) Mechanical and toxicological effects of deep-sea mining sediment plumes on a habitat-forming cold-water octocoral [Original Research]. *Frontiers in Marine Science*, 9.
<https://doi.org/10.3389/fmars.2022.915650>

- Carter, L., McCave, I.N. (1997) The sedimentary regime beneath the Deep Western Boundary Current inflow to the Southwest Pacific Ocean. *Journal of Sedimentary Research*, 67(6), 1005-1017. <https://doi.org/10.1306/d42686b2-2b26-11d7-8648000102c1865d>
- Cavan, E., Laurenceau-Cornec, E., Bressac, M., Boyd, P. (2019) Exploring the ecology of the mesopelagic biological pump. *Progress in Oceanography*, 176, 102125.
- Cecchetto, M.M., Moser, A., Smith, C.R., van Oevelen, D., Sweetman, A.K. (2023) Abyssal seafloor response to fresh phytodetrital input in three areas of particular environmental interest (APEIs) in the western clarion-clipperton zone (CCZ). *Deep Sea Research Part I: Oceanographic Research Papers*, 195, 103970. <https://doi.org/https://doi.org/10.1016/j.dsr.2023.103970>
- Chiswell, S.M., Bostock, H.C., Sutton, P.J.H., Williams, M.J.M. (2015) Physical oceanography of the deep seas around New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research*, 49(2), 286-317. <https://doi.org/10.1080/00288330.2014.992918>
- Christensen, J.P. (2000) A relationship between deep-sea benthic oxygen demand and oceanic primary productivity. *Oceanologica Acta*, 23(1), 65-82. [https://doi.org/https://doi.org/10.1016/S0399-1784\(00\)00101-8](https://doi.org/https://doi.org/10.1016/S0399-1784(00)00101-8)
- Clark, M.R., Rowden, A.A. (2009) Effect of deepwater trawling on the macro-invertebrate assemblages of seamounts on the Chatham Rise, New Zealand. *Deep Sea Research Part I: Oceanographic Research Papers*, 56(9), 1540-1554. <https://doi.org/https://doi.org/10.1016/j.dsr.2009.04.015>
- Clark, M.R., Rowden, A.A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K.I., Rogers, A.D., O'Hara, T.D., White, M., Shank, T.M., Hall-Spencer, J.M. (2010) The Ecology of Seamounts: Structure, Function, and Human Impacts. *Annual Review of Marine Science*, 2(1), 253-278. <https://doi.org/10.1146/annurev-marine-120308-081109>
- Collins, J.R., Edwards, B.R., Thamatrakoln, K., Ossolinski, J.E., DiTullio, G.R., Bidle, K.D., Doney, S.C., Van Mooy, B.A.S. (2015) The multiple fates of sinking particles in the North Atlantic Ocean. *Global Biogeochemical Cycles*, 29(9), 1471-1494. <https://doi.org/https://doi.org/10.1002/2014GB005037>
- Consalvey, M., Mackay, K., Tracey, D. (2006) Information Review for Protected Deep-Sea Coral Species in the New Zealand Region (Prepared for Department of Conservation) (WLG2006-85). <https://www.doc.govt.nz/documents/conservation/marine-and-coastal/fishing/protected-coral-information-review.pdf>
- Cook, A.A., Lamshead, P.J.D., Hawkins, L.E., Mitchell, N., Levin, L.A. (2000) Nematode abundance at the oxygen minimum zone in the Arabian Sea. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 47(1-2), 75-85. <Go to ISI>://WOS:000084501100005

- Cram, J.A., Fuchsman, C.A., Duffy, M.E., Pretty, J.L., Lekanoff, R.M., Neibauer, J.A., Leung, S.W., Huebert, K.B., Weber, T.S., Bianchi, D. (2022) Slow particle remineralization, rather than suppressed disaggregation, drives efficient flux transfer through the Eastern Tropical North Pacific Oxygen Deficient Zone. *Global Biogeochemical Cycles*, 36(1), e2021GB007080.
- Daufresne, M., Lengfellner, K., Sommer, U. (2009) Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 106(31), 12788-12793.
- Davison, P., Checkley Jr, D., Koslow, J., Barlow, J. (2013) Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Progress in Oceanography*, 116, 14-30.
- de Jonge, D.S.W., Gaurisas, D.Y., Smith, A.J., Holmes, E., Orejas, C., Mosquera Giménez, Á., Murray Roberts, J., Bernardino, A.F., Sweetman, A.K. (2024) In situ benthic community response to a phytodetritus pulse in the Cabo Verde Abyssal Basin (tropical NE Atlantic). *Progress in Oceanography*, 229, 103340.
<https://doi.org/https://doi.org/10.1016/j.pocean.2024.103340>
- De La Rocha, C.L., Passow, U. (2007) Factors influencing the sinking of POC and the efficiency of the biological carbon pump. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(5), 639-658.
<https://doi.org/https://doi.org/10.1016/j.dsr2.2007.01.004>
- De Leo, F.C., Smith, C.R., Rowden, A.A., Bowden, D.A., Clark, M.R. (2010) Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proceedings of the Royal Society B: Biological Sciences*.
<https://doi.org/10.1098/rspb.2010.0462>
- Décima, M., Stukel, M.R., Nodder, S.D., Gutiérrez-Rodríguez, A., Selph, K.E., Dos Santos, A.L., Safi, K., Kelly, T.B., Deans, F., Morales, S.E. (2023) Salp blooms drive strong increases in passive carbon export in the Southern Ocean. *Nature communications*, 14(1), 425.
- Diaz, R. J., Rosenberg, R. (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna.
- Dithugoe, C.D., Bezuidt, O.K., Cavan, E.L., Froneman, W.P., Thomalla, S.J., Makhalanyane, T.P. (2023) Bacteria and archaea regulate particulate organic matter export in suspended and sinking marine particle fractions. *Mosphere*, 8(3), e00420-00422.
- Donald, G.W. (1996) Response of macro- and meiobenthos from a carbon-poor sand to phytodetrital sedimentation. *Journal of Experimental Marine Biology and Ecology*.
[https://doi.org/10.1016/0022-0981\(96\)02581-6](https://doi.org/10.1016/0022-0981(96)02581-6)
- Durden, J.M., Clare, M.A., Vad, J., Gates, A.R. (2023) First in-situ monitoring of sponge response and recovery to an industrial sedimentation event. *Marine Pollution Bulletin*, 191, 114870.
<https://doi.org/https://doi.org/10.1016/j.marpolbul.2023.114870>

- Eerkes-Medrano, D.I., Leys, S.P. (2006) Ultrastructure and embryonic development of a syconoid calcareous sponge. *Invertebrate Biology*, 125(3), 177-194.
<https://doi.org/https://doi.org/10.1111/j.1744-7410.2006.00051.x>
- Emig, C.C. (1997) Ecology of inarticulated brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 129(1-2), 33-50.
- EPA. (2014) Decision on the marine consent application by Chatham Rock Phosphate Limited.
https://www.epa.govt.nz/assets/FileAPI/proposal/EEZ000006/EEZ000006_Decision_Decision.pdf
- EPA. (2017) Decision on marine consents and marine discharge consents application, Trans-Tasman Resources Limited, Extracting and processing iron sand within the South Taranaki Bight.
<https://www.epa.govt.nz/assets/Uploads/Documents/Marine-Activities-EEZ/Activities/7f11a030cb/TTRL-Marine-Consent-Decision-EEZ000011-FINAL-version.pdf>
- EPA. (2019) Decision on marine discharge consent application; OMV New Zealand Limited.
- Fernandez, D. (in prep.) Characterising ocean oxygen content around Aotearoa New Zealand over the last 20 years from observations.
- Fok-Pun, L. (1981) Settling velocities of planktonic foraminifera: density variations and shape effects.
- Foley, M.M., Martone, R.G., Fox, M.D., Kappel, C.V., Mease, L.A., Erickson, A.L., Halpern, B.S., Selkoe, K.A., Taylor, P., Scarborough, C. (2015) Using ecological thresholds to inform resource management: current options and future possibilities. *Frontiers in Marine Science*, 2, 95.
- Foster, M.W. (1974) Recent Antarctic and sub-Antarctic brachiopods (Vol. 63).
- Frontin-Rollet, G.E., Handler, M.R., Wysoczanski, R.J., Gazley, M.F., Hickey, C.W. (2022). Geochemical characterisation of offshore New Zealand phosphorites, and mechanisms for their formation. *Marine Geology*, 445, 106751.
- Gadeken, K.J., Dorgan, K.M. (2024) Effects of Diel Oxygen Cycling and Benthic Macrofauna on Sediment Oxygen Demand. *Estuaries and coasts*, 47(8), 2377-2388.
<https://doi.org/10.1007/s12237-024-01404-0>
- Gage, J.D., Tyler, P.A. (1992) Deep-Sea Biology: a Natural History of organisms at the Deep-Sea floor. Cambridge University Press.
- Gardner, W.D., Chung, S.P., Richardson, M.J., Walsh, I.D. (1995) The oceanic mixed-layer pump. *Deep Sea Research Part II: Topical Studies in Oceanography*, 42(2-3), 757-775.

- Gibbs, M., Leduc, D., Nodder, S.D., Kingston, A., Swales, A., Rowden, A.A., Mountjoy, J., Olsen, G., Ovenden, R., Brown, J. (2020) Novel application of a compound-specific stable isotope (CSSI) tracking technique demonstrates connectivity between terrestrial and deep-sea ecosystems via submarine canyons. *Frontiers in Marine Science*, 7, 608.
- Giering, S.L.C., Sanders, R., Lampitt, R.S., Anderson, T.R., Tamburini, C., Boutrif, M., Zubkov, M.V., Marsay, C.M., Henson, S.A., Saw, K., Cook, K., Mayor, D.J. (2014) Reconciliation of the carbon budget in the ocean's twilight zone. *Nature*, 507(7493), 480-483. <https://doi.org/10.1038/nature13123>
- Glasson, J. (2008) Principles and Purposes of Standards and Thresholds in the EIA Process. In (pp. 3-17). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-31141-6_1
- Glud, R. N. (2008). Oxygen dynamics of marine sediments. *Marine Biology Research*, 4(4), 243-289. <https://doi.org/10.1080/17451000801888726>
- Gooday, A.J. (1993) Deep-sea benthic foraminiferal species which exploit phytodetritus: Characteristic features and controls on distribution. *Marine Micropaleontology*, 22(3), 187-205. [https://doi.org/https://doi.org/10.1016/0377-8398\(93\)90043-W](https://doi.org/https://doi.org/10.1016/0377-8398(93)90043-W)
- Gooday, A.J. (2002) Biological responses to seasonally varying fluxes of organic matter to the ocean floor: A review [Review]. *Journal of Oceanography*, 58(2), 305-332. <Go to ISI>://000175729100008
- Gooday, A.J., Aranda da Silva, A., Pawlowski, J. (2011) Xenophyophores (Rhizaria, Foraminifera) from the Nazare Canyon (Portuguese margin, NE Atlantic). *Deep Sea Research Part II: Topical Studies in Oceanography*, 58(23-24), 2401-2419. <http://www.sciencedirect.com/science/article/pii/S096706451100107X>
- Gooday, A. J., Durden, J. M., Holzmman, M., Pawlowski, J., & Smith, C. R. (2020). Xenophyophores (Rhizaria, Foraminifera), including four new species and two new genera, from the western Clarion-Clipperton Zone (abyssal equatorial Pacific). *European Journal of Protistology*, 75, 125715. <https://doi.org/https://doi.org/10.1016/j.ejop.2020.125715>
- Gooday, A.J., Goineau, A., Voltski, I. (2017) Large agglutinated foraminifera in the Southwest Pacific: xenophyophores and deep-sea biodiversity. *Deep-Sea Research Part II*, 137, 6-13. <https://doi.org/10.1016/j.dsr2.2016.07.004>
- Gooday, A.J., Holzmman, M., Caille, C., Goineau, A., Jones, D.O., Kamenskaya, O., Simon-Lledó, E., Weber, A.A.-T., Pawlowski, J. (2017) New species of the xenophyophore genus Aschemonella (Rhizaria: Foraminifera) from areas of the abyssal eastern Pacific licensed for polymetallic nodule exploration. *Zoological Journal of the Linnean Society*, 182(3), 479-499.

- Gooday, A.J., Holzmann, M., Caille, C., Goineau, A., Kamenskaya, O., Weber, A.A.T., Pawlowskii, J. (2017) Giant protists (xenophyophores, Foraminifera) are exceptionally diverse in parts of the abyssal eastern Pacific licensed for polymetallic nodule exploration. *Biological Conservation*, 207, 106-116. <http://doi.org/10.1016/j.biocon.2017.01.006>.
- Gooday, A.J., Pfannkuche, O., Lambshead, P.J.D. (1996) An apparent lack of response by metazoan meiofauna to phytodetritus deposition in the bathyal north-eastern Atlantic [Article]. *Journal of the Marine Biological Association of the United Kingdom*, 76(2), 297-310. <Go to ISI>://A1996UQ46200003
- Gooday, A.J., Turley, C.M., Allen, J.A. (1990) Responses by benthic organisms to inputs of organic material to the ocean floor - a review. *Philosophical Transactions of the Royal Society of London Series a-Mathematical Physical and Engineering Sciences*, 331(1616), 119-138. <Go to ISI>://WOS:A1990DK63500009
- Graf, G. (1989) Benthic pelagic coupling in a deep-sea benthic community. *Nature*, 341(6241), 437-439. <Go to ISI>://WOS:A1989AT97600055
- Grant, N., Matveev, E., Kahn, A.S., Leys, S.P. (2018) Suspended sediment causes feeding current arrests in situ in the glass sponge *Aphrocallistes vastus*. *Marine Environmental Research*, 137, 111-120.
- Graves, K.P., Grano, E., Last, E.K. (2022a) Atlantic lower bathyal live *Solenosmilia variabilis* reef (biogenic structure). In H. Tyler-Walters (Ed.), *Marine Life Information Network: Biology and Sensitivity Key Information Reviews* online. <https://www.marlin.ac.uk/habitat/detail/1234>.
- Graves, K.P., Grano, E., Last, E.K. (2022b) Discrete *Solenosmilia variabilis* colonies on Atlantic lower bathyal rock and other hard substrata. In H. Tyler-Walters (Ed.), *Marine Life Information Network: Biology and Sensitivity Key Information Reviews* online. <https://www.marlin.ac.uk/habitat/detail/1235>
- Groffman, P.M., Baron, J.S., Blett, T., Gold, A.J., Goodman, I., Gunderson, L.H., Levinson, B.M., Palmer, M.A., Paerl, H.W., Peterson, G.D., Poff, N.L., Rejeski, D.W., Reynolds, J.F., Turner, M.G., Weathers, K.C., Wiens, J. (2006) Ecological Thresholds: The Key to Successful Environmental Management or an Important Concept with No Practical Application? *Ecosystems*, 9(1), 1-13. <https://doi.org/10.1007/s10021-003-0142-z>
- Gutiérrez-Rodríguez, A., Latasa, M., Safi, K., Pinkerton, M.H., Nodder, S.D. (2023) Decoupled growth and grazing rates of diatoms and green algae drive increased phytoplankton productivity on HNLC sub-Antarctic plateaux. *Limnology and Oceanography Letters*, 8(6), 896-905. <https://doi.org/https://doi.org/10.1002/lol2.10355>
- Hale, R., Leduc, D., Murray, C., Rowden, A.A. (2025) Effects of an experimental in situ seabed disturbance on deep-sea benthic ecosystem function and macro-infaunal community structure on the Chatham Rise, Southwest Pacific. *New Zealand Journal of Marine and Freshwater Research*. <https://doi.org/10.1080/00288330.2025.0000000>

- Harrold, C., Light, K., Lisin, S. (1998) Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. *Limnology and Oceanography*, 43(4), 669-678.
- Hayward, B.W., Grenfell, H.R., Sabaa, A.T., Neil, H.L. (2007) Factors influencing the distribution of Subantarctic deep-sea benthic foraminifera, Campbell and Bounty Plateaux, New Zealand. *Marine Micropaleontology*, 62(3), 141-166.
- Henry, L.-A., Roberts, J.M. (2007) Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers*, 54(4), 654-672.
- Henson, S., Laufkötter, C., Leung, S., Giering, S., Palevsky, H., Cavan, E. (2022) Uncertain response of ocean biological carbon export in a changing world, *Nat. Geosci.*, 15, 248–254. In.
- Hewitt, J.E., Lohrer, A.M. (2013) Impacts of sedimentation arising from mining on the Chatham Rise. *NIWA Client Report HAM2012-132* prepared for Chatham Rock Phosphate Ltd.
<https://www.epa.govt.nz/assets/FileAPI/proposal/EEZ000006/Applicants-proposal-documents/c82889b07f/EEZ000006-Appendix29-Hewitt-Lohrer-Sedimentation-Impacts.pdf>
- Hillebrand, H., Donohue, I., Harpole, W.S., Hodapp, D., Kucera, M., Lewandowska, A.M., Merder, J., Montoya, J.M., Freund, J.A. (2020) Thresholds for ecological responses to global change do not emerge from empirical data. *Nature Ecology & Evolution*, 4(11), 1502-1509. <https://doi.org/10.1038/s41559-020-1256-9>
- Hitchin, B., Smith, S., Kröger, K., Jones, D.O.B., Jaeckel, A., Mestre, N.C., Ardron, J., Escobar, E., van der Grient, J., Amaro, T. (2023) Thresholds in deep-seabed mining: A primer for their development. *Marine Policy*, 149, 105505.
<https://doi.org/https://doi.org/10.1016/j.marpol.2023.105505>
- Holland, L.P., Rowden, A.A., Hamilton, J.Z., Clark, M.R., Chiswell, S.M., Gardner, J.P.A. (2020) Genetic connectivity of deep-sea corals in the New Zealand region (New Zealand Aquatic Environment and Biodiversity Report No. 245).
<https://www.mpi.govt.nz/dmsdocument/41872-AEBR-245-Genetic-connectivity-of-deep-sea-corals-in-the-New-Zealand-region/>
- Honda, M.C., Watanabe, S. (2010) Importance of biogenic opal as ballast of particulate organic carbon (POC) transport and existence of mineral ballast-associated and residual POC in the Western Pacific Subarctic Gyre. *Geophysical research letters*, 37(2), L02605. <https://doi.org/10.1029/2009GL041521>
- Honjo, S., Manganini, S.J., Krishfield, R.A., Francois, R. (2008) Particulate organic carbon fluxes to the ocean interior and factors controlling the biological pump: A synthesis of global sediment trap programs since 1983. *Progress in Oceanography*, 76(3), 217-285. <https://doi.org/10.1016/j.pocean.2007.11.003>

- Hopwood, J.D., Mann, S., Gooday, A.J. (1997) The Crystallography and Possible Origin of Barium Sulphate in Deep Sea Rhizopod Protists (Xenophyophorea). *Journal of the Marine Biological Association of the United Kingdom*, 77(4), 969-987. <https://doi.org/10.1017/S002531540003856X>
- Ingels, J., Billett, D.S.M., Van Gaever, S., Vanreusel, A. (2011) An insight into the feeding ecology of deep-sea canyon nematodes - Results from field observations and the first in-situ C-13 feeding experiment in the Nazare Canyon. *Journal of Experimental Marine Biology and Ecology*, 396(2), 185-193. <https://doi.org/10.1016/j.jembe.2010.10.018>
- Ingels, J., Van den Driessche, P., De Mesel, I., Vanhove, S., Moens, T., Vanreusel, A. (2010) Preferred use of bacteria over phytoplankton by deep-sea nematodes in polar regions. *Marine Ecology Progress Series*, 406, 121-133. <https://doi.org/10.3354/meps08535>
- Ingels, J., Zeppilli, D., Giere, O. (2023) Meiofauna—Adapted to Life at the Limits. In *New Horizons in Meiobenthos Research: Profiles, Patterns and Potentials* (pp. 363-400). Springer International Publishing Cham.
- Jackson, A. (2000) *Novocrania anomala* A brachiopod. In H. Tyler-Walters & K. Hiscock (Eds.), *Marine Life Information Network: Biology and Sensitivity Key Information Reviews* online. <https://www.marlin.ac.uk/species/detail/1331>
- Jahnke, R.A. (1996) The global ocean flux of particulate organic carbon: Areal distribution and magnitude. *Global Biogeochemical Cycles*, 10(1), 71-88.
- Johnson, G.C. (2008) Quantifying Antarctic bottom water and North Atlantic deep water volumes. *Journal of Geophysical Research: Oceans*, 113(C5).
- Jónasdóttir, S.H., Visser, A.W., Richardson, K., Heath, M.R. (2015) Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Proceedings of the National Academy of Sciences*, 112(39), 12122-12126.
- Jones, D.O.B., Kaiser, S., Sweetman, A.K., Smith, C.R., Menot, L., Vink, A., Trueblood, D., Greinert, J., Billett, D.S.M., Arbizu, P.M., Radziejewska, T., Singh, R., Ingole, B., Stratmann, T., Simon-Lledó, E., Durden, J.M., Clark, M.R. (2017) Biological responses to disturbance from simulated deep-sea polymetallic nodule mining. *PLoS ONE*, 12(2), e0171750. <https://doi.org/10.1371/journal.pone.0171750>
- Jørgensen, B.B., Wenzhöfer, F., Egger, M., Glud, R.N. (2022) Sediment oxygen consumption: Role in the global marine carbon cycle. *Earth-Science Reviews*, 228, 103987. <https://doi.org/https://doi.org/10.1016/j.earscirev.2022.103987>
- Kahn, A.S., Leys, S.P. (2012) The potential role of nutrition on the resilience of deep-sea sponges. *Marine Biology*, 159, 1001-1016. <https://doi.org/10.1007/s00227-011-1863-8>

- Kahn, A.S., Ruhl, H.A., Smith, K.L. (2012) Temporal changes in deep-sea sponge populations are correlated to changes in surface climate and food supply. *Deep Sea Research Part I: Oceanographic Research Papers*, 70, 36-41.
<https://doi.org/https://doi.org/10.1016/j.dsr.2012.08.001>
- Kaikkonen, L., Clark, M.R., Leduc, D., Nodder, S.D., Rowden, A.A., Bowden, D.A., Beaumont, J., Cummings, V. (2025) Probabilistic ecological risk assessment for deep-sea mining: A Bayesian network for Chatham Rise, Pacific Ocean. *Ecological Applications*, 35(1), e3064.
- Kamenskaya, O.E., Gooday, A.J., Tendal, O.S., Melnik, V.F. (2015) Xenophyophores (Protista, Foraminifera) from the Clarion-Clipperton Fracture Zone with description of three new species. *Marine Biodiversity*. <http://link.springer.com/10.1007/s12526-015-0330-z>
- Kamenskaya, O.E., Melnik, V.F., Gooday, A.J. (2013) Giant protists (xenophyophores and komokiaceans) from the Clarion-Clipperton ferromanganese nodule field (Eastern Pacific). *ZHURNAL OBSHCHEI BIOLOGII*, 73(5), 377-388.
http://apps.webofknowledge.com.proxy-ub.rug.nl/full_record.do?product=UA&search_mode=GeneralSearch&qid=1&SID=T15EYVKBZuXlHfTAVsm&page=24&doc=233&cacheurlFromRightClick=no
- Kendrick, G.A., Renton, M., Wahab, M.A.A., Webster, N.S., Clode, P.L. (2017) Sediment tolerance mechanisms identified in sponges using advanced imaging techniques.
- Klaas, C., Archer, D.E. (2002) Association of sinking organic matter with various types of mineral ballast in the deep sea: Implications for the rain ratio. *Global Biogeochemical Cycles*, 16(4), 63-61-63-14.
<https://doi.org/10.1029/2001GB001765>
- Lampitt, R.S., Antia, A.N. (1997) Particle flux in deep seas: regional characteristics and temporal variability. *Deep-Sea Research Part I: Oceanographic Research Papers*, 44(8), 1377-1403. <Go to ISI>://WOS:A1997YD20700006
- Lampitt, R.S., Briggs, N., Cael, B.B., Espinola, B., Hélaouët, P., Henson, S.A., Norrbin, F., Pebody, C.A., Smeed, D. (2023) Deep ocean particle flux in the Northeast Atlantic over the past 30 years: carbon sequestration is controlled by ecosystem structure in the upper ocean. *Frontiers in Earth Science*, 11.
<https://doi.org/10.3389/feart.2023.1176196>
- Larsson, A.I., van Oevelen, D., Purser, A., Thomsen, L. (2013) Tolerance to long-term exposure of suspended benthic sediments and drill cuttings in the cold-water coral *Lophelia pertusa*. *Marine Pollution Bulletin*, 70(1), 176-188.
<https://doi.org/https://doi.org/10.1016/j.marpolbul.2013.02.033>
- Law, C.S., Rickard, G.J., Mikaloff-Fletcher, S.E., Pinkerton, M.H., Gorman, R., Behrens, E., Chiswell, S.M., Bostock, H.C., Anderson, O., Currie, K. (2016) The New Zealand EEZ and South West Pacific. Synthesis Report RA2, Marine Case Study. Climate Changes, Impacts and Implications (CCII) for New Zealand to 2100. MBIE contract CO1X1225.

- Lawrence, J., Blackett, P., Cradock-Henry, N., Flood, S., Greenaway, A., Dunningham, A. (2016) Climate Change Impacts and Implications for New Zealand to 2100. Synthesis report RA4: enhancing capacity and increasing coordination to support decision making, Wellington.
- Leduc, D., Clark, M.R., Rowden, A.A., Hyman, J., Dambacher, J.M., Dunstan, P.K., Connolly, R., Fulton, E.A., Hosack, G.R., O'Hara, T., Parr, J.M., Schlacher, T.A., Woolley, S.N.C. (2024) Moving towards an operational framework for defining serious harm for management of seabed mining. *Ocean & Coastal Management*, 255, 107252. <https://doi.org/https://doi.org/10.1016/j.ocecoaman.2024.107252>
- Leduc, D., Nodder, S. D., Pinkerton, M., & Pilditch, C. A. (2020) Benthic metabolism on Chatham Rise, New Zealand continental margin: Temporal and spatial variability, and relationships with macrofauna and environmental factors. *Deep Sea Research Part I: Oceanographic Research Papers*, 159, 103239. <https://doi.org/https://doi.org/10.1016/j.dsr.2020.103239>
- Leduc, D., Nodder, S.D., Rowden, A.A., Gibbs, M., Berkenbusch, K., Wood, A., De Leo, F., Smith, C., Brown, J., Bury, S. J., Pallentin, A. (2020) Structure of infaunal communities in New Zealand submarine canyons is linked to origins of sediment organic matter. *Limnology and Oceanography*, 65(10), 2303-2327. <https://doi.org/https://doi.org/10.1002/lno.11454>
- Leduc, D., Rowden, A.A., Bowden, D.A. (2012) Food supply as a driver of nematode and polychaete diversity in the deep Southwest Pacific. *Deep-Sea Research Part II*, 70, 70-80. <https://doi.org/10.1016/j.dsr2.2012.03.004>
- Leduc, D., Rowden, A.A., Clark, M.R., Bowden, D.A., Thurber, A.R. (2016) Limited differences among habitats in deep-sea macro-infaunal communities off New Zealand: implications for their vulnerability to anthropogenic disturbance. *Marine Ecology*, 37(4), 845-866. <https://doi.org/https://doi.org/10.1111/maec.12363>
- Leduc, D., Rowden, A.A., Nodder, S.D., Berkenbusch, K., Probert, P.K., Hadfield, M.G. (2014) Unusually high food availability in Kaikoura Canyon linked to distinct deep-sea nematode community. *Deep Sea Research Part II: Topical Studies in Oceanography*(0). <https://doi.org/http://dx.doi.org/10.1016/j.dsr2.2013.06.003>
- Lee, D.E., Robinson, J.H., Crame, J.A. (2022) Brachiopods of New Zealand: Diversity and Distribution. *New Zealand journal of geology and geophysics*, 65(1), 12-33. <https://doi.org/10.1080/00288306.2021.2017740>
- Levin, L.A. (1994) Paleoecology and Ecology of Xenophyophores. *PALAIOS*, 9(1), 32-41. <https://doi.org/10.2307/3515076>
- Levin, L.A. (2003) Oxygen minimum zone benthos: Adaptation and community response to hypoxia. *Oceanography and Marine Biology*, Vol 41, 41, 1-45. <Go to ISI>://WOS:000185182700001

- Levin, L.A., Alfaro-Lucas, J.M., Colaço, A., Cordes, E.E., Craik, N., Danovaro, R., Hoving, H.-J., Ingels, J., Mestre, N.C., Seabrook, S., Thurber, A.R., Vivian, C., Yasuhara, M. (2023) Deep-sea impacts of climate interventions. *Science*, 379(6636), 978-981. <https://doi.org/doi:10.1126/science.ade7521>
- Levin, L.A., Demaster, D.J., McCann, L.D., Thomas, C.L. (1986) Effects of giant protozoans (Class Xenophyophorea) on deep-seamount benthos. *MARINE ECOLOGY-PROGRESS SERIES*, 29(1), 99-104. <Go to ISI>://WOS:A1986A243600013
- Levin, L.A., Gooday, A.J. (1992) Possible roles for xenophyophores in deep-sea carbon cycling. In G. T. Rowe & V. Pariente (Eds.), *Deep-Sea Food Chains and the Global Carbon Cycle* (Vol. 360, pp. 93-104). <Go to ISI>://WOS:A1992BV47D00006
- Levin, L.A., Rouse, G.W. (2020) Giant protists (xenophyophores) function as fish nurseries. *Ecology*, 101(4), e02933. <https://doi.org/10.1002/ecy.2933>
- Levinton, J.S., Bambach, R.K. (1975) A comparative study of Silurian and recent deposit-feeding bivalve communities. *Paleobiology*, 1(1), 97-124. <https://doi.org/10.1017/S0094837300002232>
- Leys, S.P., Eerkes-Medrano, D.I. (2006) Feeding in a Calcareous Sponge: Particle Uptake by Pseudopodia. *The Biological Bulletin*, 211(2), 157-171. <https://doi.org/10.2307/4134590>
- Little, C., Trowbridge, C.D., Pilling, G.M., Cottrell, D.M., Plowman, C.Q., Stirling, P., Morritt, D., Williams, G.A. (2018) Long-term fluctuations in epibiotic bryozoan and hydroid abundances in an Irish sea lough. *Estuarine, Coastal and Shelf Science*, 210, 142-152. <https://doi.org/https://doi.org/10.1016/j.ecss.2018.06.007>
- Liu, Q., Rogers, A.D., Roch, C., Gordon, J.D.M., Duarte, C.M., Robinson, L.F., Waller, R. G., Ferrier-Pages, C., Brooke, S., Carreiro-Silva, M., Benson, K., De Carvalho Ferreira, M.L., Du Preez, C., Banks, S., Barry, J.P., Cordeiro, R.T.S, Cordes, E., Hennige, S., Hourigan, T.F., Kitahara, M.V., Kutti, T., Larsson, A.I., Lauretta, D.M., Matsumoto, A.K., Ross, R.E., Ramirez-Llodra, E., Yáñez Suárez, A.B., Edinger, E., Metaxas, A., Filander, Z.N.P., Taylor, M.L. (2024) CORDAP RandD roadmap for conservation and restoration of cold-water corals. https://cordap.org/wp-content/uploads/CORDAP-Cold-Water-Corals_Aug2024.pdf
- Logan, A. (2007) Geographic distribution of extant articulated brachiopods. *Deep-Sea Research II*, 54(16-17), 1691-1709.
- Lohrer, A.M., Hewitt, J.E., Thrush, S.F. (2006) Assessing far-field effects of terrigenous sediment loading in the coastal marine environment. *Marine Ecology Progress Series*, 315, 13-18.
- Lohrer, A.M., Thrush, S.F., Gibbs, M.M. (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature*, 431(7012), 1092-1095. <https://doi.org/10.1038/nature03042>

- Lohrer, A.M., Thrush, S.F., Hewitt, J.E., Berkenbusch, K., Ahrens, M., Cummings, V.J. (2004) Terrestrially derived sediment: response of marine macrobenthic communities to thin terrigenous deposits. *Marine Ecology Progress Series*, 273, 121-138.
- Lohrer, A.M., Thrush, S.F., Lundquist, C.J., Vopel, K., Hewitt, J.E., Nicholls, P.E. (2006) Deposition of terrigenous sediment on subtidal marine macrobenthos: response of two contrasting community types. *Marine Ecology Progress Series*, 307, 115-125.
- Luigi, V., Daniela, M., Mariapaola, M., Mauro, F. (2003) Sediment organic matter and meiofauna community response to long-term fish-farm impact in the Ligurian Sea (Western Mediterranean). *Chemistry and Ecology*.
<https://doi.org/10.1080/02757540310001609361>
- Lunden, J.J., McNicholl, C.G., Sears, C.R., Morrison, C.L., Cordes, E.E. (2014) Acute survivorship of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico under acidification, warming, and deoxygenation [Original Research]. *Frontiers in Marine Science*, Volume 1 - 2014. <https://doi.org/10.3389/fmars.2014.00078>
- Lutz, M.J., Caldeira, K., Dunbar, R.B., Behrenfeld, M.J. (2007) Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. *J. Geophys. Res.*, 112(C10), C10011. <https://doi.org/10.1029/2006jc003706>
- MacDiarmid, A. (2007) Treasures of the Sea: A Summary of Biodiversity in the New Zealand Marine Ecoregion. WWF-New Zealand.
- MacDiarmid, A., Bowden, D., Cummings, V., Morrison, M., Jones, E., Kelly, M., Neil, H., Nelson, W.S., Rowden, A. (2013) Sensitive marine benthic habitats defined (Prepared for the Ministry for the Environment).
<https://www.qualityplanning.org.nz/sites/default/files/Sensitive%20marine%20benthic%20habitats%20defined.pdf#:~:text=obtaining%20specimens%20from%20rock%20faces,The%20Chatham%20Rise%20represents%20a>
- MacFarlan, D., Bradshaw, M., Campbell, H., Cooper, R., Lee, D., MacKinnon, D., Waterhouse, J., Wright, A.J., Robinson, J. (2009) Phylum Brachiopoda: lamp shells.
- Maier, S.R., Brooke, S., De Clippele, L.H., de Froe, E., van der Kaaden, A.S., Kutti, T., Mienis, F., van Oevelen, D. (2023) On the paradox of thriving cold-water coral reefs in the food-limited deep sea. *Biol Rev Camb Philos Soc*, 98(5), 1768-1795.
<https://doi.org/10.1111/brv.12976>
- Maier, S.R., Kutti, T., Bannister, R.J., Fang, J.K.-H., van Breugel, P., van Rijswijk, P., van Oevelen, D. (2020) Recycling pathways in cold-water coral reefs: Use of dissolved organic matter and bacteria by key suspension feeding taxa. *Scientific reports*, 10(1), 9942. <https://doi.org/10.1038/s41598-020-66463-2>
- Maldonado, M., Aguilar, R., Bannister, R.J., Bell, J.J., Conway, K.W., Dayton, P.K., Díaz, C., Gutt, J., Kelly, M., Kenchington, E.L. (2015) Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles, and conservation concerns. *Marine animal forests*, 1-39.

- Maldonado, M., Giraud, K., Carmona, C. (2008) Effects of sediment on the survival of asexually produced sponge recruits. *Marine Biology*, 154(4), 631-641.
- Maldonado, M., López-Acosta, M., Sitjà, C., García-Puig, M., Galobart, C., Ercilla, G., Leynaert, A. (2019) Sponge skeletons as an important sink of silicon in the global oceans. *Nature geoscience*, 12(10), 815-822. <https://doi.org/10.1038/s41561-019-0430-7>
- Marc, T., Matthias, B., Walter, T. (2007) Factors influencing the vertical distribution of nematodes in Sediments. *Journal of Freshwater Ecology*.
<https://doi.org/10.1080/02705060.2007.9664173>
- Martin, A.P., Lucas, M.I., Painter, S.C., Pidcock, R., Prandke, H., Prandke, H., Stinchcombe, M.C. (2010) The supply of nutrients due to vertical turbulent mixing: A study at the Porcupine Abyssal Plain study site in the northeast Atlantic. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 57(15), 1293-1302.
<http://www.sciencedirect.com/science/article/B6VGC-4YC1K1C-1/2/4a59638bb395397d49bbb15bb28d2d90>
- Martin, J.H., Knauer, G.A., Karl, D.M., Broenkow, W.W. (1987) VERTEX: carbon cycling in the northeast Pacific. *Deep Sea Research Part A. Oceanographic Research Papers*, 34(2), 267-285. [https://doi.org/https://doi.org/10.1016/0198-0149\(87\)90086-0](https://doi.org/https://doi.org/10.1016/0198-0149(87)90086-0)
- McCave, I., Carter, L., Hall, I.R. (2008) Glacial–interglacial changes in water mass structure and flow in the SW Pacific Ocean. *Quaternary Science Reviews*, 27(19-20), 1886-1908.
- McDonnell, A.M.P., Buesseler, K.O. (2010) Variability in the average sinking velocity of marine particles. *Limnology and Oceanography*, 55(5), 2085-2096.
<https://doi.org/https://doi.org/10.4319/lo.2010.55.5.2085>
- Meysman, F.J.R., Middelburg, J.J., Heip, C.H.R. (2006) Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology & Evolution*, 21(12), 688-695.
- Micaroni, V., Strano, F., McAllen, R., Woods, L., Turner, J., Harman, L., Bell, J.J. (2022) Adaptive strategies of sponges to deoxygenated oceans. *Glob Chang Biol*, 28(6), 1972-1989. <https://doi.org/10.1111/gcb.16013>
- Middelburg, J.J. (2019) Carbon Processing at the Seafloor. In J. J. Middelburg (Ed.), *Marine Carbon Biogeochemistry : A Primer for Earth System Scientists* (pp. 57-75). Springer International Publishing. https://doi.org/10.1007/978-3-030-10822-9_4
- Middelburg, J.J., Barranguet, C., Boschker, H.T.S., Herman, P.M.J., Moens, T., Heip, C.H.R. (2000) The fate of intertidal microphytobenthos carbon: An in situ C-13-labeling study [Article]. *Limnology and Oceanography*, 45(6), 1224-1234. <Go to ISI>://000089396500002
- Miklasz, K.A., Denny, M.W. (2010) Diatom sinkings speeds: Improved predictions and insight from a modified Stokes' law. *Limnology and Oceanography*, 55(6), 2513-2525.

- Mobilia, V., Cummings, V.J., Clark, M.R., Tracey, D., Bell, J.J. (2021) Short-term physiological responses of the New Zealand deep-sea sponge *Ecionemia novaezealandiae* to elevated concentrations of suspended sediments. *Journal of Experimental Marine Biology and Ecology*, 541, 151579.
<https://doi.org/https://doi.org/10.1016/j.jembe.2021.151579>
- Mobilia, V., Tracey, D.M., Cummings, V., Clark, M.R., Woods, L., Bell, J. (2023) Effects of sediment pulses on the deep-sea coral *Goniocorella dumosa*. *New Zealand Journal of Marine and Freshwater Research*, 1-17.
<https://doi.org/10.1080/00288330.2023.2230154>
- Moodley, L., Middelburg, J.J., Boschker, H.T.S., Duineveld, G.C.A., Pel, R., Herman, P. M. J., Heip, C.H.R. (2002) Bacteria and Foraminifera: key players in a short-term deep-sea benthic response to phytodetritus. *MARINE ECOLOGY-PROGRESS SERIES*, 236, 23-29. <Go to ISI>://WOS:000177007100003
- Moodley, L., Middelburg, J.J., Soetaert, K., Boschker, H.T.S., Herman, P.M.J., Heip, C.H.R. (2005) Similar rapid response to phytodetritus deposition in shallow and deep-sea sediments. *Journal of Marine Research*, 63(2), 457-469. <Go to ISI>://WOS:000228959100006
- Mora, C., Wei, C.L., Rollo, A., Amaro, T., Baco, A.R., Billett, D., Bopp, L., Chen, Q., Collier, M., Danovaro, R., Gooday, A.J., Grupe, B.M., Halloran, P.R., Ingels, J., Jones, D.O., Levin, L.A., Nakano, H., Norling, K., Ramirez-Llodra, E., Rex, M., Ruhl, H.A., Smith, C.R., Sweetman, A.K., Thurber, A.R., Tjiputra, J.F., Usseglio, P., Watling, L., Wu, T., Yasuhara, M. (2013) Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st century. *PLoS Biol*, 11(10), e1001682.
<https://doi.org/10.1371/journal.pbio.1001682>
- Morrison, K.M., Meyer, H.K., Roberts, E.M., Rapp, H.T., Colaço, A., Pham, C.K. (2020) The First Cut Is the Deepest: Trawl Effects on a Deep-Sea Sponge Ground Are Pronounced Four Years on [Original Research]. *Frontiers in Marine Science*, Volume 7 - 2020. <https://doi.org/10.3389/fmars.2020.605281>
- Mountjoy, J., Howarth, J.D., Orpin, A.R., Barnes, P.M., Bowden, D.A., Rowden, A.A., Schimel, A.C.G., Holden, C., Horgan, H.J., Nodder, S.D., Patton, J.R., Lamarche, G., Gerstenberger, M., Micallef, A., Pallentin, A., Kane, T. (2018) Earthquakes drive large-scale submarine canyon development and sediment supply to deep-ocean basins. *Science Advances*, 4(3), eaar3748.
<https://doi.org/doi:10.1126/sciadv.aar3748>
- Murphy, R., Pinkerton, M., Richardson, K., Bradford-Grieve, J., Boyd, P. (2001) Phytoplankton distributions around New Zealand derived from SeaWiFS remotely-sensed ocean colour data. *New Zealand Journal of Marine and Freshwater Research*, 35(2), 343-362.
- Neira, C., Ingels, J., Mendoza, G., Hernandez-Lopez, E., Levin, L.A. (2018) Distribution of Meiofauna in Bathyal Sediments Influenced by the Oxygen Minimum Zone Off Costa Rica [Original Research]. *Frontiers in Marine Science*, 5(448).
<https://doi.org/10.3389/fmars.2018.00448>

- Nielsen, S.H.H., McKenzie, C., Miller, A., Partington, G., Payne, C., Puccioni, E., Stokes, M., Wildman, C., Falconer, R.K.H., Wood, R. (2015) Chatham Rise nodular phosphate — Modelling the prospectivity of a lag deposit (off-shore New Zealand): A critical tool for use in resource development and deep sea mining. *Ore Geology Reviews*, 71, 545-557.
<https://doi.org/https://doi.org/10.1016/j.oregeorev.2014.10.013>
- Nodder, S., Alexander, B. (1998) Sources of variability in geographical and seasonal differences in particulate fluxes from short-term sediment trap deployments, east of New Zealand. *Deep Sea Research Part I: Oceanographic Research Papers*, 45(10), 1739-1764.
- Nodder, S., Gall, M. (1998) Pigment fluxes from the Subtropical Convergence region, east of New Zealand: relationships to planktonic community structure. *New Zealand Journal of Marine and Freshwater Research*, 32(3), 441-465.
- Nodder, S. D., Eager, C.A., O'Callaghan, J., Leduc, D., Davidson, S., Deppeler, S., Frontin-Rollett, G., Gerring, P., Searson, S., Quinn, W., George, S., Ovenden, R., Bury, S.J., Brown, J., Clark, M.R. (2025) Near-seabed sediment dynamics and fluxes on Chatham Rise, the effects of seabed disturbance, and implications for deep-sea bottom trawling and seabed mining. *New Zealand Journal of Marine and Freshwater Research*, 1-36. <https://doi.org/10.1080/00288330.2025.2461290>
- Nodder, S.D., Alexander, B.L. (1999) The effects of multiple trap spacing, baffles and brine volume on sediment trap collection efficiency.
- Nodder, S.D., Chiswell, S.M., Northcote, L.C. (2016) Annual cycles of deep-ocean biogeochemical export fluxes in subtropical and subantarctic waters, southwest Pacific Ocean. *Journal of Geophysical Research: Oceans*, 121(4), 2405-2424.
<https://doi.org/https://doi.org/10.1002/2015JC011243>
- Nodder, S.D., Duineveld, G.C.A., Pilditch, C.A., Sutton, P.J., Probert, P.K., Lavaleye, M. S.S., Witbaard, R., Chang, F.H., Hall, J.A., Richardson, K.M. (2007) Focusing of phytodetritus deposition beneath a deep-ocean front, Chatham Rise, New Zealand. *Limnology and Oceanography*, 52(1), 299-314.
<https://doi.org/10.4319/lo.2007.52.1.0299>
- Nodder, S.D., Northcote, L.C. (2001) Episodic particulate fluxes at southern temperate mid-latitudes (42–45°S) in the Subtropical Front region, east of New Zealand. *Deep Sea Research Part I: Oceanographic Research Papers*, 48(3), 833-864.
[https://doi.org/https://doi.org/10.1016/S0967-0637\(00\)00062-5](https://doi.org/https://doi.org/10.1016/S0967-0637(00)00062-5)
- NZODN. (2022) New Zealand Ocean Data Network. <https://nzodn.nz>
- Oschlies, A., Brandt, P., Stramma, L., Schmidtko, S. (2018) Drivers and mechanisms of ocean deoxygenation. *Nature geoscience*, 11(7), 467-473.
- Passow, U., De La Rocha, C.L. (2006) Accumulation of mineral ballast on organic aggregates. *Global Biogeochemical Cycles*, 20(1).

- Peck, L.S., Barnes, D.K.A. (2004) Metabolic flexibility: the key to long-term evolutionary success in Bryozoa? *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, S18-S21. <https://doi.org/10.1098/rsbl.2003.0053>
- Pham, C.K., Murillo, F.J., Lirette, C., Maldonado, M., Colaço, A., Ottaviani, D., Kenchington, E. (2019) Removal of deep-sea sponges by bottom trawling in the Flemish Cap area: conservation, ecology and economic assessment. *Scientific reports*, 9(1), 15843. <https://doi.org/10.1038/s41598-019-52250-1>
- Pierrejean, M., Grant, C., Neves, B., Chaillou, G., Edinger, E., Blanchet, F.G., Maps, F., Nozais, C., Archambault, P. (2020) Influence of Deep-Water Corals and Sponge Gardens on Infaunal Community Composition and Ecosystem Functioning in the Eastern Canadian Arctic [Original Research]. *Frontiers in Marine Science*, Volume 7 - 2020. <https://doi.org/10.3389/fmars.2020.00495>
- Pilditch, C., Leduc, D., Nodder, S., Probert, P., Bowden, D. (2015) Spatial patterns and environmental drivers of benthic infaunal community structure and ecosystem function on the New Zealand continental margin. *New Zealand Journal of Marine and Freshwater Research*, 49(2), 224-246.
- Pineda, M.-C., Strehlow, B., Sternel, M., Duckworth, A., Haan, J.d., Jones, R., Webster, N.S. (2017) Effects of sediment smothering on the sponge holobiont with implications for dredging management. *Scientific reports*, 7(1), 5156.
- Pineda, M.C., Duckworth, A., Webster, N. (2016) Appearance matters: sedimentation effects on different sponge morphologies. *Journal of the Marine Biological Association of the United Kingdom*, 96(2), 481-492.
- Pinkerton, M., Gall, M., Thorat, F., Sutton, P., Wood, S. (2024) Monitoring ocean health: 2023 update on satellite indicators for surface temperature, productivity and suspended solids. Prepared for Ministry for the Environment (July 2024). *NIWA Client Report 2023217WN_rev2* (NIWA Project: MFE22302).
- Pinkerton, M., Rickard, G., Nodder, S., Macdonald, H. (2016) Climate change impacts and implications: net primary production, particulate flux and impacts on fish species in the New Zealand region. NIWA report.
- Probert, P.K., Glasby, C.J., Grove, S.L., Paavo, B.L. (2009) Bathyal polychaete assemblages in the region of the Subtropical Front, Chatham Rise, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 43(5), 1121-1135. <https://doi.org/10.1080/00288330.2009.9626535>
- Probert, P.K., Grove, S.L., McKnight, D.G., Read, G.B. (1996) Polychaete Distribution on the Chatham Rise, Southwest Pacific. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 81(4), 577-588. <https://doi.org/https://doi.org/10.1002/iroh.19960810411>
- Probert, P.K., Read, G.B., Grove, S.L., Rowden, A.A. (2001) Macrobenthic polychaete assemblages of the continental shelf and upper slope off the west coast of the South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 35(5), 971-984. <https://doi.org/10.1080/00288330.2001.9517057>

- Puro.Earth. (2025) Microalgae Carbon Fixation and Sinking Methodology for CO₂ Removal [Draft for public consultation](Puro Standard, Issue.
- Putnam, H.M., Barott, K.L., Ainsworth, T.D., Gates, R.D. (2017) The Vulnerability and Resilience of Reef-Building Corals. *Current Biology*, 27(11), R528-R540. <https://doi.org/https://doi.org/10.1016/j.cub.2017.04.047>
- Readman, J.A.J., Lloyd, K.A., Watson, A. (2023) *Flustra foliacea* on slightly scoured silty circalittoral rock. In H. Tyler-Walters (Ed.), *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. [cited 01-08-2025]. Available from: <https://www.marlin.ac.uk/habitat/detail/24>.
- Roberts, J.M., Wheeler, A.J., Freiwald, A. (2006) Reefs of the Deep: The Biology and Geology of Cold-Water Coral Ecosystems. *Science*, 312(5773), 543-547. <https://doi.org/10.1126/science.1119861>
- Rogers, A.D., Clark, M.R., Hall-Spencer, J.M., Gjerde, K. (2008) The science behind the guidelines: A scientific guide to the FAO Draft International Guidelines (December 2007) for the management of Deep-Sea Fisheries in the high Seas and examples of how the guidelines may be practically implemented. <https://portals.iucn.org/library/sites/library/files/documents/2008-115-En.pdf>
- Rooks, C., Fang, J.K.-H., Mørkved, P.T., Zhao, R., Rapp, H.T., Xavier, J.R., Hoffmann, F. (2020) Deep-sea sponge grounds as nutrient sinks: denitrification is common in boreo-Arctic sponges. *Biogeosciences*, 17(5), 1231-1245. <https://doi.org/10.5194/bg-17-1231-2020>
- Rothe, N., Gooday, A.J., Pearce, R.B. (2011) Intracellular mineral grains in the xenophyophore *Nazareammina tenera* (Rhizaria, Foraminifera) from the Nazaré Canyon (Portuguese margin, NE Atlantic). *Deep Sea Research Part I: Oceanographic Research Papers*, 58(12), 1189-1195. <http://www.sciencedirect.com/science/article/pii/S0967063711001695>
- Rowden, A., Leduc, D., Torres, L., Bowden, D., Hart, A., Chin, C., Davey, N., Nodder, S., Pallentin, A., Mackay, K., Northcote, L., Sturman, J. (2014) Benthic epifauna communities of the central Chatham Rise crest. *NIWA Client Report WLG2014-9* prepared for Chatham Rock Phosphate Ltd.
- Rowden, A., Leduc, D., Torres, L., Bowden, D., Hart, A., Chin, C., Davey, N., Wright, J., Carter, M., Crocker, B., Halliday, J., Loerz, A.-N., Read, G., Mills, S., Anderson, O., Neill, K., Kelly, M., Tracey, D., Kaiser, S., Gordon, D., Wilkins, S., Horn, P., Pallentin, A., Nodder, S., Mackay, K., Northcote, L. (2013) Benthic communities of MPL area 50270 on the Chatham Rise. *NIWA Client Report WLG2012-25* prepared for Chatham Rock Phosphate Ltd.
- Ruhl, H.A. (2008) Community change in the variable resource habitat of the abyssal northeast Pacific. *Ecology*, 89(4), 991-1000. <https://doi.org/doi:10.1890/06-2025.1>

- Ruhl, H.A., Smith, K.L. (2004) Shifts in Deep-Sea Community Structure Linked to Climate and Food Supply. *Science*, 305(5683), 513-515.
<https://doi.org/10.1126/science.1099759>
- Ruppert, E.E., Barnes, R.D., Fox, R.S. (1994) Invertebrate zoology (Vol. 1). Saunders College Publishing Fort Worth.
- Russell, J.L., Dickson, A.G. (2003) Variability in oxygen and nutrients in South Pacific Antarctic Intermediate Water. *Global Biogeochemical Cycles*, 17(2).
<https://doi.org/10.1029/2000GB001317>
- Russon, T., Elliot, M., Kissel, C., Cabioch, G., De Deckker, P., Corrège, T. (2009) Middle-late Pleistocene deep water circulation in the southwest subtropical Pacific. *Paleoceanography*, 24(4). <https://doi.org/10.1029/2009PA001755>
- Sapir, A. (2021) Why are nematodes so successful extremophiles? *Communicative & Integrative Biology*, 14(1), 24-26. <https://doi.org/10.1080/19420889.2021.1884343>
- Schönberg, C.H.L. (2016) Happy relationships between marine sponges and sediments—a review and some observations from Australia. *Journal of the Marine Biological Association of the United Kingdom*, 96(2), 493-514.
- Schratzberger, M., Ingels, J. (2018) Meiofauna matters: The roles of meiofauna in benthic ecosystems. *Journal of Experimental Marine Biology and Ecology*, 502, 12-25. <https://doi.org/10.1016/j.jembe.2017.01.007>
- Shumway, S.E. (1982) Oxygen consumption in brachiopods and the possible role of punctae. *Journal of Experimental Marine Biology and Ecology*, 58(2), 207-220.
[https://doi.org/10.1016/0022-0981\(82\)90130-7](https://doi.org/10.1016/0022-0981(82)90130-7)
- Siegel, D.A., DeVries, T., Cetinić, I., Bisson, K.M. (2023) Quantifying the Ocean's Biological Pump and Its Carbon Cycle Impacts on Global Scales. *Annual Review of Marine Science*, 15(Volume 15, 2023), 329-356.
<https://doi.org/10.1146/annurev-marine-040722-115226>
- Simon-Lledó, E., Bett, B.J., Huvenne, V.A., Schoening, T., Benoist, N.M., Jeffreys, R.M., Durden, J.M., Jones, D.O. (2019) Megafaunal variation in the abyssal landscape of the Clarion Clipperton Zone. *Progress in Oceanography*, 170, 119-133.
- Sloyan, B.M., Rintoul, S.R. (2001) Circulation, renewal, and modification of Antarctic mode and intermediate water. *Journal of physical oceanography*, 31(4), 1005-1030.
- Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Arbizu, P.M. (2008). Abyssal food limitation, ecosystem structure and climate change. *Trends in Ecology & Evolution*, 23(9), 518-528. <http://www.sciencedirect.com/science/article/B6VJ1-4SVBWRW-2/2/96c5e9193cfb6e8f90337341b4d4adec>
- Smith, C.R., Tunnicliffe, V., Colaço, A., Drazen, J.C., Gollner, S., Levin, L.A., Mestre, N.C., Metaxas, A., Molodtsova, T.N., Morato, T. (2020) Deep-Sea Misconceptions Cause Underestimation of Seabed-Mining Impacts. *Trends in Ecology & Evolution*.

- Smith, K., Ruhl, H., Bett, B., Billett, D., Lampitt, R., Kaufmann, R. (2009) Climate, carbon cycling, and deep-ocean ecosystems. *Proceedings of the National Academy of Sciences*, 106(46), 19211-19218.
<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2780780/pdf/zpq19211.pdf>
- Smith, K.L., Ruhl, H.A., Huffard, C.L., Messié, M., Kahru, M. (2018) Episodic organic carbon fluxes from surface ocean to abyssal depths during long-term monitoring in NE Pacific. *Proceedings of the National Academy of Sciences*, 115(48), 12235-12240. <https://doi.org/doi:10.1073/pnas.1814559115>
- Smith, K.L., Ruhl, H.A., Kahru, M., Huffard, C.L., Sherman, A.D. (2013) Deep ocean communities impacted by changing climate over 24 y in the abyssal northeast Pacific Ocean. *Proceedings of the National Academy of Sciences*.
<https://doi.org/10.1073/pnas.1315447110>
- Snelgrove, P.V., Thrush, S.F., Wall, D.H., Norkko, A. (2014) Real world biodiversity–ecosystem functioning: a seafloor perspective. *Trends in Ecology & Evolution*, 29(7), 398-405.
- Snelgrove, P.V.R., Soetaert, K., Solan, M., Thrush, S., Wei, C.L., Danovaro, R., Fulweiler, R.W., Kitazato, H., Ingole, B., Norkko, A., Parkes, R.J., Volkenborn, N. (2018) Global Carbon Cycling on a Heterogeneous Seafloor. *Trends Ecol Evol*, 33(2), 96-105. <https://doi.org/10.1016/j.tree.2017.11.004>
- Soviadan, Y.D., Beck, M., Habib, J., Baudena, A., Drago, L., Accardo, A., Laxenaire, R., Speich, S., Brandt, P., Kiko, R., Stemmann, L. (2024) Marine snow morphology drives sinking and attenuation in the ocean interior. *EGUsphere*.
<https://doi.org/10.5194/egusphere-2024-3302>
- Steinberg, D.K., Landry, M.R. (2017) Zooplankton and the ocean carbon cycle. *Annual Review of Marine Science*, 9(1), 413-444.
- Steinberg, D.K., Van Mooy, B.A., Buesseler, K.O., Boyd, P.W., Kobari, T., Karl, D.M. (2008) Bacterial vs. zooplankton control of sinking particle flux in the ocean's twilight zone. *Limnology and Oceanography*, 53(4), 1327-1338.
- Steyaert, M., Leon, M., Jan, V., Vandewiele, S., Magda, V. (2005) Laboratory experiments on the infaunal activity of intertidal nematodes. *Hydrobiologia*, <https://doi.org/10.1007/S10750-004-7145-4>
- Stramma, L., Brandt, P., Schafstall, J., Schott, F., Fischer, J., & Körtzinger, A. (2008). Oxygen minimum zone in the North Atlantic south and east of the Cape Verde Islands. *Journal of Geophysical Research: Oceans*, 113(C4).
- Stramma, L., Johnson, G. C., Sprintall, J., & Mohrholz, V. (2008). Expanding oxygen-minimum zones in the tropical oceans. *Science*, 320(5876), 655-658.
- Stramma, L., Schmidtko, S., Levin, L.A., Johnson, G.C. (2010) Ocean oxygen minima expansions and their biological impacts. *Deep Sea Research Part I: Oceanographic Research Papers*, 57(4), 587-595.

- Stratmann, T., Busch, K., de Kluijver, A., Kelly, M., Mills, S., Rossel, S., Schupp, P.J. (2024) Nutrient fluxes, oxygen consumption and fatty acid composition from deep-water demo- and hexactinellid sponges from New Zealand. *Deep Sea Research Part I: Oceanographic Research Papers*, 214, 104416. <https://doi.org/https://doi.org/10.1016/j.dsr.2024.104416>
- Stratmann, T., Mevenkamp, L., Sweetman, A.K., Vanreusel, A., van Oevelen, D. (2018) Has Phytodetritus Processing by an Abyssal Soft-Sediment Community Recovered 26 Years after an Experimental Disturbance? [Original Research]. *Frontiers in Marine Science*, Volume 5 - 2018. <https://doi.org/10.3389/fmars.2018.00059>
- Stratmann, T., Soetaert, K., Wei, C.-L., Lin, Y.-S., van Oevelen, D. (2019) The SCOC database, a large, open, and global database with sediment community oxygen consumption rates. *Scientific Data*, 6(1), 242. <https://doi.org/10.1038/s41597-019-0259-3>
- Strehlow, B.W., Pineda, M.-C., Duckworth, A., Kendrick, G.A., Renton, M., Wahab, M.A. A., Webster, N.S., Clode, P.L. (2017) Sediment tolerance mechanisms identified in sponges using advanced imaging techniques. *PeerJ*, 5, e3904.
- Stukel, M.R., Aluwihare, L.I., Barbeau, K.A., Chekalyuk, A.M., Goericke, R., Miller, A.J., Ohman, M.D., Ruacho, A., Song, H., Stephens, B.M. (2017) Mesoscale ocean fronts enhance carbon export due to gravitational sinking and subduction. *Proceedings of the National Academy of Sciences*, 114(6), 1252-1257.
- Sturdivant, S.K., Guarinello, M.L., Germano, J.D., Carey, D.A. (2024) Reshaping perspectives of deep-sea benthic function [Hypothesis and Theory]. *Frontiers in Marine Science*, Volume 11 - 2024. <https://www.frontiersin.org/journals/marine-science/articles/10.3389/fmars.2024.1383754>
- Takahashi, K., Allan, W. (1984) Planktonic foraminifera: factors controlling sinking speeds. *Deep Sea Research Part A. Oceanographic Research Papers*, 31(12), 1477-1500.
- Tendal, O. (1975) The xenophyophores of New Zealand (Rhizopodea, Protozoa). *Tuatara*, 21, 92-97.
- Tendal, O., Lewis, K. (1978) New Zealand xenophyophores: upper bathyal distribution, photographs of growth position, and a new species. *New Zealand Journal of Marine and Freshwater Research*, 12(2), 197-203.
- Tendal, O., Swinbanks, D., Shirayama, Y. (1982) A new infaunal xenophyophore (Xenophyophorea, Protozoa) with notes on its ecology and possible trace fossil analogs. *Oceanologica Acta*, 5(3), 325-329.
- Thiagarajan, N., Gerlach, D., Roberts, M.L., Burke, A., McNichol, A., Jenkins, W.J., Subhas, A.V., Thresher, R.E., Adkins, J. F. (2013) Movement of deep-sea coral populations on climatic timescales. *Paleoceanography*, 28(2), 227-236. <https://doi.org/https://doi.org/10.1002/palo.20023>

- Thresher, R., Althaus, F., Adkins, J., Gowlett-Holmes, K., Alderslade, P., Dowdney, J., Cho, W., Gagnon, A., Staples, D., McEnnulty, F., Williams, A. (2014) Strong Depth-Related Zonation of Megabenthos on a Rocky Continental Margin (~700–4000 m) off Southern Tasmania, Australia. *PLoS ONE*, 9(1), e85872.
<https://doi.org/10.1371/journal.pone.0085872>
- Thresher, R.E., Fallon, S.J. (2024) Shifting Depth Distributions of Deep-Sea Corals in the Southwest Pacific: Implications for Deglacial Dynamics of the Southern Ocean. *Paleoceanography and Paleoclimatology*, 39(4), e2023PA004824.
<https://doi.org/10.1029/2023PA004824>
- Tillin, H.M., Ashley, M. (2020) Polychaetes, including *Paraonis fulgens*, in littoral fine sand. In H. Tyler-Walters & K. Hiscock (Eds.), *Marine Life Information Network: Biology and Sensitivity Key Information Reviews* online.
<https://doi.org/https://dx.doi.org/10.17031/marlinhab.1201.1>
- Toma, M., Enrichetti, F., Bavestrello, G., Canese, S., Cau, A., Andaloro, F., Angiolillo, M., Greco, S., Bo, M. (2022) Brachiopod Fauna from the Deep Mediterranean Sea: Distribution Patterns and Ecological Preferences. *Diversity*, 14(9), 753.
<https://www.mdpi.com/1424-2818/14/9/753>
- Tompkins-MacDonald, G.J., Leys, S.P. (2008) Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. *Marine Biology*, 154(6), 973–984.
- Tracey, D.M., Hjørvarðsdóttir, F. (2019) The state of knowledge of deep-sea corals in the New Zealand region (NIWA Science & Technology Series, Issue).
https://niwa.co.nz/sites/default/files/2019_deepsea_corals_report.pdf
- Tsuchiya, M., Nomaki, H. (2021) Rapid response of the giant protist xenophyophores (Foraminifera, Rhizaria) to organic matter supply at abyssal depths revealed by an in situ dual stable isotope labeling experiment. *Deep Sea Research Part I: Oceanographic Research Papers*, 176, 103608.
<https://doi.org/https://doi.org/10.1016/j.dsr.2021.103608>
- Turner, J.T. (2015a) Zooplankton fecal pellets, marine snow and sinking phytoplankton blooms. In R. S. Lampitt & S. W. Fowler (Eds.), *Marine Snow: Biological and Physical Perspectives* (pp. 1–48). Springer.
- Turner, J.T. (2015b). Zooplankton fecal pellets, marine snow, phytodetritus and the ocean’s biological pump. *Progress in Oceanography*, 130, 205–248.
<https://doi.org/10.1016/j.pocean.2014.08.005>
- van Oevelen, D., Soetaert, K., Garcia, R., de Stigter, H.C., Cunha, M.R., Pusceddu, A., Danovaro, R. (2011) Canyon conditions impact carbon flows in food webs of three sections of the Nazaré canyon. *Deep Sea Research Part II: Topical Studies in Oceanography*, 58(23–24), 2461–2476.
<http://www.sciencedirect.com/science/article/pii/S0967064511001111>

- Veit-Köhler, G., Guilini, K., Peeken, I., Sachs, O., Sauter, E.J., Würzberg, L. (2011) Antarctic deep-sea meiofauna and bacteria react to the deposition of particulate organic matter after a phytoplankton bloom. *Deep Sea Research Part II: Topical Studies in Oceanography*, 58(19-20), 1983-1995.
<http://www.sciencedirect.com/science/article/pii/S0967064511001342>
- Vetter, E.W., Dayton, P.K. (1999) Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons [Article]. *MARINE ECOLOGY-PROGRESS SERIES*, 186, 137-148. <Go to ISI>://000083230100014
- Wahab, M.A.A., Maldonado, M., Luter, H.M., Jones, R., Ricardo, G. (2019) Effects of sediment resuspension on the larval stage of the model sponge *Carteriospongia foliascens*. *Science of The Total Environment*, 695, 133837.
- Waite, A., Gallagher, S., Dam, H.G. (1997) New measurements of phytoplankton aggregation in a flocculator using videography and image analysis. *Marine Ecology Progress Series*, 155, 77-88.
- Waite, A.M., Safi, K.A., Hall, J.A., Nodder, S.D. (2000) Mass sedimentation of picoplankton embedded in organic aggregates. *Limnology and Oceanography*, 45(1), 87-97.
- Walker, M., Hammel, J.U., Wilde, F., Hoehfurtner, T., Humphries, S., Schuech, R. (2021) Estimation of sinking velocity using free-falling dynamically scaled models: Foraminifera as a test case. *Journal of Experimental biology*, 224(2), jeb230961.
- Wijffels, S.E., Toole, J.M., Davis, R. (2001) Revisiting the South Pacific subtropical circulation: A synthesis of World Ocean Circulation Experiment observations along 32 S. *Journal of Geophysical Research: Oceans*, 106(C9), 19481-19513.
- Wijgerde, T., Jurriaans, S., Hoofd, M., Verreth, J.A., Osinga, R. (2012) Oxygen and heterotrophy affect calcification of the scleractinian coral *Galaxea fascicularis*. *PLoS ONE*, 7(12), e52702.
- Wilks, J.V., Nodder, S.D., Rigual-Hernández, A. (2021) Diatom and coccolithophore species fluxes in the Subtropical Frontal Zone, east of New Zealand. *Deep Sea Research Part I: Oceanographic Research Papers*, 169, 103455.
- Williams, U.-M.M.-C. (2022) The effects of sedimentation on the physiology of living New Zealand brachiopods University of Otago].
- Witte, U., Aberle, N., Sand, M., Wenzhofer, F. (2003) Rapid response of a deep-sea benthic community to POM enrichment: an in situ experimental study [Article]. *MARINE ECOLOGY-PROGRESS SERIES*, 251, 27-36. <Go to ISI>://000182917300003
- Witte, U., Wenzhofer, F., Sommer, S., Boetius, A., Heinz, P., Aberle, N., Sand, M., Cremer, A., Abraham, W.R., Jorgensen, B.B., Pfannkuche, O. (2003) In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. *Nature*, 424(6950), 763-766. <https://doi.org/10.1038/nature01799>|ISSN 0028-0836

- Wood, A.C.L., Rowden, A.A., Compton, T.J., Gordon, D.P., Probert, P.K. (2013) Habitat-Forming Bryozoans in New Zealand: Their Known and Predicted Distribution in Relation to Broad-Scale Environmental Variables and Fishing Effort. *PLoS ONE*, 8(9), e75160. <https://doi.org/10.1371/journal.pone.0075160>
- Wurz, E., Beazley, L., MacDonald, B., Kenchington, E., Rapp, H.T., Osinga, R. (2021) The hexactinellid deep-water sponge *Vazella pourtalesii* (Schmidt, 1870)(Rossellidae) copes with temporarily elevated concentrations of suspended natural sediment. *Frontiers in Marine Science*, 8, 611539.
- Yang, W., Zhao, X., Zheng, M. (2022) Slow-sinking particulate organic carbon and its attenuation in the mesopelagic water of the South China Sea [Original Research]. *Frontiers in Marine Science*, Volume 9 - 2022. <https://doi.org/10.3389/fmars.2022.1018825>
- Yuan-Hui, L., Gregory, S. (1974) Diffusion of ions in sea water and in deep-sea sediments. *Geochimica et Cosmochimica Acta*, 38(5), 703-714. [https://doi.org/https://doi.org/10.1016/0016-7037\(74\)90145-8](https://doi.org/https://doi.org/10.1016/0016-7037(74)90145-8)
- Ziveri, P., de Bernardi, B., Baumann, K.H., Stoll, H.M., Mortyn, P.G. (2007) Sinking of coccolith carbonate and potential contribution to organic carbon ballasting in the deep ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(5-7), 659-675. <https://doi.org/10.1016/j.dsr2.2007.01.006>