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The role of *Chaetopterus* sp. in reshaping sediment characteristics and benthic communities in Queen Charlotte Sound

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

Master of Science (Research) in Ecology and Biodiversity

at

The University of Waikato

by

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THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2025

Abstract

Soft-sediment habitats are critical to marine ecosystems, supporting diverse benthic communities and key processes such as nutrient cycling, sediment stabilisation, and energy transfer. Among these habitats, tube-building polychaetes like *Chaetopterus* act as ecosystem engineers, modifying sediment properties and influencing community structure and functioning. This study investigated the ecological impacts of *Chaetopterus* in East Bay, Queen Charlotte Sound, focusing on its role in sediment modification, macrofaunal biodiversity, and functional group composition.

Field surveys were conducted across ten paired *Chaetopterus* and control sites, selected to capture a gradient in tube mat density and depth. At each site, five sediment and macrofaunal samples were collected using coring techniques, enabling a robust comparison of *Chaetopterus*-modified and unmodified habitats.

Results showed significantly higher organic content (3.1% ± 0.2 vs. 2.0% ± 0.1) and mud content (19.8% ± 2.0 vs. 7.7% ± 0.5) in *Chaetopterus* habitats, highlighting its role in sediment enrichment and stabilisation. Macrofaunal communities exhibited significantly greater species richness (20.0 ± 0.8 vs. 14.5 ± 0.7 species per core) and diversity (Shannon diversity: 2.48 ± 0.05 vs. 2.16 ± 0.06), driven by increased structural complexity and organic matter retention.

Functional group analysis revealed a shift towards surface-oriented taxa in *Chaetopterus* habitats, including increased surface-feeding deposit feeders (e.g., amphipods) and scavengers (e.g., *Halicarcinus cookii*), alongside a relative reduction in deeper-burrowing taxa such as bioturbating polychaetes (*Prionospio multicristata*) and burrowing bivalves (*Tawera spissa*). This suggests that *Chaetopterus* tube mats promote surface-associated processes like organic matter turnover and detritus retention, while potentially suppressing sediment-mixing and oxygenation functions.

Chaetopterus habitats exhibited significantly lower dispersion (PERMDISP), indicating more functionally homogeneous assemblages compared to control sites, where greater within-group variability reflected a broader range of functional traits, including suspension feeders and opportunistic burrowers (e.g., Phoxocephalidae amphipods). *Chaetopterus* density was significantly correlated with macrofaunal community composition, reinforcing the role of tube mats as a key driver of functional trait distributions. However, the extent of these effects varied across sites, suggesting that local environmental factors, particularly sediment properties (mud content, organic matter) and *Chaetopterus* density, mediate its influence on benthic communities.

These findings advance understanding of habitat-modifying polychaetes by demonstrating that *Chaetopterus* effects are highly context-dependent, shaped by habitat × site interactions and environmental conditions. While previous studies have identified *Chaetopterus* as a biodiversity enhancer, this study highlights its dual role as both a facilitator of surface-dominated processes and a potential suppressor of deeper sediment functions. These findings provide critical insights into its ecological role within New Zealand's coastal ecosystems and underscore the need for site-specific management strategies that balance local biodiversity benefits with broader ecosystem functions.

Acknowledgments

This research would not have been possible without the support and contributions of many individuals. I am profoundly grateful to Conrad Pilditch for his invaluable guidance, thoughtful advice, and assistance throughout my thesis journey, which were instrumental in shaping this work.

Special thanks to Rob Davidson (Davidson Environmental) for his generous help with fieldwork and for sharing his extensive local knowledge. I also deeply appreciate Rod Asher (Biolive) for his expertise in macroinvertebrate identifications—facilitated through an exchange of seafood—which played a key role in this study. My appreciation also extends to Jack Hamilton for his meticulous sediment analysis and invaluable expertise.

I am sincerely thankful to Leigh Harding (who sorted half a sample), and Alexander Scott-Simmonds for their diligent assistance in sorting macroinvertebrates. I am also grateful to Barrie Forrest (Salt Ecology) for his insightful discussions, which greatly enriched this research, and to Karen Tricklebank (University of Auckland) for providing essential background knowledge and insights from past studies.

My gratitude extends to Jono Underwood (Marlborough District Council) for facilitating an Envirolink grant that supported the literature review, which laid the foundation for this research. I also want to thank my mum for her constant encouragement and steadfast support throughout this journey.

Finally, I express my deepest appreciation to my partner, Courtney Rayes. Her belief in my abilities, invaluable assistance with fieldwork, and dedication to managing our business to enable my studies has been nothing short of extraordinary. Her humour and patience brought balance and motivation when it was most needed.

To everyone who contributed, directly or indirectly, to the completion of this thesis, I offer my heartfelt thanks for your generosity and support.

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Chapter 1: General introduction and literature review

1.1 General introduction

Soft-sediment environments are critical components of marine ecosystems, supporting diverse assemblages of benthic organisms and underpinning essential ecological processes such as nutrient cycling, sediment stabilisation, and energy transfer (Snelgrove, 1998; Thrush et al., 2001, 2006). These habitats, often perceived as homogenous, are far from uniform. They are shaped by environmental gradients and the activities of ecosystem engineers, such as tube-building polychaetes, which enhance habitat complexity and mediate ecological interactions (Passarelli et al., 2012; Thomsen et al., 2011). Understanding the biodiversity and ecological processes of these habitats is essential for predicting and managing the impacts of environmental change, yet many areas, including those in New Zealand, remain understudied.

The study of cryptogenic species adds another layer of complexity to understanding soft-sediment ecosystems. Cryptogenic species, organisms of uncertain origin, challenge traditional categorisations of native versus non-indigenous species. Their ambiguous status complicates biosecurity frameworks and conservation planning, yet they may play pivotal roles in ecosystem dynamics. In soft-sediment habitats, cryptogenic species may unknowingly alter ecological balance by competing with native species, modifying habitat structure, or influencing sediment properties. This highlights the significance of their study in ecosystem management, where the challenge lies in balancing conservation and resource use despite the absence of clear guidelines for handling these enigmatic organisms.

In New Zealand, the parchment tubeworm *Chaetopterus* sp. (herein '*Chaetopterus'* unless otherwise stated) exemplifies this intersection of cryptogenesis and soft-sediment ecosystem dynamics. First recorded in the 1960s, its population remained sparse until the mid-1990s, when it began forming dense aggregations in the Hauraki Gulf and other regions (Tricklebank et al., 2001; Acosta, 2001). These mats cover large areas of the seafloor, fundamentally altering the physical and biological properties of soft-sediment habitats (Schaffner, 1990). While *Chaetopterus*' ecological impacts have been studied internationally, research within New

Zealand’s unique marine environment is limited, leaving significant gaps in the understanding of its role as an ecosystem modifier.

Studying cryptogenic species like *Chaetopterus* within the context of soft-sediment environments is crucial for several reasons. First, it enhances our knowledge of how these habitats function and respond to biogenic modification. Second, it provides insights into the potential consequences of introducing or facilitating the spread of species with uncertain origins. Finally, it informs management practices aimed at preserving ecosystem integrity while accommodating the dynamic nature of coastal and marine ecosystems.

1.1.1 Thesis structure

This thesis is structured into two main chapters, each addressing critical questions through a combination of comprehensive literature review and targeted investigation into the ecological impact of *Chaetopterus* within New Zealand's soft-sediment habitats:

The first chapter provides an overview of the biology and ecological significance of *Chaetopterus*, a tube-building polychaete widely distributed across diverse habitats, including soft-sediment and hard-substrate environments. It examines the species' role as an ecosystem engineer, focusing on its influence on habitat structure, sediment properties, and community dynamics. Key biological traits, such as tube construction, feeding mechanisms, reproductive strategies, and commensal association, are reviewed to highlight its ecological importance. This chapter also addresses the implications of *Chaetopterus* as a cryptogenic species, emphasising its potential ecological and biosecurity impacts, particularly in New Zealand, where its role in marine ecosystems remains poorly understood. By synthesising international and local research, this chapter identifies critical knowledge gaps related to the species’ ecological functions and interactions within New Zealand’s marine environments. These insights lay the foundation for the field study presented in Chapter Two.

Chapter Two investigates the ecological impact of *Chaetopterus* within Queen Charlotte Sound (QCS), Marlborough, with a focus on its role in shaping sediment properties and influencing benthic community composition in East Bay. Using a subtidal field survey, the study examines how *Chaetopterus* modifies habitat conditions, affects biodiversity, and impacts ecosystem function through changes in functional group composition. By situating these findings within the broader framework of international research and New Zealand's unique ecological context, the chapter underscores the potential of *Chaetopterus* as a cryptogenic driver of ecological change. The results offer valuable insights into the dynamic interplay between biogenic habitats, biodiversity, functional traits, and ecological processes, providing a foundation for future research and management strategies.

1.2 Literature review of *Chaetopterus* sp.

1.2.1 Identification history and related species

The Chaetopteridae family (commonly known as parchment worms) presents a persistent challenge in taxonomy and systematics. A comprehensive revision of this family has yet to be undertaken, resulting in ongoing uncertainty and confusion regarding the number of recognised species. Moore (2019) conducted a phylogenetic and morphological review of the genus *Chaetopterus*, but much of this research remains unpublished. The lack of a thorough taxonomic update has contributed to ambiguities in the classification and identification of Chaetopterid species (Osborn et al., 2007; Helm et al., 2022). More recently, Chaetopterids have been reclassified as part of the clade Chaetopteriformia, along with Apistobranchidae and Psammodrilidae (Helm et al., 2018), reflecting advances in molecular and morphological analyses. However, considerable uncertainty remains, necessitating further taxonomic clarification.

Historically, *Chaetopterus* was regarded as a single, morphologically variable, cosmopolitan species, *Chaetopterus variopedatus* (Fauvel, 1919). While a partial taxonomic revision was conducted for Pacific species (Nishi, 2001), further work is required to resolve species identities, particularly those used as model organisms and those described from non-Pacific regions (Moore, 2019). At present, the Chaetopteridae family comprises four recognised genera; *Chaetopterus* Cuvier, *Spiochaetopterus* Sars, *Phyllochaetopterus* Grube, and *Mesochaetopterus* Potts, encompassing 75 valid species, including several cryptic species complexes (Martin et al., 2022). Addressing these taxonomic uncertainties is critical for ecological studies, as species misidentifications could influence assessments of biodiversity, biogeography, and functional roles within benthic ecosystems.

1.2.2 Global distribution and history

Chaetopterids are frequently encountered marine annelids, inhabiting environments ranging from intertidal zones to abyssal depths (Moore et al., 2017). Many Chaetopterid species are regarded as having a cosmopolitan distribution, though the historical nature of their dispersal complicates determining their precise origins. These complex distribution patterns make it challenging to identify the sources of their evolutionary development and geographic spread.

Chaetopterus have been extensively studied over the last century, spanning back to 1890 when the first detailed descriptions of *C. variopedatus* were made (Joyeux-Laffuie, 1890). *Chaetopterus* research has been diverse, included many species and have focussed extensively on cell biology and biochemistry of gametes (e.g., Merriam, 1959; Inoué et al., 1974; Swalla et al., 1985), early cleavage and embryogenesis (e.g., Henry, 1986, 1989; Eckberg & Anderson, 1996; Eckberg & Hill, 1996; Yang et al., 2004; Lanza & Seaver, 2020), reproduction and early development (e.g. Enders, 1909; Irvine et al., 1999; Petersen et al., 2000), filter-feeding and fluid mechanics (e.g., Sumida & Case, 1983; Jorgensen et al., 1984; Riisgärd, 1989; Cresson et al., 2016), nervous system (e.g., Martin & Anctil, 1984; Helm et al., 2022), bioluminescence (e.g., Mikheyskaya et al., 1995; Wang et al., 2006; Deheyn et al., 2013; Branchini et al., 2014; Rawat & Deheyn, 2016; De Meulenaere et al., 2017; Purtov et al., 2019) and commensalism (e.g. Petersen & Britayev, 1997; Grove et al., 2000; Britayev et al., 2017).

1.2.3 New Zealand distribution and background studies

Research specifically focusing on *Chaetopterus* within New Zealand is limited, with the primary studies being an MSc thesis by Acosta (2001) and a report by Tricklebank et al. (2001). Acosta (2001) explored the taxonomic identity and reasons behind the rapid spread of *Chaetopterus* (often referred to as the 'Hauraki' *Chaetopterus*) in the northeastern region, covering various aspects of the species' biology, including luminescence, tube growth and repair, reproduction, and regeneration patterns. Tricklebank et al. (2001) build on this study, providing a systematic status of the Hauraki *Chaetopterus*, a brief literature review, and an analysis of the distribution and abundance in northeastern New Zealand. It also includes a species description, included in Appendix A.

Most records of *Chaetopterus* in New Zealand originate from historic commercial trawl surveys or marine biosecurity surveillance reports, with the latter resulting in a concentration of records around the main New Zealand ports and harbours (e.g. Inglis et al., 2006; MAF, 2008; MPI, 2012, 2017; MacGibbon et al., 2024; MBP, 2024). While limited, there are a few ecological reports that note *Chaetopterus* in New Zealand, however details regarding their fundamental biology are often brief (e.g., Davidson et al., 2019, 2020a, 2020b, 2022; Brook et al., 2001; Hayward & Morley, 2008).

Chaetopterid records are widely distributed around New Zealand across all depths, although most are not identified to species (Jones et al., 2018). Within this family, seven species are found in New Zealand waters, two of which are distinct *Chaetopterus* species. These include the following:

1. *Chaetopterus* sp. (*Chaetopterus-A*, NIWA 122959)
2. *Chaetopterus* sp. (*Chaetopterus-B*, NIWA 27271)
3. *Mesochaetopterus sagittarius* (Claparède, 1870)
4. *Phyllochaetopterus socialis* (Claparède, 1870)
5. *Spiochaetopterus* sp. (*Spiochaetopterus-B*, NIWA 78014)
6. *Spiochaetopterus* sp. (*Spiochaetopterus-C*, NIWA 73695)
7. *Spiochaetopterus* sp. Stull, 1979

A formal species description meeting the requirements of the Zoological Code of Nomenclature has yet to be published for New Zealand *Chaetopterus*. Consequently, the two known species (*Chaetopterus chaetopterus-A* and *Chaetopterus chaetopterus-B*) lack complete Latin binomial names. Although limited genome sequencing has been conducted on New Zealand Chaetopterus, more recent genetic studies are underway, with publications currently in preparation (G. Read, personal communication, July 12, 2023).

1.2.3.1 Chaetopterus chaetopterus-A

Chaetopterus chaetopterus-A is widely distributed in New Zealand, occurring from the Bay of Islands to Bluff Harbour, including the Top of the South region (Brook et al., 2001; MPI, 2012; MBP, 2024). While commonly found in shallow waters from 15-40 m, it has been recorded at depths down to 69 m around the Poor Knight Islands (Acosta, 2001; Brook et al., 2001). It is also a dominant component of fouling assemblages on wharf piles and structures in major New Zealand ports (MAF, 2008; MPI, 2017; MPI, 2023). It has been previously suggested that *C. chaetopterus-A* is new to science (Tricklebank et al., 2001). However, the inadequate preservation of museum specimens and holotypes posed significant challenges for conducting taxonomic comparisons of this species with other Chaetopterids.

Chaetopterus chaetopterus-A is considered a 'Category 1' cryptogenic species (MAF, 2008; MPI, 2017). Category 1 cryptogenic species are those "previously recorded from New Zealand, whose identity as either native or non-indigenous is unclear. This includes species that may have been introduced to New Zealand before scientific records began, as well as newly described species exhibiting invasive behaviour in New Zealand but with no known records outside the New Zealand region" (MAF, 2008).

1.2.3.2 Chaetopterus chaetopterus-B

Chaetopterus chaetopterus-B has a more restricted distribution compared to *C. chaetopterus*-A in New Zealand, being confined to the Marlborough Sounds and Nelson region (MBP, 2024). This species prefers shallow areas (<16 m) with mixed sand and broken shells, but avoids glutinous mud (R. Davidson, personal communication, March 12, 2023). Records show that *C. chaetopterus-B* is widespread in these regions, with large populations scattered throughout Queen Charlotte and Pelorus Sound (S. Cunningham, personal communication, June 1, 2023; Davidson et al., 2022; MBP, 2024).

Chaetopterus chaetopterus-B is classified as a 'Category 2' cryptogenic species, referring to newly discovered species for which there is insufficient information to determine whether New Zealand lies within their native distribution (MAF, 2008). Given its limited distribution and uncertain origins, further research is needed to clarify its biogeographic history and ecological role within New Zealand's soft-sediment habitats.

1.2.4 History of invasion in New Zealand

Historical records of *Chaetopterus* in New Zealand are limited. The first documented instances date to 1966 when a university student at the Leigh Marine Laboratory discovered three specimens, initially identified as *C. variopedatus* (Acosta, 2001). However, given the taxonomic complexities within the genus, there is a possibility that they were misidentified at that time.

Northeastern New Zealand

Chaetopterus populations across the country remained sparse until the mid-1990s (Tricklebank et al., 2001). It was during this period that *Chaetopterus* suddenly became exceptionally abundant in the Hauraki Gulf, where it began to inhabit rock crevices and cover extensive areas of sheltered sediment seafloor (Acosta, 2001). In 1997, the empty tubes of *Chaetopterus* began washing up dead in large numbers, disintegrating into parchment fragments that slowly decayed and littered beaches (Acosta, 2001; Tricklebank et al., 2001; Anthoni, n.d.). During the same time, *Chaetopterus* caused problems for scallop dredge fishers, and concerns arose about the exclusion of other benthic species within the Hauraki Gulf (Tricklebank et al., 2001; Cryer, 2002).

In 2001, an examination of the Hauraki Gulf *Chaetopterus* (now formally known as *C. chaetopterus-A*) was conducted to clarify its taxonomic status, which suggested that the species was previously unknown to science (Tricklebank et al., 2001). Confusion remains regarding whether *C. chaetopterus-A* is a species endemic to New Zealand, with some suggestions that it may be an introduced species (Tricklebank et al., 2001; Davidson et al., 2022). This suggestion is based on its rapid spread, ability to colonise a wide variety of habitats, threat to indigenous species, and capacity to achieve high population densities, which are characteristic of invasive or introduced species. However, the spread observed in the Hauraki Gulf may have been facilitated by widespread bottom trawling, which creates numerous worm fragments capable of regenerating into full-bodied adults (Acosta, 2001).

Benthic surveys conducted at the Poor Knights Islands in 2001 recorded *Chaetopterus* densities of up to ~20,000 ind./m^2 on coarse soft sediments at Maroro Bay, Skull Bay, and Shag Bay at depths down to 69 m (Sim-Smith & Kelly, 2008). The worm was also found on rocky reefs at much lower densities (Brook et al., 2001). However, abundance of *Chaetopterus* at the Poor Knights Islands drastically decreased in the years following, and dense mats of the tubeworm were no longer present by 2004 (Brook et al., 2001). The ecological effects of *Chaetopterus* on the benthic community at the Poor Knights Islands were not examined. *Chaetopterus* has now formed populations in various locations, including the Hauraki Gulf, Whangarei, and Tauranga where it has become a notable element of soft-bottom ecosystems (Acosta, 2001; Tricklebank et al., 2001; Eager & Reid, 2004; Hayward & Morley, 2009).

Marlborough Sounds

The Hauraki *Chaetopterus* (*C. chaetopterus-A*) is distinct from a second *Chaetopterus* species, *C. chaetopterus-B*, found in the Marlborough Sounds (Sim-Smith & Kelly, 2008). Although both species coexist in the region, there is uncertainty regarding which species first established in the Marlborough Sounds largely due to their morphological similarities. Historical records reveal the presence of extensive *Chaetopterus* beds in Grove Arm, inner QCS in 1989-90 (Davidson et al., 2020b). These beds were colonised by various native seaweeds, with *Lenormandia chauvini* being particularly notable, as well as invertebrates such as *Corbula zelandica*, *Pecten novaezelandiae*, and *Chirodota* sp. (C. Duffy, as cited in Davidson et al., 2020b).

The earliest formal record of *C. chaetopterus-B* was from a sample collected in Port Underwood in 2007 (MBP, 2024). Populations remained steady until 2017, when a population explosion occurred in the outer QCS, particularly in East Bay and the side bays of Tory Channel (R. Davidson, personal communications, March 12, 2023). The appearance of these populations was notably different from the beds found in central Pelorus Sound (R. Davidson, personal communications, March 12, 2023). Since then, it has spread further into QCS, becoming very dense up to Ruakaka Bay, and then generally becoming less abundant further into the Sound. Dense beds have been observed as far as Houhou Point but distribution likely extends further (R. Davidson, personal communications, March 12, 2023).

Although concerns about a sudden population surge of *Chaetopterus* had been raised earlier, the first empirical evidence of increased abundances was recorded in 2019 during surveys assessing scallop populations in the Marlborough Sounds (Figure 1.1; Williams et al., 2021). These surveys quantified *Chaetopterus* due to their growing prevalence within the fishing grounds, where an unidentified *Chaetopterus* was recorded in the catch at 35 out of 120 survey stations, representing a 29% presence (Williams et al., 2021). Its distribution included areas of Pelorus Sound, such as Horseshoe Bay, Waitata Bank, Ketu Bay, and Guards Bay, as well as Queen Charlotte Sound (QCS) at Ship Cove. Around the same time, a local diver reported a substantial presence of tubeworms, suspected to be *Chaetopterus*, in an area of QCS. Subsequent sampling confirmed these tubeworms as *C. chaetopterus-B* (Williams et al., 2021). By 2020, *Chaetopterus* had expanded to new areas, including the Chetwodes, Bay of Many coves, and Croisilles Harbour (Williams et al., 2019).

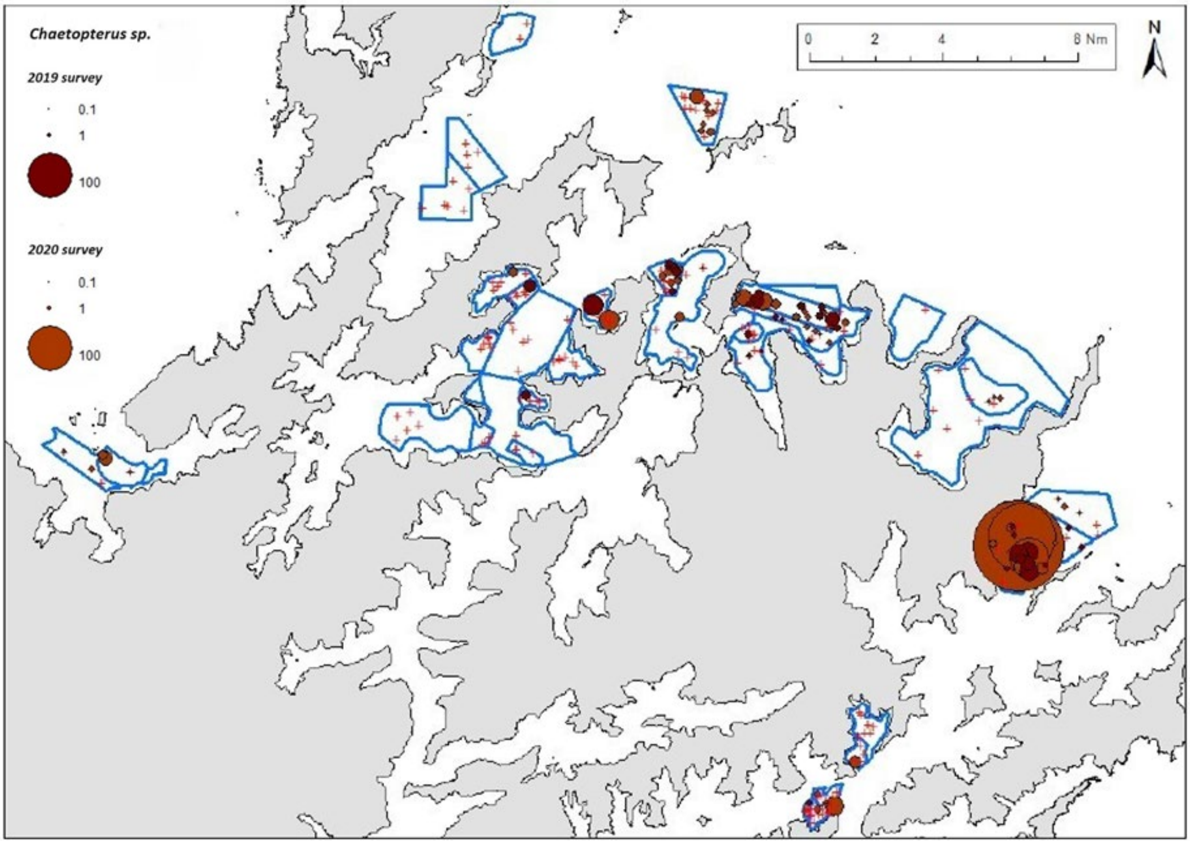

Figure 1.1. *Chaetopterus sp. catch per standard tow, Marlborough Sounds dredge surveys, May 2019 (dark brown circles) and May 2020 (light brown circles). Circle area is proportional to the estimated volume (L) caught per standard distance towed (0.4 n. miles). Values are uncorrected for dredge efficiency. Polygons denote survey strata boundaries. (Adapted from Williams et al., 2021)*

Since 2019, multiple ecological reports have documented the presence of *Chaetopterus* in areas designated as 'significant marine habitats' within the Marlborough Sounds. These sites collectively support rare or ecologically important features, habitats, and marine life (Davidson et al., 2011). A survey by Davidson et al. (2020b) confirmed the high abundance of *Chaetopterus* at Long Island marine reserve in 2019. Following this, surveys documented high densities of *Chaetopterus* sp. colonising and smothering rare calcareous tubeworm mounds (*Galeolaria hystrix)* at Perano Shoal, QCS (Davidson et al., 2020a). More recently, dense beds of *Chaetopterus* sp. have become widespread in shallow areas of East Bay less than approximately 16 m depth (Davidson et al., 2022). The study also documented a decline in giant lampshell (*Neothyris lenticularis*), scallop (*Pecten novaezealandiae*) and burrowing anemone (*Cerianthus* sp.) in the area, although the cause is unknown or related to *Chaetopterus* (Davidson et al., 2022). These observations have led to suggestions that this species of *Chaetopterus* may be introduced and could be having detrimental effects on native fauna (Davidson et al., 2022). In 2022, samples of an unidentified *Chaetopterus* species were collected from QCS and underwent morphological examination, which suggested it might be *C. chaetopterus-A* (O. Wade, personal communication, November 28, 2022). Consequently, the Ministry for Primary Industries extended its recorded range.

The observations regarding *Chaetopterus* and *G. hystrix* together coupled with ongoing localised decline of *P. novaezealandiae* in the Marlborough Sounds, has resulted in public concern that the mat-forming tubeworms may be colonising soft-sediment areas and hindering restoration (Picton Regional Forum, 2022). However, the causes behind its apparent population growth and broader ecological impact within the Top of the South region are not yet well understood. Further research is required to determine whether these expansions are driven by environmental changes, reduced predation pressure, or anthropogenic influences.

1.2.5 Biology of *Chaetopterus*

1.2.5.1 General description

The family Chaetopteridae, within the phylum Annelida, comprises tube-dwelling polychaetes that construct and inhabit self-secreted membranous tubes. Tube length and body size can vary considerably across species and populations (Tricklebank et al., 2001). *Chaetopterus* species display both infaunal and epifaunal lifestyles, with some burrowing into the substrate while others attach to hard surfaces (Tricklebank et al., 2001; Nishi et al., 2009). These species are distributed across a wide range of habitats, from intertidal zones to the deep sea (Shah et al., 2014; Moore et al., 2017).

Chaetopterus is notable for its relatively large body size, its tube with openings at each end, and three specialised middle body segments used for pumping water through the tube. The taxon name is derived from the Greek for ‘chaetae’ and ‘wing’ and refers to the long notopodia with aciculae in some taxa (Rouse et al., 2022). These features, along with the production of large gametes and bioluminescence, have made the genus a major focus of scientific interest as a laboratory organism.

1.2.5.2 The tube

Chaetopterus creates and inhabits a parchment-like tube for its entire life. As the worm grows, it enlarges the tube in both length and diameter (Enders, 1907; Faulkner, 1931). After settling, *Chaetopterus* begins building its tube by creating horizontal mucus-coated tunnels into the sediment. The initial tube is about 1 mm in diameter and 18–22 mm long (Enders, 1909). As the worm grows, it enlarges the tube by splitting it from the inside at a point where it starts to curve upward, expanding the tube laterally (Enders, 1907). This process is repeated as the worm increases in size, pushing the tube deeper into the sediment until it reaches maturity and can reproduce (Enders, 1909). The smooth internal surface and the epithelial mucus serve as a lubricant to reduce friction between the moving piston segments and the tube wall (Brown, 1977). Studies have demonstrated that these tubes can function reliably across a wide range of water temperatures (5 °C to 75 °C) and are extremely durable (Shah et al., 2014).

The tube is typically U-shaped (Figure 1.2, Figure 1.3) and features two tapered openings with diameters significantly smaller than the middle section, which enhances water velocity at the openings (Brown, 1977; Tricklebank et al., 2001). This design allows the worm to maintain a constant flow of water through the tube, providing both aeration and food. The openings are often concealed by other epiphytic organisms such as algae, ascidians, and bryozoans (Enders, 1907; Schaffner, 1990; Davidson et al., 2020). The construction of U-shaped tubes by several *Chaetopterus* species has likely contributed to ambiguities in their classification (Fauvel, 1927; Hartman, 1959). Commonly recognised for its distinctive U-shaped tube, *Chaetopterus* species exhibit significant variation in tube shape due to their ability to adapt to a wide range of habitat types (Irvine et al., 1999). Previous research has identified two groups of *Chaetopterus* based on their tube-building: infaunal species that build regular U-shaped tubes in soft sediment and epifaunal species that construct irregular tubes attached to hard surfaces (Rouse & Pleijel, 2001; Tricklebank et al., 2001; Nishi et al., 2009). Both species found in New Zealand, have adapted to inhabit both soft sediment and hard substrate environments, displaying a wide range of tube formations (Acosta, 2001; Tricklebank et al., 2001; Davidson et al., 2022). Other members of the Chaetopteridae family construct relatively straight tubes that are oriented vertically within the substratum (Barnes, 1965).

The genus *Chaetopterus* comprises several species that exhibit variation in overall tube length (Irvine et al., 1999). Tubes can reach lengths of up to 50 cm from orifice to orifice, with vertical arms protruding up to 22 cm above the seafloor (Enders, 1909). However, the length of the tube constructed by *Chaetopterus* species does not strongly correlate with the size of the worm. Instead, research suggests that the average internal diameter of the tube's main section is a more accurate indicator of the worm's size (Brown, 1977). Tricklebank et al. (2001) reported that the tube diameter of adult *C. chaetopterus-A* ranges from 10-15 mm, with lengths typically exceeding 150 mm in large adults. Specimens of *Chaetopterus* found near Aratawa Bay within the QCS have been observed by divers to exceed 250mm (pers. obs. 2023).

Chaetopterus invests significant energy in tube construction (Thompson & Schaffner, 2001). Due to the continuous production of tube material, *Chaetopterus* can rapidly repair damage to its tube. This repair ability is facilitated by specialised chaetae on their fourth anterior segment, which are used to cut or tear the tubes for growth and remodelling (Barnes, 1965). Local experiments have demonstrated that *C. chaetopterus-A* can rebuild and repair its tube, sometimes in less than an hour (Acosta, 2001). Both juvenile and adult *Chaetopterus* were able to construct new tubes when removed from their original ones (Acosta, 2001).

Figure 1.2. *Typical example of an adult Chaetopterus tube from East Bay, Queen Charlotte Sound.*

Figure 1.3*. A dense aggregation of Chaetopterus from East Bay, Queen Charlotte Sound, 2023.*

1.2.5.3 Body structure

The Chaetopteridae family exhibits a wide range of body sizes, from less than 10 mm to over 400 mm in length (Moore, 2019). The most common, *C. variopedatus,* can reach 150–200 mm in length when mature (Mirza et al., 2020). The maximum preserved length of *C. chaetopterus-A* is 79mm (Tricklebank et al., 2001), although a specimen of an unidentified *Chaetopterus* collected in the Marlborough Sounds measured over 160 mm (Figure 1.4; pers. obs. 2023).

Figure 1.4. *Body of Chaetopterus sp. collected in East Bay, Queen Charlotte Sound, 2023. Note: Measuring board is in 2cm increments.*

Chaetopterus is renowned for its highly specialised filter-feeding mechanism (Osborn et al., 2007). Their bodies can be divided into three distinct regions (Figure 1.5): a short anterior region that includes the head and mouth (Region A), a mid-region containing feeding structures (Region B), and a longer regularly segmented posterior end (Region C). The number of chaetigers or segments within the posterior section increases with age (Enders, 1909; Osborn et al., 2007; Mirza et al., 2020).

Region A comprises a morphologically fused prostomium and peristomium with 9 chaetigers, with the ninth bearing an uncinal torus, or, less commonly, 10 chaetigers (Tricklebank et al., 2001). The mouth is spade-shaped and neatly matches the inner curve of the tube. Region B consists of 5 chaetigers that function as an efficient pumping system and includes a digestive organ, which is usually green in colour due to the presence of chlorophyll (Alvarez et al., 1928). Region C can have up to 28 chaetigers, depending on the age of the individual, and includes the anus, which is surrounded by two pairs of dorsal cirri (Tricklebank et al., 2001). The body of *C. chaetopterus-A* exhibits a very pale-yellow coloration, which is slightly more intense on the ventral plastron notopodia of region A and the dorsal cupule of B2 (Tricklebank et al., 2001).

Sexually mature males and females of mature worms can be identified by the swollen and opaque parapodia in their posterior sections, caused by the accumulation of gametes (Thompson & Schaffner, 2001). In *C. variopedatus*, the sex can also be distinguished by the colour of the gonads (Enders, 1909). Fertile males have milky-white gonadal parapodia, while females have yellow-tinted ovaries (Enders, 1909; Eckberg & Hill, 1996). The sex of immature or young specimens cannot be determined (Enders, 1909).

The eyes are situated on each side, external to the antenna, though they are less noticeable in larvae (Enders, 1909). The eyes in Chaetopteridae species are simple pigment spot eyes, which can either form a flat patch or be embedded in a tube-like invagination (Purschke et al., 2022).

Various characteristics have been used to compare species recorded from the Pacific region (Nishi et al., 2009). Some traits, such as body width, the ratio of length to width of the ventral shield, and the number of teeth on the uncini in each region, show overlapping ranges. However, other features, including the shape and composition of tubes, the presence or absence of eye spots, the number of chaetigers in regions A and C, the number and shape of pairs of A4 modified chaetae, and the shape of neuropodial cirri, can be used to distinguish *Chaetopterus* species (Sun & Qui, 2014).

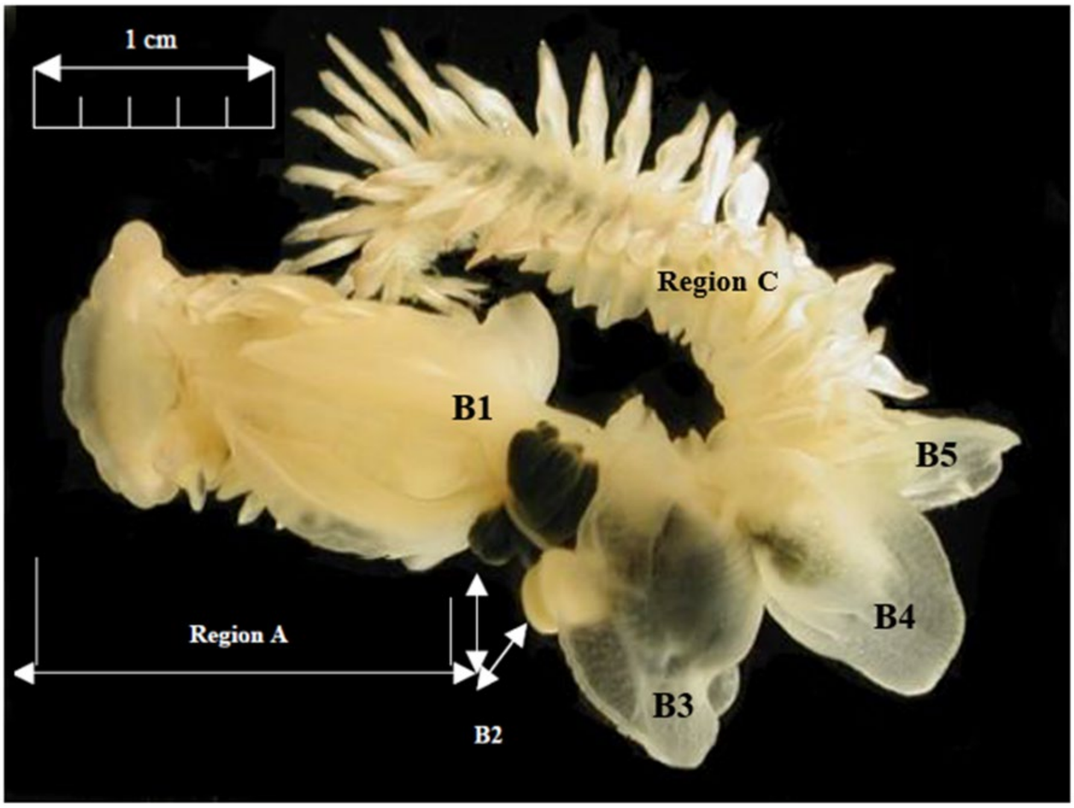

Figure 1.5. *Adult C. chaetopterus-A from northeastern New Zealand after removal from the tube. Regions A, B (segments B1 – B5) and region C are shown. (adapted from Tricklebank et al., 2001).*

1.2.5.4 Regeneration

The ability of *Chaetopterus* species to regenerate damaged or lost body segments has been documented in various studies, with several authors providing brief descriptions of the process (Berrill, 1928, 1952; Faulkner, 1931; Hill, 1972; Eckberg & Hill, 1996). More detailed investigations into the regenerative capabilities of *Chaetopterus* have been conducted, including studies by Acosta (2001) and Seaver et al. (2001).

Chaetopterus has the capability to regenerate all its body segments. While regeneration is common among annelids, the process in *Chaetopterus* is notably unique. The entire body can regenerate from just the single segment B2 (Berrill, 1928; Eckberg & Hill, 1996). Anterior regeneration within *Chaetopterus* is accomplished through epimorphosis, where all missing segments are replaced by the direct outgrowth and differentiation of the blastema. For posterior regeneration, a pygidium forms from the blastema and establishes a growth zone immediately in front of it. New segments are then added anteriorly to the pygidium and undergo differentiation to replace the lost segments (Eckberg & Hill, 1996). Given sufficient time, the new segments eventually occupy the same relative positions in the regenerated worm as they did in the original worm (Berrill, 1928). Furthermore, each somite in *Chaetopterus* retains its own identity and is directly replaced during the regeneration process (Eckberg & Hill, 1996).

Acosta (2001) conducted experiments in New Zealand on *C. chaetopterus-A*, revealing a regeneration pattern consistent with other *Chaetopterus* species. The study demonstrated that both posterior and anterior segments could regenerate, and when the body was cut into two pieces, each fragment developed into a separate individual. The time required for regeneration depended on the size of the missing segment, with larger sections taking longer to regrow. Juveniles regenerated more quickly than adults, and under laboratory conditions, adults removed from their tubes fully regenerated within 30 to 120 days.

1.2.5.5 Feeding and filtration

Chaetoperidae have been the focus of many studies due to their significant variation in their functional morphological specialisation for mucus net suspension feeding (e.g., MacGinitie, 1939; Flood & Fiala-Médioni, 1982; Jørgensen et al., 1984; Riisgård & Larsen, 2010). Food recognition is carried out through both particulate (tactile) and chemical stimuli (Faulkner, 1931; Sumida & Case, 1983; Irvine et al., 1999). When *Chaetopterus* recognises potential food, usually plankton, it stimulates the pumping and filtering process (Werner, 1953). The worm creates a water current through its tube using modified parapodial "fans" (Figure 1.6). It traps and filters suspended organisms in a mucous net, which it produces using the aliform notopodia of segment 12 (Jorgensen et al., 1984). The filter consists of longitudinal and transverse mucus fibres that create a network of rectangular meshes (Flood & Fiala-Médioni, 1982). Once full, it then rolls up the net with an accessory feeding organ and directs it to the mouth via the mid-dorsal ciliary groove for ingestion (MacGinitie, 1939). The feeding net is continuously produced, with the posterior end being rolled into a ball within the dorsal cupule and consumed at intervals of about 15 minutes (Jorgensen et al., 1984).

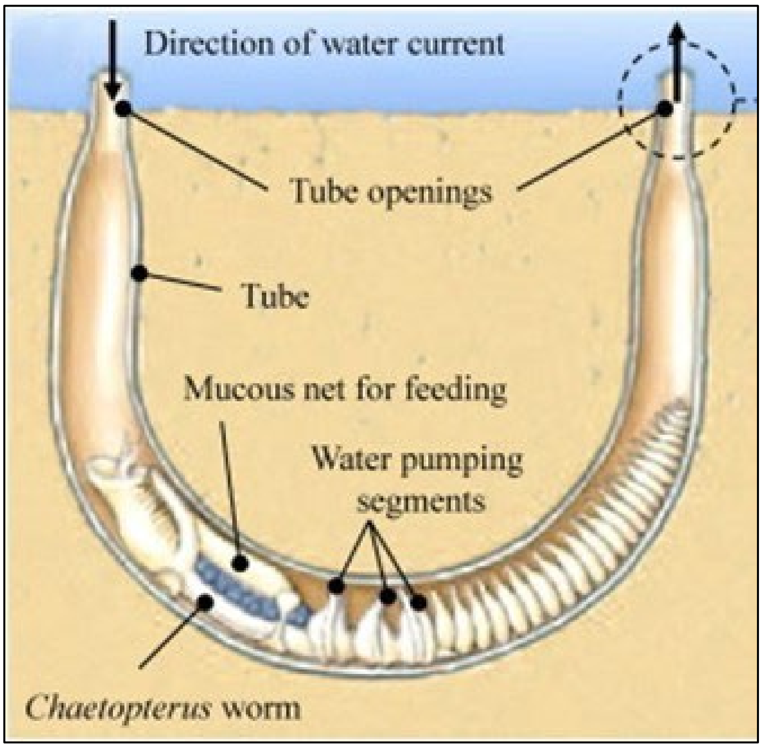

Figure 1.6. *Schematic illustration, adapted from Hickman et al. (2001), depicting a Chaetopterus worm generating water flow within its tube to feed, utilising an elongated mucous net.*

Polychaetes are known to have limited sorting capabilities and can utilise a diverse array of potential food sources (Dubois & Colombo, 2014). Enders (1909) noted that the water passing through the tube of the *C. variopedatus* carries a significant amount of organic matter. The abundance of faeces indicates that much of this organic matter is filtered out as the water flows through the worm's feeding regions. The faeces, typically 6 to 8 mm long and 1 mm in diameter in an average-sized worm, contain the tests of many diatoms, which are also known to serve as food for oysters in the same waters (Enders, 1909). Mucus nets of *C. variopedatus* have demonstrated a 100% retention efficiency of particles as small as 0.5 µm, with an overall retention efficiency that is generally higher than other mucous-net filter feeders like bivalves and ascidians (Flood & Médioni, 1984; Jorgensen et al., 1984; Riisgard, 1989).

Previous studies have also observed that *Chaetopterus* can reverse its position within the tube, causing the water current to change direction and allowing it to feed from either opening (Enders, 1909; Wells & Dales, 1951).

1.2.5.6 Nervous system

The nervous system of Chaetopteridae has been studied less extensively compared to other components. Martin and Anctil (1984) discovered that the central nervous system of *C. variopedatus* is located in the sub-epidermis. While their observations clearly establish that the anterior nervous system of *Chaetopterus* is highly modified compared to other polychaete groups, the basic neural organisation remains a simplified version of what is seen in other polychaete species. The stomatogastric nervous system, which includes the pharyngeal nerves, ganglion, and plexus, is well developed in *C. variopedatus* and is believed to regulate their specialised feeding activities (Martin & Anctil, 1984).

More recent studies found that the nervous system includes a medullary and intraepidermal anterior brain, lacking major commissures and containing only one type of neuron (Helm et al., 2022). Larval specimens lack nuchal organs and complex cup-shaped eyes. Developmental studies indicate that the larval nervous system originates in an antero-posterior manner, suggesting this trait is an ancient characteristic for Annelida (Helm et al., 2022).

1.2.5.7 Reproduction and development

Several aspects of the reproduction and development of *Chaetopterus* have been investigated in detail, with most studies conducted in laboratory settings. This extensive research is largely due to the relatively large size of their larvae, which can reach up to 2.5 mm, making them one of the largest larval forms among polychaetes (Osborn et al., 2007). The studies cover a wide range of topics, including: oocytes and fertilisation (e.g., Pease, 1940; Carroll & Eckberg, 1983; Sato et al., 1985; Eckberg & Palazzo, 1992; Eckberg & Szuts, 1993; Eckberg & Miller, 1995; Swalla et al., 1985; Thomas, 2000; Yin, 2007), embryogenesis and early cleavage (e.g., Fry, 1932; Eckberg & Anderson, 1996; Yang, 2004; Yin & Eckberg, 2009), parthenogenesis (e.g., Loeb, 1901), and early development (e.g., Enders, 1909; Irvine et al., 1999; Irvine & Martindale, 2000; Peterson et al., 2000; Thompson & Schaffner, 2001; Osborn et al., 2007). The fundamental processes of reproduction and larval development into adulthood have been described by Enders (1907, 1909). This summary combines information from these studies and other relevant research.

Chaetopterus progresses through multiple larval stages before reaching adulthood. When mature adults are fertile, the eggs and sperm are released into the water column using the parapodia at their posterior end (Enders, 1909). *Chaetopterus* species spawn in response to environmental cues, with timing varying by location. In temperate regions like North America, *C. variopedatus* typically spawns in early summer as water temperatures rise, with rapid growth to adulthood by season's end (Enders, 1909; Thompson & Schaffner, 2001). In New Zealand, spawning has been observed occurring in late November and mid-December during high tides (Acosta, 2001). Conversely, McNulty and Lopez (1969) observed year-round recruitment in Florida, indicating continuous or multiple spawning events in warmer climates. In situ spawning has been observed to occur both synchronously and asynchronously, depending on the species and location (Acosta, 2001; Thompson & Schaffner, 2001).

Following external fertilisation, the larva escapes from its membrane after approximately five hours and begins to swim actively (Enders, 1909). Over the next 30 days, the stomach enlarges significantly, occupying most of the larva's body, and a pair of eyes develop (Irvine et al., 1999). Between days 30 and 60, two major changes occur: a second trochal band appears, and overt segmentation develops between the posterior mesotroch and the pygidium (Irvine et al., 1999). The central nervous system also develops the basic components of the juvenile form. Approximately 60 days post-fertilisation, the larva reaches about 1 mm in size and begins to metamorphose. By the end of metamorphosis, the juvenile worm has acquired the general form of the adult, with the head and feeding organ taking on their mature structures (Figure 1.7; Irvine et al., 1999).

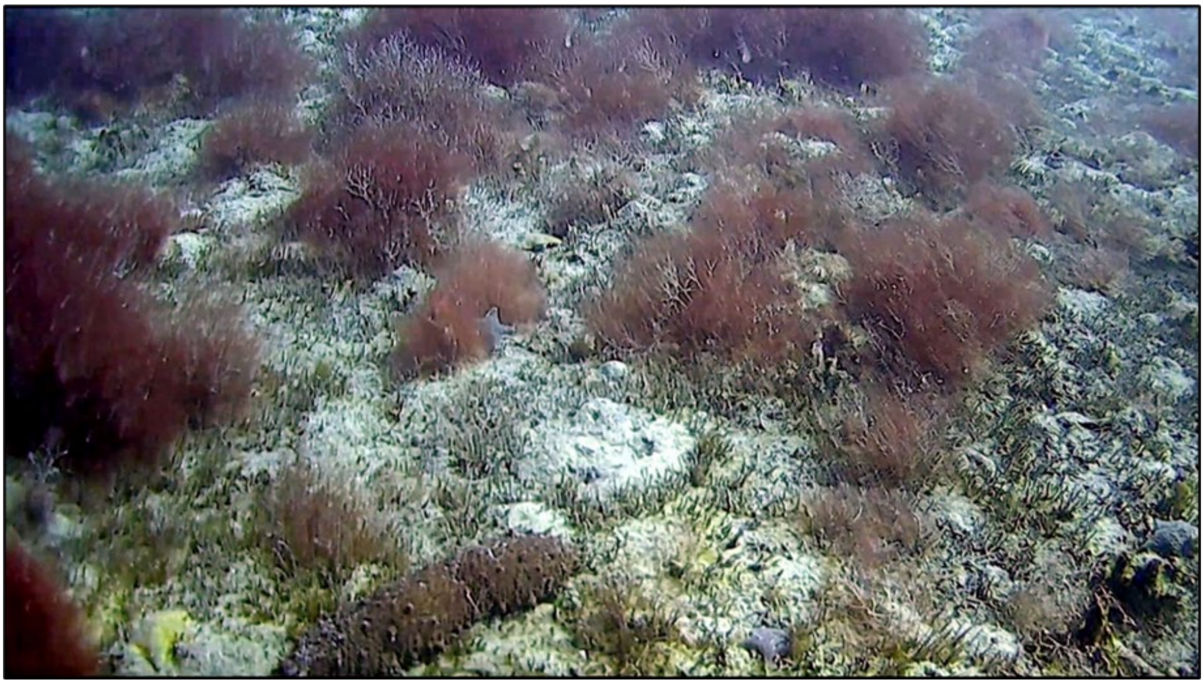

Figure 1.7. *Juvenile Chaetopterus in East Bay, Queen Chalotte Sound, 2023.*

1.2.5.8 Bioluminescence

Bioluminescence is widespread among species within the Class Polychaeta, spanning families such as Acrocirridae, Chaetopteridae, Cirratulidae, Flabelligeridae, Polynoidae, Syllidae, Tomopteridae, and Terebellidae (Nicol, 1957; Verdes & Gruber, 2017). Among these, *Chaetopterus* exhibits notable bioluminescent capabilities, with variations in luminescent parts and colours across different species (Figure 1.8; Harvey, 1926; Branchini et al., 2014; Deheyn, 2020). This diversity in bioluminescent traits has led to numerous studies aimed at understanding their mechanisms and potential applications (e.g., Nicol, 1957; Martin & Anctil, 1984; Branchini et al., 2014; Purtov et al., 2019) and includes a comprehensive review of bioluminescence in *C. variopedatus* (Mirza et al., 2020). The following is a general overview of the bioluminescent characteristics of *Chaetopterus* (namely *C. variopedatus)*, highlighting some of the key findings to date.

Chaetopterus exhibits at least two forms of luminescence: one from the body tissue (Shimomura & Johnson, 1966; Deheyn et al., 2013) and another from the mucus secreted by the animal (Branchini et al., 2014). Light emission can be induced by mechanical and electrical stimulation or by the addition of chemicals such as potassium chloride (Nicol, 1952; Mirza et al., 2020). When severely disturbed, the entire worm can display either constant or flashing light, releasing glowing (460 nm) clouds of mucus and causing the parapodia to glow brightly

(Marin & Anctil, 1984; Shimomura, 2007; Mirza et al., 2020; Purtov et al., 2019). However, experiments on *C. chaetopterus-A* demonstrated that induced bioluminescence is confined to segment B1 and region C (Acosta, 2001).

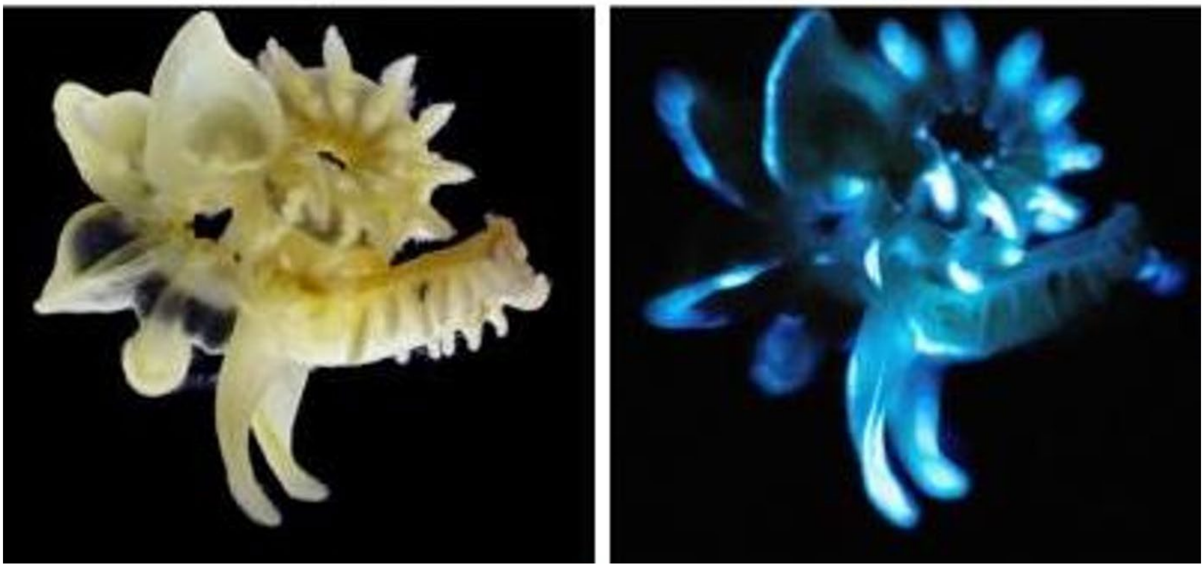

Figure 1.8. *Chaetopterus* under natural light (left), and in the dark (right) showing blue bioluminescent slime it produces. Photo credit: David Liittschwager.

The duration of light emission from *Chaetopterus* varies from a few seconds to several minutes, depending on the stimulus and environmental conditions. Martin and Anctil (1984) observed that the luminescent mucus can glow for several minutes before fading. Recent studies suggest that ferritin, known for its efficiency and reduction capabilities, supplies the long-lasting energy required for light production (Deheyn, 2020). Additionally, a study by Deheyn (2020) isolated a new protein from the worm mucus, distinct from ferritin, which exhibits an affinity for iron and, when reintroduced to the mucus, enhances light production. These findings imply that this protein plays an important role in the bioluminescence mechanism, although its exact identity remains to be determined. While the luminescence in *Chaetopterus* is usually blue, it sometimes reveals green fluorescence as it decays (Branchini et al., 2014). Additionally, *Chaetopterus* livers have been found to contain an orange, fluorescent material in their liver (Harvey, 1926).

Despite extensive research, the exact reasons for bioluminescence in *Chaetopterus* remain largely speculative. Bioluminescence in *C. variopedatus* has been hypothesised to serve various functions, though some argue it may have no specific visual function and could be merely a metabolic by-product of a reaction (Mirza et al., 2020). One hypothesis suggests that luminescence is used as a lure at night to attract zooplankton toward the mucous net, facilitating predation for larvae (Mirza et al., 2020). Additionally, Grove et al. (2000) suggested that light emission from the tissue might help maintain water circulation within the worm's tube by deterring commensal crabs, which may interfere with its feeding strategies.

Furthermore, body luminescence may be a predator defence reaction, with flashes employed to startle or distract predators, like other light-emitting animals (Burkenroad, 1943; Sumida & Case, 1983 Martin & Anctil, 1984; Mirza et al., 2020). Early studies (e.g., Enders, 1909; Berrill, 1928) have shown that *Chaetopterus* can protrude their anterior or posterior sections from their tubes and regenerate lost body segments, except for the 13th segment, which emits little to no light. This has led to suggestions that other body parts might emit light to act as sacrificial tags, allowing the worm to survive partial destruction by diverting attacks from critical areas (Mirza et al., 2020). Further research is needed to understand the purpose of bioluminescence in *Chaetopterus*, including identifying natural predators to validate these theories.

1.2.5.9 Commensal associations

Chaetopterus are known to form commensal associations, as their tubes offer suitable shelter with a continuous flow of oxygen-rich water for various organisms (Martin & Britayev, 2018). Approximately 28 species of symbionts have been reported living inside tubes of *Chaetopterus* (Petersen & Britayev, 1997). These relationships often involve complex communities that are not well understood. A study by Britayev et al. (2017) revealed that crab and nudibranch symbionts of *Chaetopterus* frequently share a host and live in pairs, thereby partitioning resources. This arrangement allows the species to coexist within the tubes, forming a tightly packed community (Britayev et al., 2017). Similarly, Werding & Hiller (2019) found two species of crabs co-habiting the tubes of *Chaetopterus* in Vietnam waters.

The commensal organisms associated with *Chaetopterus* are predominantly decapods and polychaetes but also include fish, gastropods, and ostracods (Britayev et al. 2017; Eagar & Read, 2004). For example, the pea crab *Pinnixia chaetopterana* is commonly found inhabiting the tubes of *C. variopedatus* in North America (Grove et al., 2000; McDermott, 2005) and several species of polychaete have been described living inside the tubes of *Chaetopterus* in Vietnam and Chilean Patagonia (Britayev & Martin 2018; Werding & Hiller, 2019; Soto & San Martin, 2018). In New Zealand, a new species of Ostracoda, *Pontocypria omaha*, was found attached to the head of *Chaetopterus* in Omaha Bay (Eagar & Read, 2004). And more recently, a new species of nudibranch, *Tenellia chaetopterana* sp. nov., was discovered within an unidentified *Chaetopterus* in Vietnam (Ekimova et al., 2019). This discovery was the first documented example of a symbiotic association between a mollusc and an annelid host among cladobranch sea slugs.

Grove et al. (2000) conducted a study examining the impact of symbiotic crabs on the pumping activity and growth rates of *C. variopedatus*, revealing that these crabs do not significantly hinder host growth and reproduction. Although worms hosting *Polyonyx gibbesi* were generally larger than those hosting *Pinnixa chaetopterana*, this difference was likely attributed to competition between crab species for hosts rather than varying effects on host growth.

1.2.5.10 Habitat preference and environmental tolerances

Chaetopterus are widely distributed in temperate to tropical waters, occurring in regions such as North America, Caribbean, Japan, the Galapagos Islands, Australia, New Zealand, and Hong Kong (Dean et al, 2012; Enders, 1909; Thompson & Schaffner, 2001; Tricklebank et al., 2001; Sun & Qui, 2014, Moore et al., 2020). The *Chaetopterus* genus includes not only benthic and epibenthic species but also a pelagic species, *Chaetopterus pugaporcinus* (Osborn et al., 2007), discovered in Monterey Bay, California, at depths ranging from 875 to 3000 m. However, the life stage of these specimens remains uncertain as no reproductive organs were present in any of the specimens collected.

Chaetopterus variopedatus are frequently observed in higher concentrations in calm waters with soft, fine sediment, showing a preference for sheltered bays and harbours over areas with rough wave action and coarse sands (Mirza et al., 2020). Early observations by Enders (1909) noted that *C. variopedatus* thrives in environments characterised by extensive sand flats, often covered with dense diatom growth or regularly exposed to currents rich in diatoms. Other studies emphasise the species' need for stable salinity levels, as fluctuations can affect their physiological functions (Rouse & Pleijel, 2001). Adequate oxygenation of water is crucial for supporting both aeration and nutrient transport (Enders, 1909; Acosta, 2001).

Some *Chaetopterus* sp. found in the Pacific region such *Chaetopterus charlesdarwinii* and *Chaetopterus aduncus* sp. nov are characterised by a parchment tube attached to hard substrates (Nishi et al., 2009). On the Argentine Sea's shelf-break, *Chaetopterus antarcticus*, typically an infaunal species, unexpectedly exhibited significant settlement on *Zygochlamys patagonica* scallops in 2007 (Bremec & Schejter, 2019). This variability in life habits was attributed to fishing disturbances, highlighting the adaptations of *C. antarcticus* in response to environmental changes caused by human activities.

In northeastern New Zealand, *C. chaetopterus-A* typically inhabits sandy-shell and sandy-foul environments at depths ranging from 15 to 35 m (Acosta, 2001; Tricklebank et al., 2001), with documented occurrences as deep as 69 meters near the Poor Knight Islands (Brook et al., 2001). These worms display both infaunal and epifaunal behaviours, being found buried in sediment with exposed tube ends or attached to hard substrates like foul and gravel; they have also been observed attached to horse mussels *Atrina zelandica* (Acosta, 2001; Tricklebank et al., 2001). This dual behaviour is uncommon within the *Chaetopterus* genus (Tricklebank et al., 2001). *Chaetopterus chaetopterus-A* has demonstrated the ability to form large aggregations or mats in various locations in New Zealand, such as the Hauraki Gulf, Whangarei Harbour, and Great Barrier Island (Tricklebank et al., 2001).

Tricklebank et al. (2001) examined the relationship between *C. chaetopterus-A* distribution and environmental factors such as depth, exposure, and sediment type. Their findings indicated that exposure level had no significant influence on *Chaetopterus* presence, but a strong association was observed with sediment type, particularly with coarse substrates like sand, sand-gravel, and shell-gravel. Dense aggregations of *Chaetopterus* were found on these sediment types, although the mean percent cover of tube mats did not differ significantly among them. However, the widest variation in percent cover was recorded on sandy substrates. Depth was also a significant factor, with most *Chaetopterus* mats occurring between 20 and 34 m, although individuals were found across a broader depth range, from shallow waters (<10 m) to deeper areas exceeding 40 m (Tricklebank et al., 2001).

Though Tricklebank et al. (2001) provided valuable insights on *Chaetopterus* within a New Zealand context, there remains limited information on the specific habitat preferences that differentiate the two species found in the Marlborough region. Tubeworms and horse mussels constitute the most abundant filter-feeder communities in QCS and Tory Channel (Ribo et al., 2021). The distribution of these communities is influenced by factors such as depth, slope, sediment type, and rugosity, with contributions of approximately 55%, 14%, 11%, and 8%, respectively (Ribo et al., 2021). It is understood that infaunal specimens of *Chaetopterus* are common in sheltered bays with muddy-sand bottoms, while epifaunal communities are primarily found along cobble-dominated coastlines of the QCS (Davidson et al., 2019). Dense mats of tube worms are found in shallow soft sediments (>15 m) in East Bay and scattered throughout the bays of the inner and mid QCS (e.g., Grove Arm, Aratawa Bay; pers. obs., 2022). They have also been observed in exposed areas of the outer QCS, where they occur in high densities on rocky subtidal reefs (e.g., The Twins; pers. obs., 2023).

1.2.5.11 Population and community dynamics

While benthic suspension feeders play a crucial role in shallow estuarine and coastal ecosystems, global research specifically focused on the population and community dynamics of *Chaetopterus* is relatively limited compared to broader ecological studies exploring their habitat preferences and behaviours. Majority of these key studies have been carried out in Chesapeake Bay, USA where large populations of *C. variopedatus* are present (e.g., Schaffner, 1990; Thompson & Schaffner, 2000, 2001).

Global examples

Thompson and Schaffner (2001) investigated the population dynamics and secondary production of *C. variopedatus*, highlighting its role as a significant component of estuarine ecosystems. Their study found that worm densities varied seasonally, with peaks following summer recruitment periods and population densities ranging from 30 to 1000 individuals/m². Recruitment success showed notable interannual variation, best described by a two-cohort model distinguishing juveniles and adults. High secondary production was primarily driven by rapid growth and tube construction in newly settled recruits during summer. These interannual differences in production were closely linked to recruitment success, reinforcing *Chaetopterus*' role in carbon, nutrient, and energy flow within estuarine ecosystems and its influence as a benthic suspension feeder.

Schaffner (1990) further explored species diversity patterns in Chesapeake Bay's estuarine benthic communities, demonstrating positive interactions involving *C. variopedatus* and other species, particularly epifaunal organisms. These interactions contributed to enhanced species richness and diversity, suggesting that habitat quality is strongly influenced by the presence or absence of ecosystem engineers like *Chaetopterus*, rather than solely by environmental factors.

Like *C. variopedatus*, *Chaetopterus pergamentaceus* plays a crucial ecological role in the soft-sediment subtidal benthic communities of lower Chesapeake Bay (Thompson & Schaffner, 2000). Research on this species revealed temporal variations in population dynamics that significantly influence the role of benthic suspension feeders in ecosystem function. A key finding was a strong negative correlation between juvenile growth rates and total population density during periods of fluctuating recruitment, highlighting the importance of incorporating *Chaetopterus* into models of carbon, nutrient, and energy flow in benthic ecosystems.

Similarly, research by Zalmon (2011) in southern California demonstrated the influence of *Chaetopterus* worm mats on the distribution and abundance of associated fish populations.

Larger aggregations of *Chaetopterus* provided habitat for increased densities of specific fish species, particularly *Rhinogobiops nicholsii* and *Chaenopsis alepidota*. The spatial arrangement of worm patches influenced fish population patterns, with smaller and younger fish occupying the edges while larger, dominant individuals controlled the centre. Fish densities declined substantially beyond 20 cm from the worm patches, indicating a strong habitat dependency on these biogenic structures. Notably, smaller patches with less than 50% tube coverage failed to support *C. alepidota*, further emphasising the importance of patch size and structure in maintaining associated communities. This study underscores how *Chaetopterus* aggregations enhance habitat complexity in soft-sediment systems, fostering biodiversity and contributing to the patchy distribution of associated organisms.

Finally, one of the earliest studies on *Chaetopterus* by Enders (1909) observed that male and female individuals of *C. variopedatus* commonly cohabit the same shoals, usually spaced one to three meters apart. Interestingly, females predominated, making up approximately 60% of the collected specimens. Collectively, these studies highlight the substantial ecological influence of *Chaetopterus* across diverse marine environments, emphasising its role as a critical biogenic habitat-forming species that significantly shapes population structures and community dynamics.

New Zealand examples

There are no comprehensive studies focusing on the population and community dynamics of *Chaetopterus* in New Zealand. While Tricklebank et al. (2001) and Acosta (2001) offer insights into some aspects of these dynamics, these studies are limited in their scope and are localised to northeastern New Zealand. The factors contributing to the distribution of *Chaetopterus* in New Zealand and the ecological implications of dense populations of this species remain unclear. Below is a summary of the findings regarding the population dynamics of *C. chaetopterus-A* from these studies.

The extensive aggregations or mats of *Chaetopterus* observed in northeastern New Zealand are distinctive within the genus, covering substrate areas larger than 20 m^2 and reaching thicknesses of 10-20 cm (Acosta, 2001). Although, those *Chaetopterus* mats within the Marlborough Sounds are believed to extend in area well beyond what has previously been recorded (pers. obs., 2023; Figure 1.9). Similar mat-forming traits have been noted in other studies; for instance, an undescribed *Chaetopterus* species in the eastern English Channel forms dense biotope mats with *Lanice conchilega* (Rees et al., 2005), and *Chaetopterus longipes* often forms aggregations in the Galapagos Islands (Nishi et al., 2009). However, these aggregations are typically smaller compared to those observed in northeastern New Zealand (Acosta, 2001). In newly colonised areas, juveniles formed mats like adults, covering rocky areas, attaching to boulders, and are infaunal on sandy and gravelly ripples (Acosta, 2001). In the same study, juvenile *Chaetopterus* were also noted adhering to an artificial reef (HMNZS Waikato) in Tutukaka Bay. In established *Chaetopterus* habitats, newly recruited individuals settled within them, creating layers up to 20 cm thick (Acosta, 2001). Mortality has been associated with storms and large swells, which can dislodge their mats from the substrate and transport tubes to beaches or other underwater locations (Acosta, 2001). While most washed-up tubes are empty, live individuals have been occasionally found inside them (Acosta, 2001).

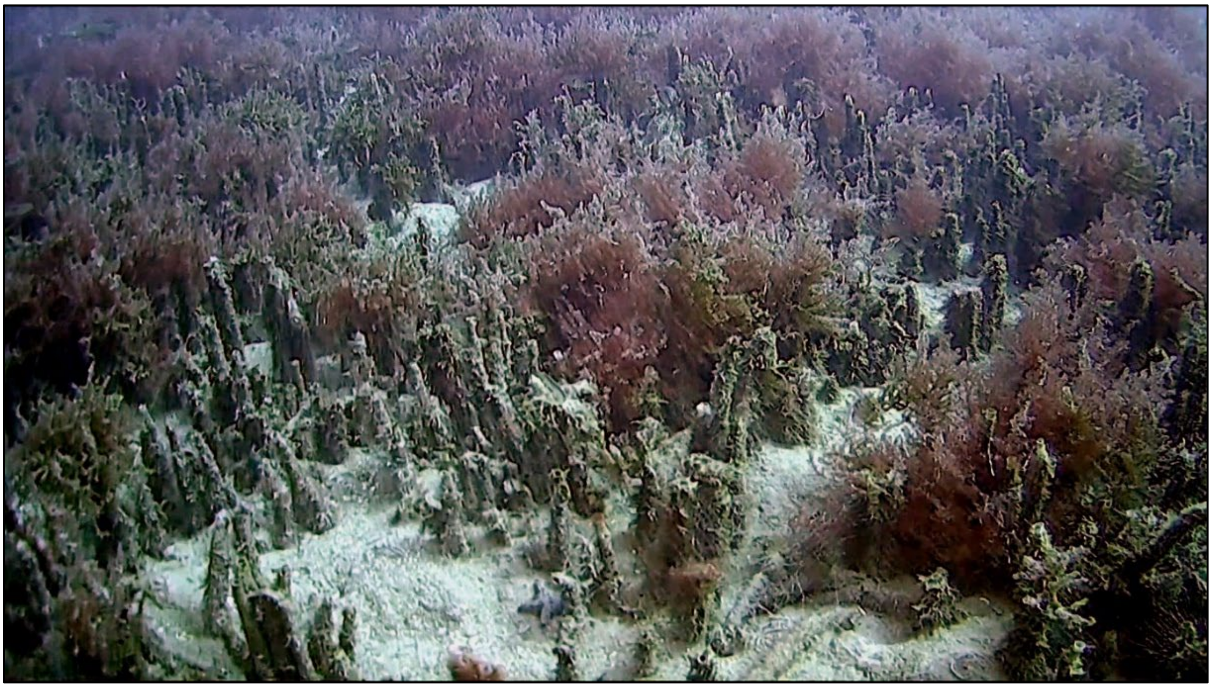

Figure 1.9. *Dense Chaetopterus mats showing attached epiphytic algae within East Bay, Queen Charlotte Sound, 2024.*

Nelson et al. (2012) identified *C. chaetopterus-A* as a prominent polychaete species within subtidal rhodolith beds at Te Miko Reef and Kahuwhera Bay in the Bay of Islands (Figure 1.10). This species was found at multiple sites, contributing to the higher biodiversity and invertebrate abundance observed in rhodolith beds compared to adjacent non-rhodolith areas. The study also recorded significant temporal variation in the abundance of molluscs, polychaetes, and flatworms. While *Chaetopterus* was among the polychaetes contributing to the faunal composition, its specific temporal dynamics were not explicitly addressed, leaving room for further exploration of its role in these biodiverse habitats.

Though the ecological significance of *Chaetopterus* tube worm mats in New Zealand remains unexplored, other Chaetopterids in New Zealand have been shown to support a diverse range of species. Jones et al. (2018) identified *Phyllochaetopterus phyllochaetopterus-A* as a key contributor to distinctive soft sediment biogenic habitats at shelf depths along the east coast of the South Island. Closely related or possibly identical species form similar biogenic habitats in shallow waters (< 50 m) within parts of the Marlborough Sounds (Jones et al., 2018).

In New Zealand, there are still gaps in our understanding of the population and community dynamics of *Chaetopterus*. These gaps include details on population size and structure, growth rates, reproductive cycles, influences of water quality, community composition, and commensal associations.

Figure 1.10. *Chaetopterus chaetopterus-A collected from Kahuwhera Bay, showing how it binds rhodoliths. Adapted from Nelson et al. (2012).*

1.2.5.12 Predators

There remains limited formal documentation on the primary predators within the *Chaetopterus* genus. Shucksmith et al. (2006) demonstrated correlations between plaice (*Pleuronectes platessa*) densities and the abundance of *Chaetopterus*, which are recognised as important prey items. Similarly, the uneven distribution of *Chaetopterus* mats has been associated with fluctuations in fish trawl catches in the English Channel, where plaice (*Pleuronectes platessa*) biomass was found to be highest in trawl tows containing tube mats (Rees et al., 2005).

A study analysing the trophic resources of dominant benthic microfauna in the lower Chesapeake Bay found that the commonly occurring *C. variopedatus* did not appear to be a significant prey item for fish (Huggett, 1987). While not directly available to higher trophic levels, *C. variopedatus* is an important structuring agent in the region, increasing habitat complexity and possibly adding biogenic refuges for infauna (Schaffner, 1990).

While there are no formal reports documenting predation on *Chaetopterus* in New Zealand, anecdotal evidence suggests that a variety of fish target this species. For example, blue cod (*Parapercis colias;* Figure 1.11) and blue moki (*Latridopsis ciliaris*) are commonly found among *Chaetopterus* beds and have been observed preying on *Chaetopterus* within QCS (C. Rayes, personal. communication, May 13, 2021). Additionally, schools of snapper (*Pagrus auratus*) have been observed feeding on newly recruited populations of *Chaetopterus* at Goat Island (Acosta, 2001). Tubes of *Chaetopterus* have also been found in the gut contents of reef fish such as red pigfish (*Bodianus unimaculatus*), sandager's wrasse (*Goris sandageri*), scarlet wrasse (*Pseudolabrus miles*), and crimson cleaner fish (*Suezichthys aylingi*) from the Mokohinau Islands (Acosta, 2001).

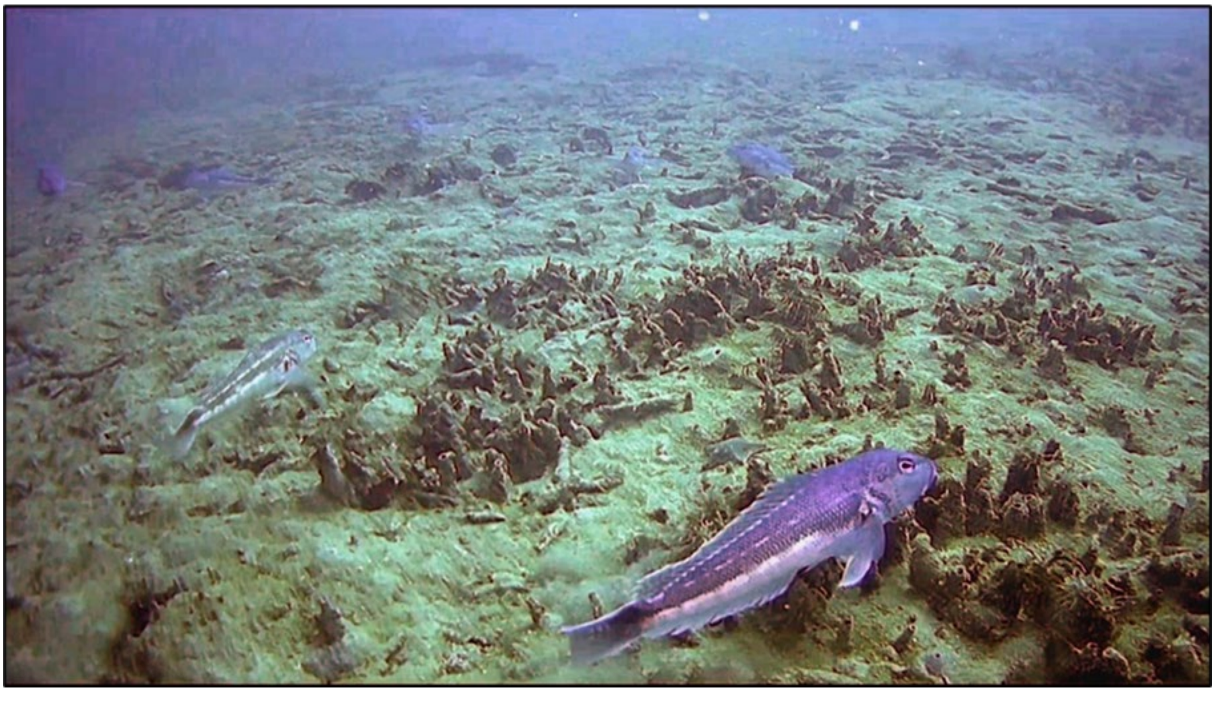

***Figure 1.11**. Blue cod (P. colias) within Chaetopterus habitat in East Bay, Queen Charlotte Sound, 2023.*

1.2.5.13 Human uses

Recent advancements in understanding the bioluminescent mechanisms and commensal relationships of *Chaetopterus* have opened promising applications in various fields, including medical biotechnology, bioengineering, and environmental monitoring. The following highlights these key findings.

A study by De Meulenaere et al. (2017) found that the ferritin in *C. variopedatus* exhibits catalytic performance nearly eight times faster than that of human ferritin. This finding has significant implications for biotechnology and human health, particularly in managing iron metabolism for those with iron deficiencies (Wood, 2017).

Additionally, a newly isolated protein from the worm's mucus, which shows an affinity for iron and enhances light production, has the potential to facilitate the use of light in applied biotechnology and bioengineering (Deheyn, 2020). Other studies suggest that the unique qualities of *Chaetopterus* tubes, characterised by their strength, flexibility, and thermomechanical properties, offer valuable insights for developing advanced materials in conventional pipe technology (Brown & McGee-Russell, 1971; Shah et al., 2014).

Eca et al. (2013) explored the symbiotic relationships involving *Chaetopterus* and their potential applications in biomonitoring. Their study highlighted how the presence of symbionts, such as *Polyonyx gibbesi*, within *C. variopedatus* tubes enhances the monitoring of environmental contaminants across various benthic compartments. Both the polychaete and its commensals accumulate trace and major elements, providing valuable insights into metal distribution and contamination in marine environments. This relationship offers significant advantages over bivalves, which typically do not accumulate metals such as aluminium and magnesium in high concentrations (Eca et al., 2013).

1.2.5.14 Pathways of spread

Natural dispersion

Several studies have demonstrated that *Chaetopterus* species are broadcast spawners, with most fertilised eggs becoming planktonic (e.g. Enders, 1909; Acosta, 2001; Rouse & Pleijel, 2001; Nishi & Rouse, 2007). Their primary mode of dispersal is through the planktonic larval stage, which can remain in the water column for extended periods, sometimes exceeding three months (Scheltema, 1971, 1974). Early observations by Petersen (1984) suggested that *Chaetopterus* is not a monotypic genus, as previously thought, but represents a species complex containing at least ten species. While maps have shown the distribution of *C. variopedatus* larvae in the north and tropical Atlantic (Scheltema, 1974), there is no direct evidence of a pan-oceanic distribution of adult individuals (Bhaud, 1998). Furthermore, Bhaud (1998) suggested that successful planktonic life and recruitment do not always lead to the continuation of the life cycle into adulthood, meaning the presence of larvae does not necessarily predict the distribution of adult populations within this species.

In addition to broadcast spawning and extended planktonic stages, *Chaetopterus* may also disperse through mechanisms influenced by environmental factors. Acosta (2001) suggests that storms could facilitate dispersal in northeastern New Zealand. This is supported by observations of live *Chaetopterus* in tubes washing up on broad-scale sampling stations, as well as the species' ability to regenerate lost body parts and repair damaged tubes, enabling them to survive and spread after being displaced.

Further research is required to determine the duration of planktonic development, the potential distance of larval dispersal, the ability of *Chaetopterus* larvae to actively select settlement sites, and the impact of storm events on dispersal patterns within New Zealand marine environments.

Human-mediated spread

Few studies address the human-mediated spread of *Chaetopterus*. While specific evidence for dispersal by vessels is lacking, ocean shipping is a significant vector for transporting species outside their native range (Ruiz and Carlton, 2003; Drake and Lodge, 2007). In New Zealand, records from the Marine Biosecurity Porthole (MBP 2024) highlight the ability of *C. chaetopterus-A* to attach to vessel hulls. However, no studies focusing specifically on these traits confirm any instances of vessel-mediated dispersal.

Other means of human-mediated spread of *Chaetopterus* have been linked to commercial fishing practices, particularly benthic trawling. Tricklebank et al. (2001) found a strong association between scallop fishing areas and dense *Chaetopterus* aggregations in New Zealand, suggesting that similar habitat preferences and scallop fishing activities might contribute to the spread of *Chaetopterus*. Disturbances from scallop dredging is likely to break and scatter *Chaetopterus* worms thus increasing the population through regenerative processes (Acosta, 2001; Tricklebank et al., 2001; Schejter et al., 2008). Fishers discarding bycatch, including *Chaetopterus*, overboard also likely aids in their dispersal (Rintoul, personal communication, as cited in Tricklebank et al., 2001). However, additional studies are needed to confirm these assumptions, particularly regarding the influence of fishing practices in facilitating the spread of *Chaetopterus* in New Zealand.

1.2.5.15 Impacts associated with Chaetopterus

Impacts on the environment

Various studies have highlighted the significant environmental impacts of *Chaetopterus* species on marine ecosystems, both positive and negative. However, research specific to these impacts within a New Zealand context remains limited.

Aggregations of tube-building organisms play a significant role in sediment stabilisation, leading to modifications within their immediate environment (Somaschini, 1993; Callaway, 2006). Likewise, mats of *Chaetopterus* in northeastern New Zealand have shown to stabilise sediments in areas with strong currents, altering sediment dynamics and potentially changing species abundance and composition (Acosta, 2001). This stabilisation affects nutrient and oxygen exchange rates, possibly reducing dissolved oxygen and nutrient levels in the water column and competing with other filter feeders such as scallops (Acosta, 2001). Furthermore, a study by Smith et al. (1995) highlights its ability to stabilise large amounts of sand, shell grit, and sediment, resulting in impacts to coral and algal dynamics in northern New South Wales, Australia.

Smith and Harriott (1998) described the formation of dense aggregations of *Chaetopterus* in the Solitary Islands Marine Park, with patches containing up to 14,000 ind./m^2. These aggregations were observed to smother branching corals, resulting in significant coral mortality and changes in benthic community structure. Furthermore, Nishi et al. (2009) documented the gregarious nature of *C. longipes*, which forms similar large clusters on hard substrates and coral rubble in regions including the Eastern Pacific, Sri Lanka, and Japan.

In New Zealand, an ecological report by Davidson et al. (2022) noted the impact of dense *Chaetopterus* populations on native tube worm mounds *Galeolaria hystrix* in QCS. Observations suggest that *Chaetopterus* colonisation in this area negatively affects *G. hystrix* by smothering and outcompeting them. In addition, adult and juvenile scallops (*P. novaezelandiae*) in parts of northeastern New Zealand have been found almost completely covered by *Chaetopterus*, which may impact their distribution and viability (Acosta, 2001).

Schaffner (1990) found that *C. variopedatus* significantly impacts species abundance and composition in estuarine communities, with positive associations among species being more common than negative ones. The presence of *C. variopedatus* enhanced species richness and diversity, particularly among near-surface fauna. This enhancement is due to the polychaete's role in providing refugia and influencing larval settlement (Huggett, 1987; Schaffner, 1990). Additionally, the sandy tubes of *Chaetopterus* also provide habitats for other macroinvertebrate species, enhancing local biodiversity temporarily (Smith & Harriott, 1998).

Benthic suspension feeders are critical components of many shallow estuarine and coastal ecosystems (Herman, 1993; Petersen, 2004). The role of *C. variopedatus* was demonstrated to significantly influence organic matter transformation, storage, and cycling processes in these environments (Thompson & Schaffner, 2001). The study by Thompson & Schaffner (2001) showed that the worm population required 35%–100% of the estimated annual net water column community production/m^2 in a region of lower Chesapeake Bay. Though, *Chaetopterus* exhibited considerable interannual variations in density, biomass, and secondary production, indicating that its impact on ecosystem stability can vary significantly. Consequently, *C. variopedatus* can be considered a keystone species, akin to bivalves, with its effects on food web dynamics and nutrient cycling being crucial for maintaining ecosystem function and stability (Thompson & Schaffner, 2001).

Impacts to industry

Marine biosecurity

Previous reports have indicated that its rapid spread, ability to colonise diverse habitats, and capacity to reach high population densities are typical characteristics of an invasive or introduced species (Tricklebank et al., 2001; Davidson et al., 2022). Additionally, their ability to rapidly colonise disturbed habitats suggests that *Chaetopterus* poses an uncertain biosecurity risk. However, neither *Chaetopterus* species in New Zealand are considered a high biosecurity risk and they are listed as non-target species in the National Marine High Risk Site Surveillance programme (MPI, 2023). According to Çinar (2013), there is only one recorded instance of *Chaetopterus* invasion, which occurred in Hawaii. Here, *Chaetopterus* was documented as abundant on reef flats, growing on algae *Dietyosphaeria eavernosa* and coral rubble (Bailey-Brock, 1979). Unfortunately, details regarding any impacts to industry are limited, and there are no studies available on their broader ecological effects.

Scallop fisheries

Previous reports (e.g., Tricklebank et al., 2001; MPI, 2012; Picton Regional Forum, 2022) have raised concerns about the potential negative impact of *Chaetopterus* on local scallop (*P. novaezelandiae*) populations, which are significant for both commercial and recreational fisheries in New Zealand. Furthermore, declining scallop densities in the region led to the closure of the southern scallop (SCA 7) fishery in 2017, which remains closed, exacerbating public concerns. While international studies provide some insights into these interactions, comprehensive ecological impact studies regarding scallops in New Zealand are lacking. The following summarises key findings, investigations, and studies regarding the associations of scallops and *Chaetopterus*.

Between 1999 and 2003, the Coromandel scallop fishery in New Zealand faced challenges from both "black gill disease" and a proliferation of *Chaetopterus* (MPI, 2012). It was suggested that these worms competed with suspension filter feeders like scallops and obstructed fishing operations by rapidly clogging dredges (MPI, 2012). However, the extent of the impact of *Chaetopterus* on scallops during this period was not investigated or quantified. Following this, the fishery showed improvement until 2012 (MPI, 2012), but experienced a significant decline in biomass in 2021, leading to a full closure in 2023. The reasons for the decline are yet to be determined but were likely a combination of both fishing and non-fishing related stressors (Fisheries NZ, 2023). *Chaetopterus* continues to be found in inshore trawl surveys including off the West Coast South Island, Tasman Bay, Golden Bay and the Marlborough Sounds (Williams et al., 2019, 2021; MacGibbon et al., 2024).

In 2019, a commercial diver reported to Fisheries New Zealand a sudden proliferation of *Chaetopterus* in QCS, coinciding with observations of dead and dying *P. novaezelandiae* (MPI, 2019). Samples of both the worms and scallops were analysed to determine the tubeworm's species, identified as *C. chaetopterus-B* and evaluate the scallops' health. Health assessments of scallops from within and outside the worm beds showed an inflammatory response in both groups, more pronounced in those within the worm beds, though no infectious agents were linked to this inflammation. Virus-like particles were found in the digestive glands of both groups, a common but not well-understood occurrence in New Zealand scallops. No definitive cause for the scallop mortality was determined, and the investigation was subsequently closed (MPI, 2019).

As previously mentioned, a study by Bremec and Schejter (2019) observed a significant relationship between the *C. antarcticus* and the scallop *Z. patagonica*. In 2007, a large settlement of *C. antarcticus* on scallops was recorded. Analysis of 892 scallops revealed that more than 50% were encrusted with *C. antarcticus*. Over time, the presence of these epibiotic worms decreased, with no occurrences noted from 2013 to 2015. Infaunal worms were observed consistently throughout the entire study area for the duration of the research. The variability in *C. antarcticus* life habits, such as shifting to epibiotic behaviour, was suggested to be attributed to intensive soft sediment disturbances due to trawling, which forced the worms to select alternative settlement substrates (Bremec & Schejter, 2019).

In a study conducted in the Patagonian scallop management area of the Argentine Sea, Schejter et al. (2019) compared fished areas and exclusion zones from 1998 to 2002, revealing significant impacts of *C. variopedatus on Z. patagonica*. While species richness and composition remained similar in both areas, scallop biomass was consistently higher in exclusion zones. Over time, fished areas exhibited signs of moderate disturbance, with increased predator biomass and decreased populations of fragile species. Based on analysis of species (dis)similarities, the founding of *C. variopedatus* in fishing grounds contributed to differences in scallop biomasses between fished areas and exclusion zones (Schejter et al., 2019).

Aquaculture

There are no documented cases of *Chaetopterus* affecting the aquaculture industry. However, recent anecdotal evidence suggests that *Chaetopterus* can attach to mussel farm infrastructure in Tasman Bay, New Zealand (Figure 1.12; S. Cunningham, personal communication, June 1, 2023). While their presence on dropper lines may not impact adult mussels, it is thought to potentially create issues for younger size classes at the primary and interseed stages (S. Cunningham, personal communication, June 1, 2023). Biofouling is typically seen as a major issue for bivalve aquaculture, leading to additional costs that can constitute up to 30% of the industry's total operational expenses (Lacoste & Gaertner-Mazouni, 2015). The presence of epibionts not only impacts the species they colonise but can also disrupt the ecological functioning of the area (Ropert & Goulletquer 2000; De Sá et al., 2007). Furthermore, the transfer of equipment and shellfish seed-stock among growing regions, have been identified to be likely mechanisms for human-mediated spread of other unwanted species (Fletcher, 2014).

Figure 1.12. *Before (left) and after (right) showing Chaetopterus tubes persisting on mussel farm ropes following machine processing, Tasman Bay, 2023. Photo credit: S. Cunningham.*

Biofouling

Chaetopterus can also attach to vessel hulls, wharf structures, and other man-made installations, contributing to biofouling (Relini et al., 2001; Inglis et al., 2006; Moura et al., 2008). In the Port of Whangarei, *C. chaetopterus-A* has been recorded as a dominant component of fouling assemblages on wharf piles (MPI, 2017; MPI, 2023) and is frequently found attached to vessel hulls (pers. obs., 2023; MPB, 2024). Although studies on their impact and associated costs are limited, their presence are likely to contribute to maintenance expenses and operational challenges for maritime infrastructure.

1.2.6 Conclusion

The current understanding of *Chaetopterus* covers various aspects of their biology, ecology, and potential applications, yet significant challenges and gaps remain. Despite extensive research on their cell biology, reproduction, filter-feeding mechanisms, bioluminescence, and commensal relationships, the taxonomy and systematics of the Chaetopteridae family are still underdeveloped. The lack of comprehensive taxonomic revisions has led to ongoing uncertainties and ambiguities in species identification and classification. Additionally, the biogeographical distribution and evolutionary origins of *Chaetopterus* species remain complex and not fully understood, complicating efforts to monitor their spread and ecological impact.

The overall impact of *Chaetopterus* on marine ecosystems is context-dependent, with both beneficial and detrimental effects. Its role as an ecosystem engineer can enhance biodiversity and stabilise sediments, but its competitive behaviour and fluctuating population dynamics can also disrupt native species and ecosystem stability. Moreover, the ecological roles and impacts of *Chaetopterus*, particularly in relation to their interactions with other species and their environment, need more comprehensive studies, especially concerning their influence on valuable species like scallops.

In summary, further research on *Chaetopterus*, particularly within a New Zealand context, is crucial due to the significant uncertainties and potential risks associated with these species. Their ability to outcompete native species, combined with natural and human-mediated dispersion, high fecundity, broad habitat preferences, wide environmental tolerance, and tendency to attach to vessel hulls, poses considerable threats if they are non-indigenous. Conversely, they are also considered keystone species, providing essential biogenic habitats that support diverse marine life. Although their extensive spread within the Top of the South region limits certain management options, addressing these ambiguities through focused research is vital for understanding their broader ecological implications, assisting in decision-making, and exploring potential applications of *Chaetopterus* in marine ecosystems.

1.2.6.1 Research priorities for the Top of the South region

Comprehensive mapping and long-term monitoring:

- Conduct detailed spatial mapping of *C. chaetopterus-A* and *C. chaetopterus-B* populations within the Top of the South region, focusing on areas like QCS, Pelorus Sound, and surrounding bays.

- Implement long-term monitoring programmes to identify population trends, range expansions, and seasonal dynamics, particularly in response to environmental variables such as depth, sediment composition, and hydrodynamics.

Impacts on community dynamics and benthic interactions:

- Investigate the role of *Chaetopterus* tube mats in structuring macroinvertebrate communities, specifically examining changes in species abundance, diversity, and functional composition.
- Assess interactions between *Chaetopterus* and native benthic fauna (e.g., *P. novaezelandiae*, *G. hystrix*), including potential competition for space, resource availability, and impacts on recruitment and survival rates.

Effects on seafloor functioning and sediment properties:

- Quantify the physical and chemical changes in benthic sediments caused by *Chaetopterus* tube mats, including organic matter accumulation, sediment particle size distribution, and oxygen penetration depth.
- Evaluate how these sediment modifications influence key ecological processes, such as nutrient cycling, organic matter turnover, and sediment stability, and their broader implications for benthic ecosystem functioning.

Population dynamics, growth rates, and reproductive cycles:

- Examine growth rates, reproductive cycles, and dispersal traits of *Chaetopterus* in New Zealand waters to better understand their population structure and recruitment patterns.
- Investigate factors influencing larval settlement and survival, including hydrodynamic conditions, substrate availability, and anthropogenic disturbances.

Influence of fishing practices on Chaetopterus colonisation and spread:

- Assess the role of bottom trawling, dredging, and other fishing activities in facilitating *Chaetopterus* dispersal through fragmentation, resuspension, and regeneration of individuals.
- Evaluate the spatial overlap between fishing grounds and *Chaetopterus* aggregations to determine potential risks to benthic habitats and fisheries resources.

Impacts on aquaculture infrastructure and operations:

- Monitor mussel farm infrastructure, including dropper lines and equipment, to determine the extent of *Chaetopterus* colonisation and biofouling impacts on bivalve growth and survival, particularly at the primary and interseed stages.
- Investigate the potential for *Chaetopterus* to spread via aquaculture operations, including the transfer of seed stock and farming equipment between growing regions.

Chapter 2: Effects of *Chaetopterus* on sediment properties and benthic biodiversity in East Bay, Marlborough Sounds

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2.1 Introduction

Understanding the factors that shape soft-sediment ecosystems is essential for assessing changes in benthic biodiversity and habitat stability. In coastal environments, species that modify the seafloor can have profound ecological impacts by altering sediment properties and influencing species interactions. Among these, tube-building polychaetes such as *Chaetopterus* play a particularly influential role by stabilising sediments, increasing organic matter accumulation, and creating structurally complex microhabitats (Passarelli et al., 2012; Thomsen et al., 2011). In areas where *Chaetopterus* forms dense aggregations, its presence may significantly reshape soft-sediment communities, affecting both physical habitat conditions and the composition of associated fauna (Schaffner, 1990).

The ecological effects of *Chaetopterus* are shaped by environmental gradients and population dynamics. For instance, Thompson and Schaffner (2000) demonstrated that *C. pergamentaceus* populations in Chesapeake Bay exhibit density-dependent growth patterns influenced by depth, circulation eddies, and food availability. These findings highlight how environmental conditions regulate population structure and growth, ultimately determining the species' role as an ecosystem engineer. Given this complexity, understanding the interactions between *Chaetopterus* and its environment is essential for predicting its broader ecological impacts.

Like other tube-building polychaetes, *Chaetopterus* constructs rigid tubes that extend above the sediment surface, enhancing habitat complexity, stabilising sediments, and modifying biogeochemical cycling (Thomsen et al., 2011; Passarelli et al., 2012). These effects are dependent on population density and patch size, with larger aggregations amplifying stabilisation effects and promoting species richness (Zühlke, 2001; Hughes, 2009; Rabaut, 2009; Thomsen et al., 2011). Similar impacts have been observed in *L. conchilega* populations, where tube formations influence sedimentary processes and enhance stability beyond their immediate physical extent (Borsje et al., 2014).

In addition to their structural role, *Chaetopterus* and other tube-building polychaetes alter sediment properties through their feeding, burrowing, and tube-building activities. Their tubes bind sediment particles, reducing erosion and increasing stability (Thomsen et al., 2011; Passarelli et al., 2012). These structures also promote the accumulation of fine particles and organic material by trapping detritus and faecal deposits, resulting in microscale habitat heterogeneity (Schaffner, 1990; Passarelli et al., 2012). Changes in sediment compaction, permeability, and nutrient retention influence microbial activity, sediment-water exchanges, and broader benthic processes (Hughes, 2009; Thomsen et al., 2011).

While *Chaetopterus* aggregations can enhance biodiversity by providing habitat for certain species, they may also exclude organisms less tolerant of compacted or organic-rich sediments (Schaffner, 1990; Passarelli et al., 2012). High-density tube mats can monopolise space, limiting the abundance of other organisms and altering community structure (Rabaut, 2009; Tricklebank et al., 2001). In Chesapeake Bay, *C. variopedatus* mats have been shown to increase suspension feeders and detritivores while reducing mobile predators and deposit feeders, illustrating their dual role as biodiversity enhancers and agents of exclusion (Schaffner, 1990).

Despite extensive international research on *Chaetopterus*, its ecological role in New Zealand remains poorly understood. The only significant study, conducted by Tricklebank et al. (2001), provided baseline data on distribution, habitat preferences, and densities in northeastern New Zealand, where populations have been recorded at over 120 ind./0.02 m^2 in sandy and shell gravel sediments at depths of 15 to 30 m (Tricklebank et al., 2001; Acosta, 2001). However, while *Chaetopterus* has formed dense aggregations in the Marlborough Sounds, the extent and density of these populations remain unquantified, leaving significant knowledge gaps regarding their ecological influence in this region (Tricklebank et al., 2001).

Beyond sedimentary effects, *Chaetopterus* aggregations may alter macrobenthic community composition, including interactions with economically important species such as scallops. Observations suggest that scallop fishing activities may facilitate the spread of *Chaetopterus*, raising concerns about both ecological and economic consequences (Tricklebank et al., 2001). Given the species' increasing presence in New Zealand waters, further research is needed to assess its role as an ecosystem engineer and its potential impact on soft-sediment habitats.

2.1.1 Study aims and hypotheses

This study investigates the ecological role of *Chaetopterus* in New Zealand's soft-sediment ecosystems, addressing key knowledge gaps in the literature. Focusing on East Bay in the Marlborough Sounds, where dense aggregations have recently been observed, this research examines the effects of *Chaetopterus* tube mats on sediment properties, macroinvertebrate community composition, and ecosystem processes using functional trait analysis. Through structured sampling at multiple sites, this study will:

- Assess the impacts of *Chaetopterus* tube mats on sediment properties, including grain size distribution and organic matter content.
- Examine macroinvertebrate community composition, functional traits, and diversity within and outside *Chaetopterus* mats.
- Identify key environmental drivers such as *Chaetopterus* density, depth, and sediment composition that mediate the observed effects.

The following hypotheses guide this research:

1. **Sediment modification**: *Chaetopterus* tube mats significantly alter benthic sediment properties by increasing organic matter content and the proportion of fine particles. These changes arise from sediment stabilisation and the enhanced retention of fine and organic material facilitated by the physical structure of the tubes.
2. **Community composition and ecosystem functioning:** *Chaetopterus* tube mats alter macroinvertebrate community composition and enhance taxonomic diversity by creating complex biogenic habitats. These changes, driven by environmental factors such as tube presence, water depth, organic matter content, and sediment mud content, promote surface-dominated ecological processes while reducing deeper sediment mixing and its associated benthic functions.

This study takes an integrative approach, linking environmental drivers to sedimentary impacts and functional trait analyses to assess ecosystem-level consequences. By addressing these knowledge gaps, this research advances the understanding of *Chaetopterus* as an ecosystem engineer in New Zealand and contributes insights applicable to soft-sediment ecosystem management globally.

2.2 Methodology

2.2.1 Study area and site selection

The Marlborough Sounds encompass approximately 4,000 km², extending northward into Cook Strait—a passage 22–60 km wide that separates New Zealand's North and South Islands. This region comprises a network of deep, drowned river valleys formed through river incision followed by marine inundation and flooding, driven by post-glacial sea level rise and land subsidence (Lauder, 1987; Hume et al., 2016). At the southeastern edge of this network lies Queen Charlotte Sound (QCS), spanning ~40 km in length and up to 26 km in width, with water depths ranging from the coastline to approximately 350 m (Ribo et al., 2021). Sediments within the Marlborough Sounds are predominantly muds in the deep valleys, grading into silts and very fine sands, while coarser substrates are characteristic of the outer regions of QCS and Tory Channel (Boyce, 1971; Lewis & Mitchell, 1980; Lauder, 1987).

Furthermore, the Marlborough Sounds support various subtidal biogenic habitat-forming species, including giant kelp forests (*Macrocystis pyrifera*), horse mussel beds (*A. zelandica*), tubeworm towers (*G. hystrix*), rhodolith or maerl beds, and communities of bryozoans, hydroids, and sponges (Davidson et al., 2011). The extent and distribution of these biogenic habitats have significantly declined from their historical ranges (Handley, 2015, 2016) and remain vulnerable to ongoing damage (Davidson & Richards, 2015). Today, these habitats primarily persist in high-current areas, where conditions such as strong tidal currents limit bottom-trawling and dredging activities, prevent anchoring, and resuspend fine terrigenous sediments. In other locations, biogenic habitats endure either because of the protective characteristics of the surrounding topography, marine reserves, or, in some cases, by chance (Willis, 2013; Urlich & Handley, 2020).

Key economic activities in QCS include ecotourism, recreational fishing, finfish aquaculture, forestry, and maritime operations such as port facilities, passenger ferries, and cargo shipping. These industries coexist with the region's natural and cultural values, making sustainable management of the marine environment crucial.

The study was conducted in East Bay (41°09′S, 174°18′E; Figure 2.1) within Queen Charlotte Sound (QCS), New Zealand. Although "East Bay" refers to three different bays in QCS, this research specifically focuses on outer East Bay, also known as Onauku Bay. The area's distinctive geological features and ecological richness make it well-suited for investigating the effects of *Chaetopterus* on sediment properties and benthic communities. Its spatial extent and environmental heterogeneity provided sufficient separation between sampling sites, enabling the capture of environmental variability while minimising spatial autocorrelation.

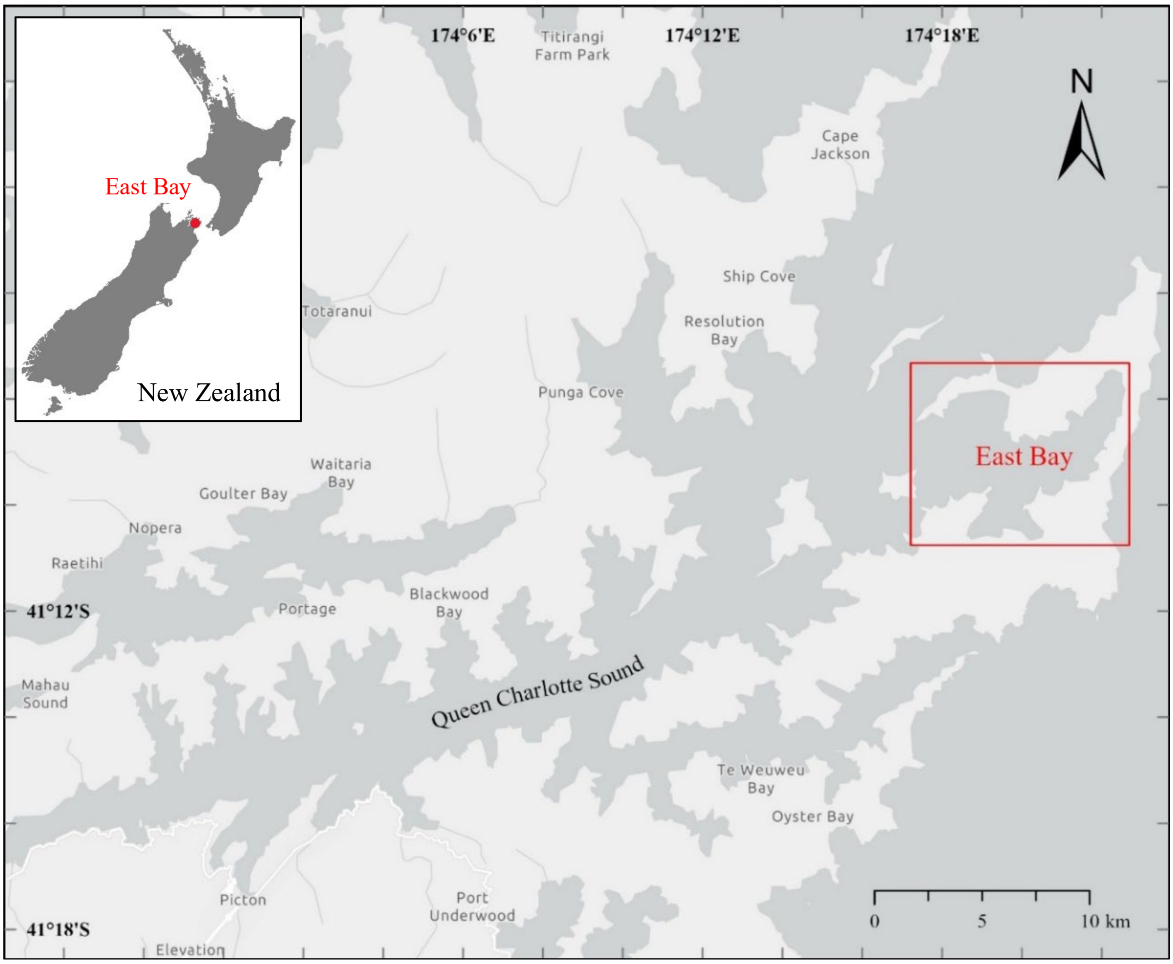


Figure 2.1. *Map depicting the study site location in East Bay, Marlborough Sounds, New Zealand.*

To assess *Chaetopterus* impacts, study sites were selected based on key environmental variables, including tube mat density, water depth, sediment composition, and exposure. These gradients are critical for understanding how *Chaetopterus* modifies benthic habitats and influences macroinvertebrate communities (Schaffner, 1990; Thompson & Schaffner, 2001). Site selection ensured a robust comparison between *Chaetopterus*-dominated areas and corresponding control sites without *Chaetopterus*, directly addressing the study's objective of quantifying its role as an ecosystem engineer in New Zealand's soft-sediment habitats.

Sampling locations were strategically spaced to minimise confounding environmental overlap while encompassing a broad range of conditions to assess how *Chaetopterus* impacts vary across different contexts. The presence of extensive *Chaetopterus* mats in the area allowed for randomised sampling replication, with control sites paired and depth strata matched to reduce variability from external factors. This approach ensured consistent comparisons across environmental gradients, enhancing the reliability and robustness of the study's findings.

By integrating spatial and environmental variability, the study design enabled a comprehensive assessment of *Chaetopterus* effects on sediment properties and macroinvertebrate communities. The structured site selection process accounted for local environmental factors, strengthening the ecological validity of the study's conclusions.

2.2.2 Sampling methodologies and data acquisition

2.2.2.1 Field sampling methods

Two ecological surveys were conducted in East Bay to gather data for this study. The first survey, conducted on 18 August 2023, focused on identifying suitable study sites by locating established *Chaetopterus* tube worm beds and corresponding control sites. A low-definition drop-camera system was employed in conjunction with the mapping software TUMONZ Professional, integrated with a Simrad NSS16 EVO3S chart plotter and echosounder. This setup was connected to an externally mounted Lowrance Point-1 high-sensitivity GPS, enabling real-time visualisation of drop-camera imagery with GPS accuracy to within ± 5 m.

A total of 51 drop-camera photographs were captured during this survey, from which ten control sites and ten *Chaetopterus* sites were selected (Figure 2.2; Table 2.1). Site details and field notes are provided in Appendix B. *Chaetopterus* sites were characterised by visible *Chaetopterus* tubes with an estimated minimum percent cover of 20% and a spatial extent of at least 1,000 m^2. Control sites were located at least 10 m beyond the boundary of the *Chaetopterus* habitat and within 50 m of their corresponding *Chaetopterus* sites, ensuring they were positioned within the same depth strata to minimise variability from confounding environmental factors.

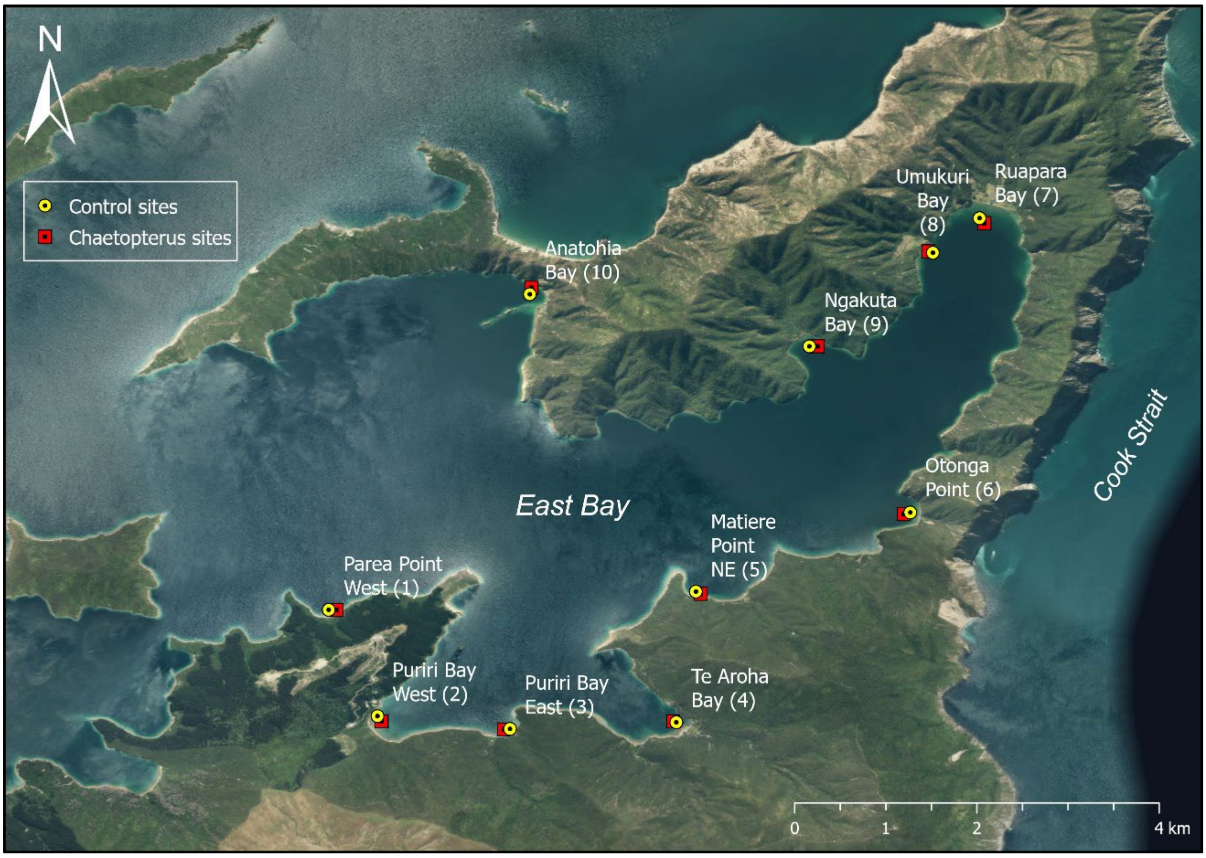


***Figure 2.2**. Study locations including site names and corresponding site number (shown in brackets) within East Bay, Marlborough. Yellow circles represent study control sites (*Chaetopterus *absent), and red squares illustrate* Chaetopterus *habitat sites.*

***Table 2.1**. Latitude and longitude coordinates of control and* Chaetopterus *sampling sites.*

Site number	Control habitat	*Chaetopterus* habitat
1	41°09.860'S 174°18.397'E	41°09.861'S 174°18.443'E
2	41°10.489'S 174°18.686'E	41°10.519'S 174°18.711'E
3	41°10.565'S 174°19.470'E	41°10.568'S 174°19.434'E
4	41°10.526'S 174°20.454'E	41°10.519'S 174°20.436'E
5	41°09.752'S 174°20.570'E	41°09.765'S 174°20.598'E
6	41°09.283'S 174°21.838'E	41°09.293'S 174°21.801'E
7	41°07.540'S 174°22.248'E	41°07.570'S 174°22.277'E
8	41°07.745'S 174°21.972'E	41°07.737'S 174°21.945'E
9	41°08.280'S 174°21.241'E	41°08.279'S 174°21.289'E
10	41°07.991'S 174°19.587'E	41°07.952'S 174°19.597'E

The second survey was conducted on the 19th and 20th of November 2023 to collect macroinvertebrate and sediment samples from the 20 selected sites. Each site was precisely located using GPS, with a drop line and buoy deployed to mark its position. Prior to sampling, site conditions were verified through SCUBA surveys. Divers conducted a systematic swim within a 20-meter radius, capturing video footage to assess the area, covering approximately 1,256 m² per site.

Depth at each sampling site was recorded by SCUBA divers using Shearwater Perdix 2 TI dive computers and adjusted to Mean High Water Springs (MHWS) based on the time of day and tidal range. On 19 November 2023, low tide occurred at 5:08 am (0.1 m) and high tide at 12:09 pm (1.6 m). On 20 November 2023, low tide occurred at 5:52 am (0.1 m) and high tide at 12:53 pm (1.6 m).

Sampling was carried out using a 1 m² quadrat divided into 16 equal sections, which was randomly placed on the seafloor for each of the five replicates at each site (Figure 2.3). SCUBA divers collected five sediment samples from random locations within each quadrat, targeting the top 20 mm of sediment. Samples were extracted using labelled 60 mL Luer Lock syringes fitted with rubber stoppers. The five samples from each quadrat were combined to create a single composite sediment sample representing that replicate. Replicates were spaced approximately 5 m apart. A total of 50 composite sediment samples were collected, with five replicates taken from each of the ten sites within both habitat groups. All samples were frozen at -21°C for later analysis.

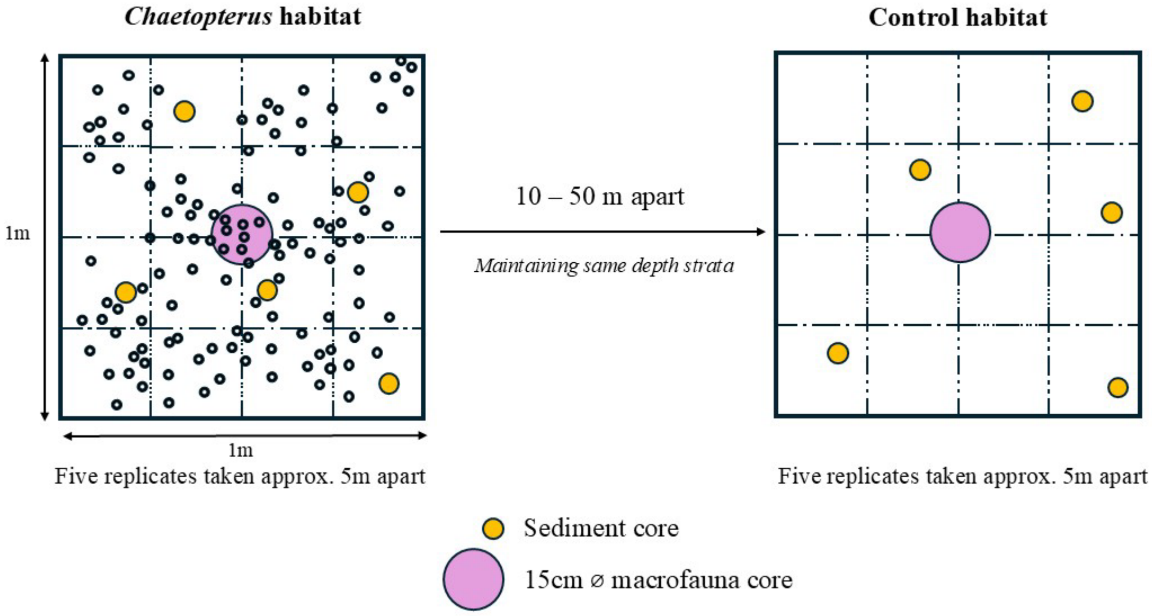


Figure 2.3. *Schematic representation of sampling site methodology for* Chaetopterus *and control habitats.*

Macrofauna samples were collected using a 15 cm diameter core, taken to a depth of 15 cm. Each core was positioned near the centre of the quadrat, capped, and placed in a catch bag. Five macrofauna cores were collected per site, resulting in 50 cores per habitat group and 100 cores overall. At sites with dense but patchy *Chaetopterus* beds, the quadrat was placed within an area of at least 20% tubeworm coverage to ensure sampling was representative of dense patches. Macrofauna samples were sieved using a 0.5 mm mesh to isolate macroinvertebrates for analysis. *Chaetopterus* specimens were carefully removed from their tubes due to preservation challenges. Tubes were cut laterally with scissors to expose live worms, and abundance data were recorded in situ.

Macroinvertebrates were preserved in a diluted isopropyl solution (~70% isopropyl alcohol mixed with seawater) and identified to the lowest possible taxonomic resolution by experts. Preserved organisms were counted, and taxonomic classifications followed the standards of the World Register of Marine Species (WoRMS; https://www.marinespecies.org/). Where applicable, macrofaunal core data were incorporated into analyses. Site averages for macroinvertebrate abundance (mean abundance per core; $n = 5$) were calculated to represent community composition in specific analyses. These data were used for visualisations, including non-metric multidimensional scaling (nMDS) plots.

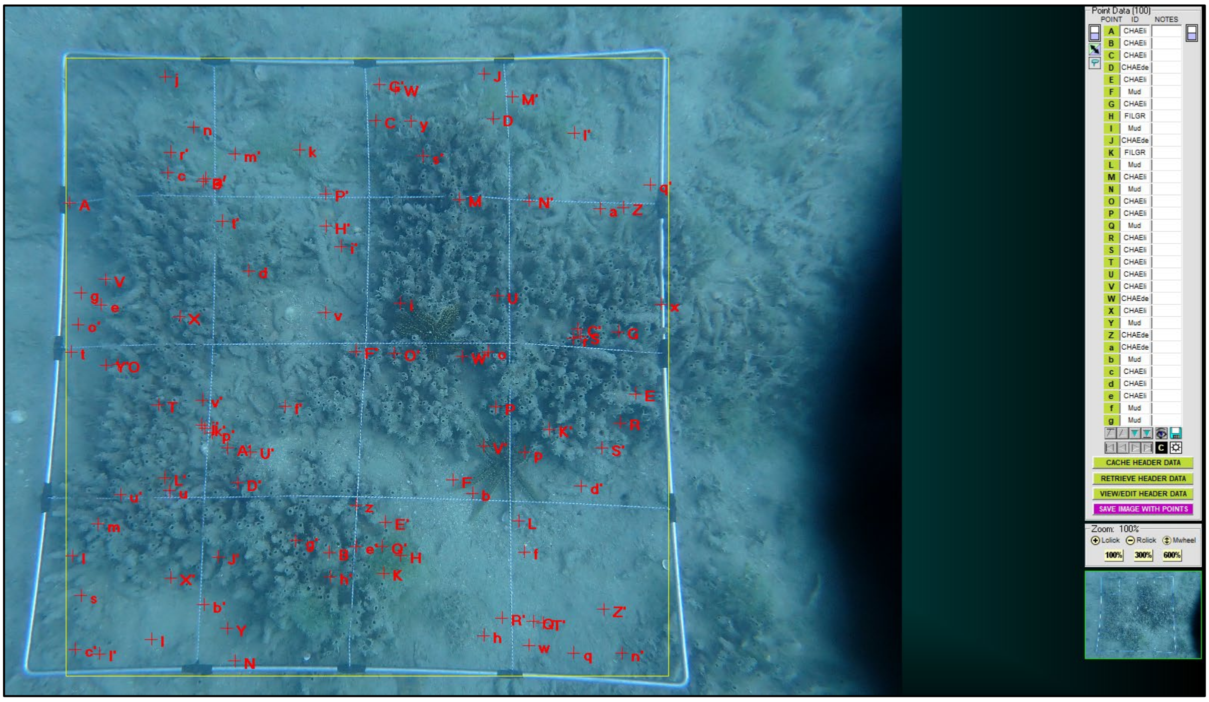
2.2.2.2 Sediment analysis

In the laboratory, each sediment sample was analysed for median grain size (µm), mud content (% < 63 µm), silt content (% grains 2–63 µm), and organic content (% AFDW) using standard sediment analysis methods, following the Wentworth scale (Wentworth, 1922). Sediments were digested with 10% H_2O_2 until bubbling ceased, and grain size was determined using a Malvern Mastersizer 3000, which measures particle sizes ranging from 0.1 to 3,500 µm. The percentage of ash-free dry weight (AFDW%) was determined to quantify the organic content of sediment samples. Sediments were dried in pre-weighed crucibles at 105°C for 24–48 h until a constant weight was achieved, and the dry weight (DW) was recorded. The dried samples were then combusted in a muffle furnace at 500–550°C for 4–6 h to remove organic material. After cooling in a desiccator to prevent moisture absorption, the ash weight (AW) of each sample was measured. The ash-free dry weight (AFDW) was calculated as the difference between the dry weight and ash weight (e.g., AFDW (g) = DW (g) − AW (g)). The percentage of AFDW relative to the sample's dry weight was then determined.

***Data Adjustment Note:** For *Chaetopterus* Site 8, silt and mud values from Quadrat 1 were identified as outliers through visual inspection and were excluded from the analysis. Averages for these parameters were recalculated using data from the remaining four samples at the site to maintain the reliability and accuracy of the dataset for subsequent analyses.

2.2.2.3 Chaetopterus percent cover

Chaetopterus percentage cover, defined as the visible coverage of protruding tubes, was recorded at each of the *Chaetopterus* sites. SCUBA divers captured labelled, oblique photographs of each quadrat, where macrofauna and sediment samples were collected. Percentage cover was quantitatively assessed using CPCe (Coral Point Count with Excel extensions; Kohler & Gill, 2006; Figure 2.4), a software tool originally developed for analysing coral cover in transect photographs and now widely used to estimate population statistics of marine benthic communities from still images (Carleton & Done, 1995).



Point Data (100)

POINT	ID	NOTES
A	CHAEli	
B	CHAEli	
C	CHAEli	
D	CHAEde	
E	CHAEli	
F	Mud	
G	CHAEli	
H	FILGR	
I	Mud	
J	CHAEde	
K	FILGR	
L	Mud	
M	CHAEli	
N	Mud	
O	CHAEli	
P	CHAEli	
Q	Mud	
R	CHAEli	
S	CHAEli	
T	CHAEli	
U	CHAEli	
V	CHAEli	
W	CHAEde	
X	CHAEli	
Y	Mud	
Z	CHAEde	
a	CHAEde	
b	Mud	
c	CHAEli	
d	CHAEli	
e	CHAEli	
f	Mud	
g	Mud	

***Figure 2.4**. Quadrat image (from* Chaetopterus *site nine, replicate three) analysed with CPCe software to quantify percent cover. Points were classified as live or dead* Chaetopterus*, epibiota, or bare substrate, with only live tubes included in the final calculation.*

To ensure robust calculations of percent cover, 100 spatially random points were distributed across each quadrat image, as the density of points per unit area is crucial for reliable estimates (Pante & Dustan, 2012). Features underlying these points were manually identified and classified into four categories: 'live' *Chaetopterus* (i.e., sedentary, upright tubes), dead *Chaetopterus* (i.e., broken or lying on their side), conspicuous epibiota (e.g., sea cucumbers, sea stars), and bare substrate. Coverage statistics were generated using CPCe and exported to Microsoft Excel for further analysis. Only sedentary, upright *Chaetopterus* tubes were considered in the final calculation of percent cover.

2.2.2.4 Functional group assignment

The application of functional trait diversity has become a widely used method for assessing how organisms contribute to ecosystem functioning. Functional roles of species, such as productivity, nutrient cycling and sediment stabilisation, often offer a more accurate indication of ecosystem stability compared to traditional biodiversity metrics that rely solely on taxonomic diversity (Costello et al., 2015; Beauchard et al., 2017; Villnäs et al., 2018). To evaluate the potential effects of environmental changes on ecosystem function in relation to *Chaetopterus*, each taxon was assigned to a specific functional group based on the framework developed by Greenfield et al. (2016). This functional group index incorporates traits related to morphology, feeding mode, and behavioural characteristics that influence the stability of marine ecosystems.

Trait data were obtained from the New Zealand Trait Database (NZTD; Lam-Gordillo et al., 2023) and supplemented with information from WoRMS and other relevant studies where gaps existed. When taxa displayed multiple possible trait profiles (e.g., different amphipod species belonging to different functional groups), the most dominant functional group was assigned. In addition, a deliberate effort was made to ensure taxa with larger body sizes were kept distinct, as organisms with larger body sizes often play disproportionate roles in ecological processes (Hildrew et al., 2007; Norkko et al., 2013). Two taxa (*Bivalve unid.* and *Polychaeta unid.*) were excluded from the functional group analysis due to insufficient taxonomic resolution for reliable trait assignment. Their exclusion is unlikely to significantly influence the results, as *Bivalve unid.* accounted for only two individuals in the control habitat and none in the *Chaetopterus* habitat. Similarly, *Polychaeta unid.* was absent from the control sites, with just one individual recorded in the *Chaetopterus* habitat. Together, these taxa contributed only 0.06% to the total abundance across both habitats. In total, 148 species were categorised into 37 distinct functional groups (Table 2.2).

Table 2.2*. Summary of defining traits for each functional group (1 – 37) guided by the methods described by Greenfield et al (2016). The most abundant species from each functional group are given as examples.*

FG #	**Description of traits**	**Example species**
1	Calcified, deposit/suspension feeding, top 3cm, freely mobile, burrower, small/medium	*Leptomya retiaria retiaria*
2	Calcified, deposit/suspension feeding, top 3cm/deep, freely mobile, burrower, large	*Gari stangeri*
3	Calcified, suspension, attached/above surface, freely mobile, attached	*Musculus impactus*
4	Calcified, suspension feeding, above surface/top 3cm, burrower, small/medium	*Corbula zelandica*
5	Calcified, suspension feeding, top 3cm/deep, freely mobile, burrower/free living, medium/large	*Tawera spissa*
6	Calcified, deposit/grazer, above surface/top 3cm, freely mobile, burrower/free living, large	*Philine auriformis*
7	Calcified, predator/scavenger, top 3cm/deep, freely mobile, free living, large	*Cominella adspersa*
8	Calcified, grazer, above surface, freely mobile, large	*Leptochiton inquinatus*
9	Soft-bodied, deposit/suspension/predator, top 3cm/deep, freely mobile, free living, large	Nereidae
10	Soft-bodied, deposit/suspension feeding, above surface/top 3cm/deep, freely mobile, tube dweller	*Polydora* sp.
11	Soft-bodied, deposit/suspension feeding, above surface/top 3cm/deep, freely mobile, burrower, large	*Phascolosoma annulatum*
12	Soft-bodied, suspension feeding, attached/above surface, attached/sedentary, large	*Cnemidocarpa bicornuta*
13	Soft-bodied, suspension feeding, above surface/top 3cm/deep, tube dweller	Sabellidae
14	Soft-bodied, suspension feeding, top 3cm, freely mobile, burrower/free living, large	*Epigonichthys hectori*
15	Soft-bodied, suspension feeding, top 3cm, freely mobile, attached, small	*Edwardsia* sp.
16	Soft-bodied, suspension feeding, top 3cm, sessile/attached, tube dwelling, medium size	Ampharetidae
17	Soft-bodied, suspension feeding, top 3cm/deep, freely mobile, tube dweller	*Euchone pallida*
18	Soft-bodied, suspension feeding, top 3cm/deep, sedentary, free living, medium	*Phoronus* sp.
19	Soft-bodied, deposit/predator/scavenger, top 3cm, freely mobile	Syllidae
20	Soft-bodied, deposit feeding, above surface/top 3cm/deep, freely mobile, tube dwelling, small/medium	Maldanidae
21	Soft-bodied, deposit feeding, above surface/top 3cm, freely mobile, free living/burrower, large	*Chiridota nigra*
22	Soft-bodied, deposit feeding, top 3cm/deep, tube dwelling, small/medium	*Prionospio multicristata*
23	Soft-bodied, deposit feeding, top 3cm/deep, freely mobile, burrower, small/medium	Cirratulidae
24	Soft-bodied, deposit feeding, below surface, freely mobile, tube dwelling, small/medium	*Barantolla lepte*
25	Soft-bodied, predator/scavenger, above surface/top 3cm, freely mobile	Hesionidae
26	Soft-bodied, deposit/grazer/predator, top 3cm, freely mobile, free living	Amphipoda (unid.)
27	Soft-bodied, predator/scavenger, top 3cm/deep, freely mobile, free living/burrower	Goniadidae
28	Rigid, deposit/suspension feeding, above surface/top 3cm, freely mobile, free living	Ophiuroidea
29	Rigid, suspension/predator, above surface/top 3cm/deep, freely mobile, tube dwelling, medium	Tanaidacea
30	Rigid, suspension/scavenger, above surface, freely mobile, free living, small	*Petrolisthes novaezelandiae*
31	Rigid, suspension feeding, attached, sedentary, attached, large	*Galeolaria hystrix*
32	Rigid, suspension feeding, above surface/top 3cm, freely mobile, burrower/free living/tube, small/medium	*Nebalia* sp.
33	Rigid, suspension feeding, top 3cm/deep, freely mobile, burrower, large	*Upogebia danai*
34	Rigid, deposit/predator, above surface/top 3cm, freely mobile, free living	*Phoxocephalidae*
35	Rigid, deposit feeding, top 3cm/deep, freely mobile, free living/burrower	*Filhollianassa filholi*
36	Rigid, predator/scavenger, above surface, freely mobile	*Halicarcinus cookii*
37	Rigid, predator/scavenger, top 3cm/deep, freely mobile, free living/burrower	Anthuridea

2.2.3 Statistical analyses

2.2.3.1 Benthic macrofauna

Species accumulation curves (SACs) were created by plotting the cumulative number of species against the number of samples within each habitat group (control and *Chaetopterus*) to assess sampling adequacy and determine whether species richness was sufficiently captured within the collected data. To account for the inherent heterogeneity of benthic communities, the Ugland, Gray, and Ellingsen (UGE) distribution method (Ugland et al., 2003) was employed.

A series of univariate analyses were performed to assess similarities and differences in community structure across habitats (Clarke et al., 20145). These analyses utilised raw macroinvertebrate data to calculate metrics such as abundance, species richness, the Shannon-Wiener diversity index, and Pielou's evenness index.

To examine variations in community structure between habitats, non-metric multidimensional scaling (nMDS) was applied (Clarke et al., 2015). Bray-Curtis dissimilarities were calculated from square-root-transformed macroinvertebrate abundance data to reduce the influence of highly abundant species while preserving community structure patterns. Community relationships between habitats and sites were visualised in ordination space using nMDS, with habitat specified as a grouping factor. Site centroids were positioned in two- or three-dimensional space based on their dissimilarities, where the relative distances between sites represent the degree of variation in macrofaunal community composition.

To assess the robustness of the ordination, a RELATE analysis was performed, comparing the similarity matrix of community composition with the Euclidean distances between points in the nMDS plot. This test validated the accuracy of the nMDS in effectively representing dissimilarities in community structure across habitats (Clarke et al., 2015).

A two-factor Permutational Multivariate Analysis of Variance (PERMANOVA) was used to assess the effects of habitat (control vs. *Chaetopterus*) on community structure and to evaluate the interaction between habitat and site. Both analyses were performed using Bray-Curtis dissimilarity matrices derived from square-root-transformed macroinvertebrate abundance data to account for variation in species abundances. Statistical significance was assessed using 999 permutations, ensuring robust results. In addition, an ANOSIM (Analysis of Similarities) test was also performed to further evaluate the significance of habitat effects on macroinvertebrate community composition. This analysis used Bray-Curtis similarity measures to compare differences between control and *Chaetopterus* sites.

A PERMDISP (Permutational Analysis of Multivariate Dispersions) analysis was used to evaluate variability in community composition between habitats. PERMDISP distinguishes whether observed differences in community structure arise from variation in the mean composition of groups (as tested by PERMANOVA) or differences in within-group variability. The analysis calculates the average distance of individual samples from their group centroid in ordination space (e.g., Bray-Curtis dissimilarity) and assesses differences in dispersion using a permutation test (e.g., 999 permutations). This ensures that differences in dispersion are not artifacts of group size or sampling effort. In this study, PERMDISP was applied to square-root-transformed macroinvertebrate abundance data to test for homogeneity of dispersions across habitats, complementing the PERMANOVA results by determining whether differences in community composition were influenced by within-group variability.

To further evaluate overall similarities in community structure between habitat sites and determine the contribution of individual species to observed similarities and dissimilarities, a similarity percentage (SIMPER) analysis was performed on the square-root-transformed abundance data. SIMPER analysis, using Bray-Curtis dissimilarities, decomposes the contributions of each species to overall community patterns, identifying the species that are most influential in driving observed similarities and differences between groups (Clarke et al., 2015).

2.2.3.2 Statistical modelling

Environmental drivers of community structure

To investigate how macroinvertebrate community structure responded to environmental gradients, distance-based linear modelling (DISTLM) was applied, using species abundance data and environmental variables from all samples. This multivariate linear regression method is widely used for examining relationships between biological data and multiple predictor variables (McArdle & Anderson, 2001). DISTLM, based on Bray-Curtis dissimilarities, was conducted to identify the environmental variables that explained the most variation in macroinvertebrate community structure within East Bay. Since mud encompasses silt proportions, it was used as a proxy for fine sediment categorisation in the DISTLM modelling, allowing silt to be excluded to prevent redundancy in the analysis.

To minimise the dominance of abundant species while maintaining the model's ability to detect differences in community structure, abundance data were square-root transformed (Clarke & Gorley, 2014; Clarke et al., 2015). Environmental variables were normalised prior to analysis to ensure comparability. Pearson's correlations checked for multicollinearity among environmental predictors to prevent redundancy and misrepresentation in the DISTLM results. Given the relatively small sample size, the DISTLM analysis employed a forward selection procedure, using the Corrected Akaike Information Criterion (AICc) to identify key environmental predictors driving variation in community structure. The analysis was conducted separately for control and *Chaetopterus* sites to account for potential differences in environmental drivers between habitats. This approach allowed for a more detailed understanding of how environmental variables uniquely influence community structure within each habitat type. To ensure robustness, backward and stepwise selection procedures were also tested, both yielding similar final models based on AIC criteria.

This study conducted most analyses, including DISTLM and other multivariate methods, using PRIMER V7.0.13 (Clarke et al., 2015) with the PERMANOVA+ add-on (Anderson et al., 2008). Two-factor PERMANOVA tests were applied to assess habitat effects and to evaluate interactions between site and habitat. These tests were used to examine variation in environmental variables across habitats, as well as *Chaetopterus* abundance and percent cover within *Chaetopterus* sites.

Assessing changes to ecosystem functionality

To examine differences in ecosystem function associated with *Chaetopterus* presence, functional group (FG) abundance data were analysed using a combination of multivariate techniques. Square-root-transformed FG abundance data were used to reduce the dominance of highly abundant groups while still preserving the ability to detect meaningful patterns in less abundant groups.

A non-metric multidimensional scaling (nMDS) plot was constructed based on Bray-Curtis dissimilarities to visualise differences in FG community structure between control and *Chaetopterus* habitats. The stress value of the nMDS plot was assessed to confirm its reliability in representing multidimensional relationships within a two-dimensional space.

A BEST analysis was performed to identify the functional groups that best explained the observed patterns in community composition. Using Bray-Curtis similarity, the analysis identified combinations of functional groups that showed the strongest correlation with differences between control and *Chaetopterus* habitats. Key functional groups (n = 5) were subsequently overlaid as vectors on the nMDS plot to visualise their influence on community structure across the two habitat groups. Furthermore, to quantify the contributions of individual functional groups to differences in community composition, a SIMPER analysis was performed. Bray-Curtis dissimilarities were used to assess the relative importance of each functional group to overall dissimilarity, with those contributing cumulatively to 70% of the total dissimilarity considered most influential. This provided insight into the specific functional groups driving differences between control and *Chaetopterus* habitats.

Statistical differences in FG community composition were tested using PERMANOVA on square-root-transformed FG abundance data. A two-factor PERMANOVA was performed to evaluate the effects of habitat (control vs. *Chaetopterus*) on FG composition, as well as to assess the effects of site and the interaction between site and habitat. To complement this analysis, a PERMDISP was used to assess differences in within-group variability between habitats, ensuring that observed patterns were not confounded by differences in dispersion.

2.3 Results

2.3.1 *Chaetopterus* characteristics in East Bay

The distribution of *Chaetopterus* across the habitat sites, assessed through percent cover of visible tubes and the number of live individuals collected within cores, varied considerably (Table 2.3). On average (± SE), 16.8 ± 1.6 ind. core^{-1} were recorded with an inter site range 6.0 ± 1.9 to 34.0 ± 10.2 ind. core^{-1}. The percent cover of *Chaetopterus* tubes averaged 65% ± 3, with a range of 20% to 98%. A correlation analysis revealed a weak negative relationship between tube cover and individual abundance ($r = -0.286$), indicating that sites with greater tube cover did not necessarily have higher densities of live individuals.

2.3.2 Environmental variables

Water depth ranged from 2.2 m to 13.0 m across all sites, with an overall mean of 7.6 ±0.4 m (Table 2.3). Although depth differences between habitats were minimal and not statistically significant, significant environmental variation was observed among sites ($p = 0.001$) and in the habitat × site interaction (Table 2.4; $p = 0.001$).

Median grain size (MGS) differed slightly between habitats, with control sites having a mean of 245 µm ±16 and a range of 141 µm to 658 µm, compared to a mean of 216 µm ±16 and a range of 19 µm to 513 µm in *Chaetopterus* habitats (Table 2.3). While the difference in MGS between habitats was not statistically significant, site-level variability was significant, indicating that local environmental factors strongly influenced grain size distributions (Table 2.4).

Mud content (% grains < 63 µm) was significantly higher in *Chaetopterus* habitats compared to control sites (Table 2.4; $p = 0.001$). Control sites had a mean mud content of 7.7% ±0.5, with values ranging from 2.9% to 16.6%, whereas *Chaetopterus* habitats averaged 19.8% ±2.0, with a broader range of 6.2% to 61.6% (Table 2.3). The significant habitat × site interaction (Table 0.4) suggests that the extent of increased mud content varied depending on site-specific factors.

Organic matter content was also significantly higher in *Chaetopterus* habitats compared to control sites (Table 2.4; $p = 0.014$). Control sites exhibited organic matter values ranging from 1.3% to 3.4%, with a mean of 2.1% ±0.1, while *Chaetopterus* habitats ranged from 1.6% to 6.9% and had a higher mean of 3.1% ±0.2 (Table 2.4). Like mud content, the habitat × site interaction was significant (Table 2.4), highlighting variability in organic matter content across sites.

Overall, *Chaetopterus* habitats were characterised by increased organic matter and finer sediment fractions, consistent with their role in modifying sediment properties. However, the magnitude of these effects varied significantly across sites, as indicated by the habitat × site interaction in the PERMANOVA analysis. Detailed site-specific values for environmental variables are provided in Appendix C.

Table 2.3. *Mean (± SE), minimum, and maximum values of environmental variables for control and* Chaetopterus *habitats (n = 10 sites per habitat group). Variables include the number of* Chaetopterus *ind. core*$^{-1}$ *and equivalent number per m*^{2}*, percent* Chaetopterus *cover per quadrat, organic matter content, mud content, median grain size, and water depth.*

	Control habitat			***Chaetopterus* habitat**		
Variables	Mean (SE)	Min.	Max.	Mean (SE)	Min.	Max.
Number of *Chaet.* (# $0.02 m^2$)	0	0	0	16.8 (1.6)	2	47
Number of *Chaet.* (# m^2)	0	0	0	585 (59)	102	1835
Chaet. cover (% m^2)	0	0	0	65 (3)	20	98
Depth (m)	6.5 (0.4)	1.5	13.2	6.8 (0.4)	1.8	13.0
MGS (µm)	245 (16)	141	658	216 (16)	19	513
Mud (% < 63 µm)	7.7 (0.5)	2.9	16.6	19.8 (2.0)	6.2	61.6
Organic content (%afdw)	2.1 (0.1)	1.3	3.4	3.1 (0.2)	1.6	6.9

Table 2.4*. P-values from a two-factor PERMANOVA assessing differences in water depth and sediment characteristics between habitat, site and the habitat × site interaction. Variables tested include water depth, median grain size (MGS, µm), mud content (Mud, % grains < 63 µm), and organic matter content (%Afdw). The degrees of freedom (df) are specified for each source of variation. Significant p-values (α < 0.05) are highlighted in bold.*

	Source of variation (df)		
Variables	Habitat (1)	Site (9)	Habitat x Site (9)
Depth (m)	0.206	**0.001**	**0.001**
MGS (µm)	0.214	**0.001**	**0.001**
Mud (% < 63 µm)	**0.001**	**0.001**	**0.001**
Organic content (%afdw)	**0.014**	**0.001**	**0.001**

2.3.3 Community composition

2.3.3.1 Sampling effort

In the control sites, the species accumulation curve (SAC) indicated sufficient sampling, as species accumulation rates noticeably declined after approximately 20 core samples (Figure 2.5). A similar trend was observed in *Chaetopterus* sites, where sampling adequacy was reached after around 15 cores. However, both curves continued to show a gradual increase, suggesting that further sampling could still reveal additional species.

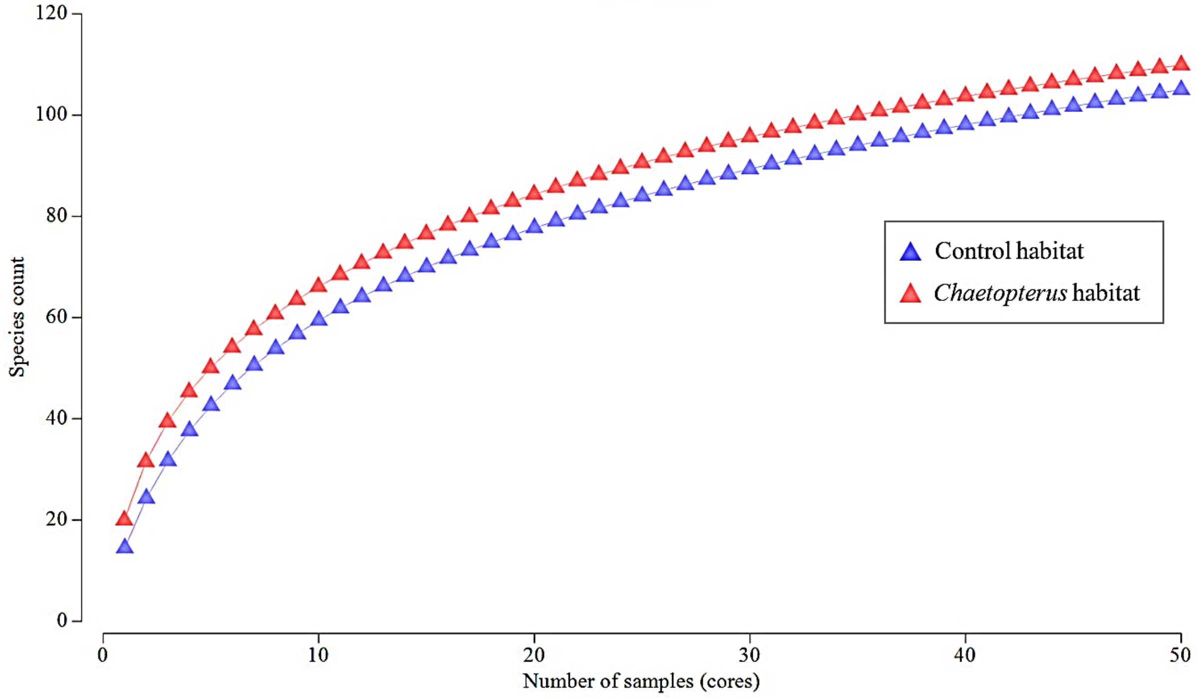


Figure 2.5*. Species accumulation curve (SAC) illustrating control group samples (n = 50) from 10 sites, represented by blue triangles, and* Chaetopterus *group samples (n = 50) from 10 sites, represented by red triangles.*

2.3.3.2 Univariate results

A total of 4,942 individuals, representing 150 species, were identified across all sites in East Bay. Detailed site-specific diversity indices are provided in Appendix C, while Appendix D contains a full species list. Notable differences in certain diversity indices were observed between control and *Chaetopterus* sites (Table 2.5; Table 2.6). Macrofaunal abundance was 30.2% higher in *Chaetopterus* habitats than in control sites, averaging 56 ± 4 and 43 ± 3 ind. core^{-1}, respectively, though this difference was not statistically significant (*p* = 0.149; Table 2.6).

Species richness was significantly higher in *Chaetopterus* habitats, with a 37.9% increase compared to control sites (*p* = 0.006). Diversity (H') was also significantly higher (14.8%) in *Chaetopterus* habitats (*p* = 0.017). Evenness (J') remained consistent across habitat types, with no significant difference observed.

Table 2.5. *Mean (±SE), minimum, and maximum values of diversity indices for control and* Chaetopterus *habitats (n = 10 sites per habitat group). N = macrofaunal abundance (individuals per 0.02 m²); S = species richness; H' = Shannon-Wiener diversity index; J' = Pielou's evenness index. Values are presented as mean (± standard error), with minimum and maximum values shown for each habitat group.*

	Control habitat			***Chaetopterus* habitat**		
Diversity index	Mean (SE)	Min.	Max.	Mean (SE)	Min.	Max.
N	43 (3)	5	121	56 (4)	17	153
S	14.5 (0.7)	5	29	20.0 (0.8)	9	32
H'	2.16 (0.06)	1.06	2.89	2.48 (0.05)	1.60	3.19
J'	0.8 (0.01)	0.5	1.0	0.8 (0.01)	0.6	1.0

Table 2.6*. P-values from two-factor PERMANOVA assessing differences in community indices between habitats, site, and the habitat × site interaction. P-values are considered significant at α < 0.05. N = macrofaunal abundance (individuals per 0.02 m²); S = species richness; H' = Shannon-Wiener diversity index; J' = Pielou's evenness index.*

	Source of variation (df)		
Diversity index	Habitat (1)	Site (9)	Habitat x Site (9)
N (# 0.02m²)	0.149	**0.001**	**0.02**
S (# 0.02m²)	**0.006**	**0.001**	**0.001**
H'	**0.017**	**0.002**	**0.002**
J'	0.662	**0.019**	**0.009**

2.3.3.3 Multivariate results

PERMANOVA analysis identified significant differences in community composition between habitat groups and among sites, as well as a notable habitat × site interaction (p<0.001). This interaction indicates that the habitat effect on community composition varied depending on the site, emphasising the potential role of local environmental conditions. Post-hoc pairwise comparisons further supported these findings, revealing significant differences in community composition between each paired control and *Chaetopterus* site, with all paired comparisons producing P(perms) values below 0.05.

Furthermore, an ANOSIM test, using Bray-Curtis similarity measures, further supported a significant habitat effect on community composition, yielding a global R-value of 0.618. This moderately strong R-value indicates a clear ecological distinction between control and *Chaetopterus* sites despite some overlap. These results were statistically robust, based on 999 permutations, and suggest that differences in community composition between the two habitat groups are unlikely to be due to chance.

A non-metric multidimensional scaling (nMDS) plot illustrates the variation in macroinvertebrate community structure between control and *Chaetopterus* sites within ordination space (Figure 2.6). Key environmental variables and diversity indices are overlaid to illustrate their influence on community composition. The stress value of 0.11 suggests that the 2D ordination provides a reliable representation of the community differences for visual interpretation. The RELATE analysis confirmed the reliability of the nMDS plot, revealing a very strong and significant correlation (Rho = 0.954, p = 0.001) between the Euclidean distances in the nMDS plot and the dissimilarities in community composition across habitat groups. This high correlation indicates that the spatial arrangement of points in the nMDS plot accurately reflects underlying differences in community structure. The distinct separation of groups within the plot highlights clear differences in community composition between the two habitat groups, with no overlap observed.

Chaetopterus sites displayed tighter clustering, reflecting a more homogeneous community structure within *Chaetopterus* areas, with a within-group similarity of 49.7% (SIMPER). In contrast, control sites showed a broader spatial distribution, indicating higher variability in community composition, with a lower within-group similarity of 40.6% (SIMPER). *Chaetopterus* site 2 is particularly distinct from other *Chaetopterus* sites, suggesting unique community characteristics. A PERMDISP test for homogeneity of multivariate dispersions revealed significant differences in dispersion between control and *Chaetopterus* sites. The average distance to the centroid, with standard errors, further supports this, showing that control sites (mean: 50.638, SE: 1.0404) are more variable than *Chaetopterus* sites (mean: 44.827, SE: 1.0503).

The nMDS plot shows a clear separation between control and *Chaetopterus* sites along the x-axis, indicating that habitat type (i.e. control vs. *Chaetopterus*) strongly influences community structure (Figure 2.6). This separation aligns with higher mud content and organic matter in *Chaetopterus* habitats, as indicated by the moderate vector lengths and directions. In contrast, variation along the y-axis appears to be primarily driven by median grain size (MGS) and depth. For example, sites with coarser sediments (e.g., control sites 10 and 8) align more closely with the MGS vector, while deeper sites (e.g., *Chaetopterus* site 10 and control site 10) show a stronger association with the depth vector. These environmental variables collectively explain the observed variation in community structure across both habitat types and spatial gradients.

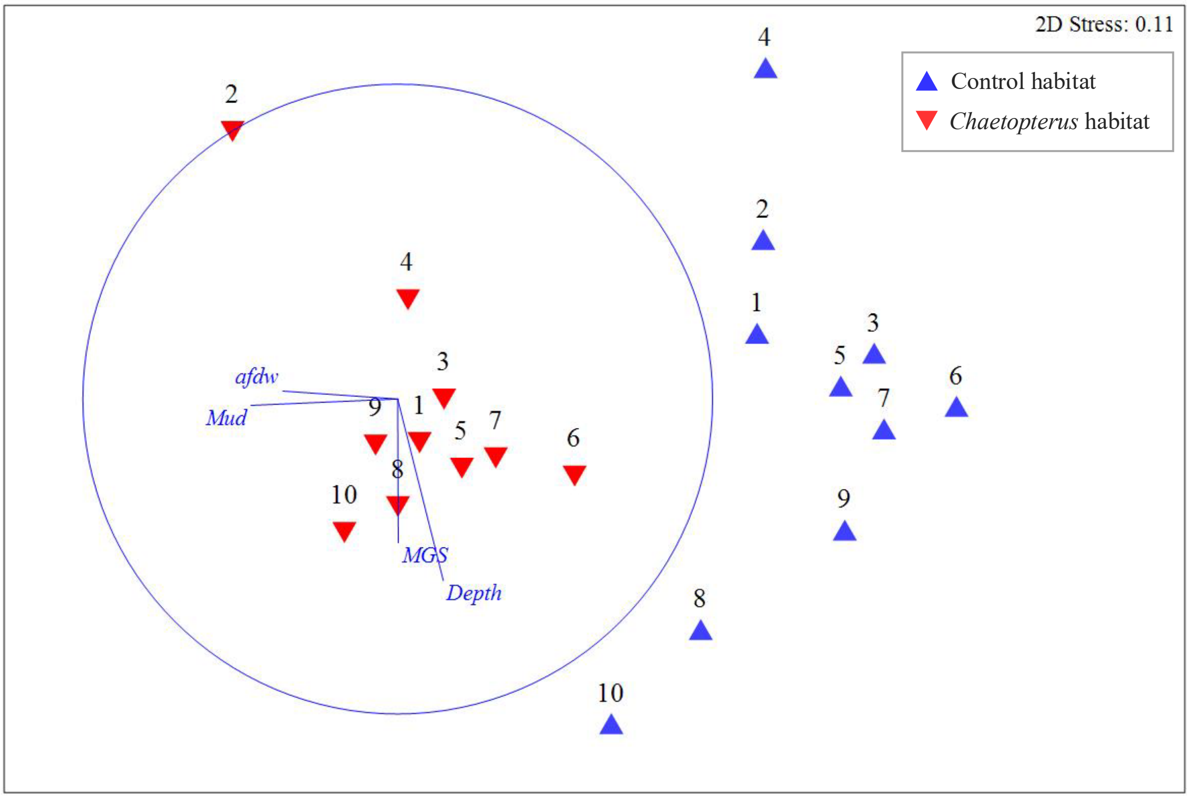


***Figure 2.6**. Non-metric multidimensional scaling ordination plot comparing macroinvertebrate community composition between control sites (blue triangles with corresponding site numbers) and* Chaetopterus *sites (red triangles). Environmental variables, including mud content (Mud), organic matter content (afdw), depth, and median grain size (MGS), are depicted as vectors. The length of the vectors is representative of the strength of the correlation. Symbol positions are based on Bray-Curtis similarities of square root transformed data collected from 5 replicate cores (stress = 0.11). The distance between samples is proportional to their relative similarity, and the axes have no units.*

SIMPER analysis revealed an overall dissimilarity of 71% between control and *Chaetopterus* sites, largely driven by differences in species abundance between habitat groups (Table 2.7). Generally, the species contributing most to this separation were also among the most abundant. A list detailing the dominant species for each habitat group is provided in Appendix E.

Amphipoda sp. was a significant contributor to the dissimilarity between habitat groups, with a higher average abundance observed in *Chaetopterus* sites (2.8 ind. core^{-1}) compared to control sites (1.6 ind. core^{-1}) (Table 2.7). This single species accounted for 5.8 % of the overall dissimilarity. *Leptomyra retaria retaria* and *Barantolla lepte* were also significant contributors to community dissimilarity, each contributing 3.39% and 3.27%, respectively. Notably, *L. retaria retaria* was more abundant in *Chaetopterus* sites (1.39 ind. core^{-1}) than in control sites (0.21 ind. core^{-1}), highlighting a shift in species dominance across habitat types. *Barantolla lepte* exhibited relatively similar mean abundances across control (1.79 ind. core^{-1}) and *Chaetopterus* sites (1.54 ind. core^{-1}; Table 2.7). However, its relatively high contribution to dissimilarity likely arises from spatial variability in its distribution across sites rather than a consistent difference between habitat types.

Additional species contributing to dissimilarity included Phoxocephalidae (3.35% contribution) and *Prionospio multicristata* (3.14%), both of which exhibited higher abundances in control sites. Phoxocephalidae had an average abundance of 1.62 ind. core^{-1}in control sites compared to 0.59 ind. core^{-1} in *Chaetopterus* sites, while *P. multicristata* recorded an average abundance of 1.22 ind. core^{-1} in control sites versus 0.2 ind. core^{-1} in *Chaetopterus* sites (Table 2.7). The top 10 contributing species collectively accounted for approximately 32.64% of the total dissimilarity between habitat groups, indicating that differences in community composition were not dominated by a few species but, rather, influenced by multiple species, each making incremental contributions to the overall dissimilarity. In total, 35 species cumulatively contributed to approximately 70% of the observed dissimilarity (Table 2.7).

Table 2.7. *Results of Similarity Percentage (SIMPER) analysis summarising key species contributing to the dissimilarities observed between macroinvertebrate communities in control and* Chaetopterus *habitats. Analysis was based on square-root transformed macroinvertebrate abundance data. The overall dissimilarity between the two habitat types was 71%. Column descriptions: Av. Abund = average abundance per site, Av. Diss = average dissimilarity, Diss/SD = ratio of average contribution to standard deviation, Contrib. % = contribution percentage, Cum. % = cumulative contribution percentage.*

Species	**Control Av.Abund**	***Chaet.* Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib. %**	**Cum.%**
Amphipoda Unid.	1.6	2.8	4.09	1.38	5.77	5.77
Leptomya retiaria retiaria	0.21	1.39	2.4	1.32	3.39	9.15
Phoxocephalidae	1.62	0.59	2.37	1.37	3.35	12.5
Prionospio multicristata	1.22	0.2	2.28	1.17	3.22	15.72
Barantolla lepte	1.79	1.54	2.17	1.36	3.06	18.78
Notomastus zeylanicus	0.42	1.44	2.15	1.84	3.03	21.81
Goniadidae	1.14	0.02	2.07	1.08	2.92	24.73
Palaemon affinis	0	1.01	2.05	2.05	2.89	27.62
Halicarcinus cookii	0.2	1.08	1.9	1.44	2.68	30.30
Terebellidae	0.05	0.84	1.66	1.55	2.34	32.64
Tanaidacea	0.11	0.87	1.57	1.14	2.21	34.85
Hesionidae	0.27	0.91	1.47	1.6	2.07	36.92
Lumbrineridae	0.61	0.99	1.46	1.17	2.07	38.99
Ophiuroidea	0.05	0.79	1.41	1.12	1.99	40.98
Dorvilleidae	0.04	0.76	1.36	1.35	1.93	42.91
Maldanidae	0.89	0.59	1.32	1.29	1.86	44.76
Lysianassidae	0.64	0.12	1.19	1.09	1.68	46.45
Glyceridae	0.42	0.96	1.18	1.23	1.67	48.11
Armandia maculata	0.34	0.65	1.15	1.31	1.62	49.73
Nucula hartvigiana	0.29	0.5	1.14	0.93	1.6	51.33
Polydora sp.	0.56	0.07	1.14	0.73	1.6	52.93
Zemysina sp.	0.1	0.61	1.05	1.02	1.49	54.42
Petrolisthes novaezelandiae	0.02	0.47	1.05	0.68	1.47	55.90
Cirratulidae	0.28	0.52	0.95	1.3	1.34	57.24
Orbinia papillosa	0.46	0	0.95	1.4	1.34	58.58
Anthuridea	0.44	0.31	0.94	1.13	1.32	59.90
Syllidae	0.24	0.39	0.93	0.89	1.31	61.21
Scintillona zelandica	0.03	0.49	0.91	1.69	1.28	62.49
Corbula zelandica	0.37	0.47	0.85	1.24	1.2	63.69
Patiriella regularis	0	0.41	0.82	1.5	1.15	64.83
Chiridota nigra	0.02	0.42	0.81	1.7	1.14	65.98
Phascolosoma annulatum	0.06	0.45	0.81	0.85	1.14	67.12
Nereidae	0.08	0.42	0.76	1.46	1.08	68.20
Diasterope grisea	0.33	0.12	0.73	1.04	1.04	69.23
Macomona liliana	0.38	0.15	0.73	0.87	1.03	70.27

In summary, the results display distinct differences between community types at control and *Chaetopterus* sites. *Chaetopterus* sites exhibited higher species richness, greater diversity, and more homogeneity in community structure compared to control sites. The nMDS plot revealed clear separations between the two habitat groups, with statistical analyses further confirming significant differences in community composition and diversity indices. These findings suggest that environmental conditions, particularly those influenced by *Chaetopterus*, play a key role in shaping these communities.

Despite these overall patterns, considerable variation in community structure was observed within and between sites, highlighting the complexity of ecological interactions in these habitats. This variability underscores the importance of splitting analyses by habitat type, as the absence of *Chaetopterus* in control sites inherently creates a different baseline for comparison. The nMDS plot visually supports this decision, showing clear groupings of control and *Chaetopterus* sites, reflecting distinct sediment characteristics and the presence or absence of *Chaetopterus*. This division enables a more focused examination of the factors driving community structure in each habitat type.

The following section investigates how the measured environmental variables, particularly those linked to *Chaetopterus*, explain the observed variation in community structure across sites. By isolating key drivers, this analysis provides deeper insights into the ecological impacts of *Chaetopterus* on benthic habitats.

2.3.4 Environmental drivers of diversity and community structure

2.3.4.1 Comparison of environmental variables

In comparing control and *Chaetopterus* sites, notable differences in correlations among environmental variables were observed (Table 2.8). At control sites (Table 2.8a), organic matter content showed a moderate positive correlation with depth (r = 0.501), suggesting that organic matter tended to increase in deeper waters. Additionally, there was a weak positive correlation between organic matter content and median grain size (r = 0.309), suggesting a slight association between organic material and coarser sediments, which is likely influenced by depth-related factors. Conversely, and as expected, mud content (% grains < 63 µm) showed negative correlations with median grain size within both habitat groups.

At *Chaetopterus* sites, the relationships between environmental variables were more pronounced. Mud content had strong positive correlations with both organic matter content (r = 0.727) and depth (r = 0.821), indicating that muddier sediments were associated with higher organic matter and were located at greater depths (Table 2.8b). Furthermore, organic matter content showed a moderate positive correlation with depth, reinforcing the trend observed in control sites but with a stronger association in *Chaetopterus* areas.

2.3.4.2 Relationships between diversity indices and environmental variables

At control sites, diversity exhibited a strong positive correlation with species richness (Table 2.8a, r = 0.775), indicating that sites with a greater number of species tended to have higher diversity. Additionally, evenness (J') was positively correlated with H', suggesting that more diverse communities were also more evenly distributed. However, J' had a negative correlation with organic matter content and N, suggesting that sites with higher organic content or larger population sizes tended to have lower species evenness. There was also a weak negative correlation between H' and organic matter content, implying that higher organic matter may slightly reduce diversity in control sites.

At *Chaetopterus* sites (Table 2.8b), different patterns emerged. Shannon-Wiener diversity showed a positive correlation with depth and mud content, indicating that deeper and muddier environments supported more diverse communities. Diversity exhibited a positive correlation with organic matter content (r = 0.518), indicating that higher levels of organic matter are associated with greater diversity. Evenness was strongly correlated with H' (r = 0.730), reflecting that higher community diversity was associated with a more even species distribution. Additionally, evenness showed a moderate positive correlation with mud content. A negative correlation between evenness and total individuals (r = -0.581) suggested that sites with higher population densities had less even species distributions in *Chaetopterus* areas.

2.3.4.3 Chaetopterus abundance, environmental variables and community indices

When considering *Chaetopterus* abundance, the results demonstrated several significant correlations with environmental and community variables (Table 2.8b). *Chaetopterus* abundance showed a significant positive correlation with organic matter content (r = 0.405), indicating that areas with higher organic matter had greater abundance of *Chaetopterus*. Additionally, there was a significant positive association between *Chaetopterus* abundance and median grain size (r = 0.396), though no significant relationship was found between *Chaetopterus* abundance and mud content. A moderate, significant positive correlation was identified between *Chaetopterus* abundance and depth (r = 0.342), suggesting that *Chaetopterus* is more abundant in deeper areas.

Regarding community indices, *Chaetopterus* abundance was strongly correlated with species richness (r = 0.658) and moderately correlated with total individuals (r = 0.523), indicating that areas with higher *Chaetopterus* presence tended to have greater species richness and higher population densities (Table 2.8b). A significant positive correlation was also found between *Chaetopterus* abundance and H' (r = 0.383), suggesting that more diverse communities contained higher numbers of *Chaetopterus* individuals.

Table 2.8. *Part A: Pearson correlation matrix of mean environmental variables and diversity indices for control sites, with significant correlations ($\alpha < 0.05$) highlighted in bold. Part B: Pearson correlation matrix of mean environmental variables, diversity indices, and* Chaetopterus *abundance for* Chaetopterus *sites, with significant correlations ($\alpha < 0.05$) highlighted in bold.*

Part A: Control habitats

Variables	%Afdw	Depth	MGS	Mud	N	S	H'
Depth (m)	**0.501**	-					
MGS (µm)	**0.309**	**0.391**	-				
Mud (% grains < 63 µm)	0.277	-0.223	**-0.485**	-			
N	0.217	0.047	**0.614**	-0.171	-		
S	-0.031	-0.059	**0.364**	-0.227	**0.708**	-	
H'	**-0.331**	-0.213	0.130	**-0.325**	0.235	**0.775**	-
J'	**-0.479**	-0.254	-0.182	-0.267	**-0.393**	0.108	**0.677**

Part B: *Chaetopterus* habitats

Variables	%Afdw	Depth	MGS	Mud	N	S	H'	J'
Depth (m)	**0.637**	-						
MGS (µm)	-0.237	**-0.364**	-					
Mud (% grains < 63 µm)	**0.727**	**0.821**	**-0.612**	-				
N	0.071	0.133	0.170	0.018	-			
S	**0.438**	**0.531**	0.123	**0.390**	**0.713**	-		
H'	**0.518**	**0.565**	-0.029	**0.505**	0.023	**0.666**	-	
J'	**0.302**	0.246	-0.144	**0.308**	**-0.581**	-0.009	**0.730**	-
Chae. Abund. ($0.02m^2$)	**0.405**	**0.342**	**0.396**	0.169	**0.523**	**0.658**	**0.383**	-0.062

2.3.4.4 Environmental drivers of community composition

In control sites, DISTLM revealed that MGS was the most influential variable, explaining approximately 12% of the variation in community composition (Table 2.9a). Depth was the second most important factor, accounting for ~10.8% of the variation, followed by organic matter content (%Afdw) at 7.7% and mud content at 6.9%. Sequential tests, which add variables stepwise based on Corrected Akaike Information Criterion (AICc), revealed that these four variables together explained 26.8% of the total variation in community composition.

Within *Chaetopterus* sites, mud content was strongly correlated with both depth and organic content, showing Pearson correlation coefficients exceeding ±0.7. Therefore, to reduce redundancy and multicollinearity in the analysis, mud content was excluded. In contrast to control sites, *Chaetopterus* abundance emerged as the dominant variable with *Chaetopterus* habitats, explaining ~9.5% of the variation in community structure (Table 2.9b). Depth closely followed, accounting for ~9%, while organic matter content explained ~7.5% of the variation. *Chaetopterus* tube coverage contributed ~4.9%, and MGS explained ~3.6%, indicating a reduced role of sediment characteristics compared to control sites. Sequential tests revealed that the combined influence of all five variables accounted for 29.5% of the total variation in community composition (Table 2.9b).

Table 2.9. *Results of distance-based linear modelling (DISTLM) using Bray-Curtis dissimilarities of square-root transformed macroinvertebrate abundance data. Part A presents results for control habitats (n = 50), while Part B shows results for* Chaetopterus *habitats (n = 50). Forward selection was applied using Corrected Akaike's Information Criterion (AICc). The variables include depth, median grain size (MGS), mud content, organic matter content (% Afdw),* Chaetopterus *abundance (Chae. Abund.), and* Chaetopterus *tube cover (%). Each predictor's sum of squares (SS(trace)), pseudo-F statistic, p-value (P), and proportion of variance explained (Prop.) are reported. Significant p-values (α < 0.05) are in bold.*

Part A: Control habitats

Variable	SS(trace)	Pseudo-F	P	Prop.
Depth (m)	14112	5.802	**0.001**	0.108
MGS (µm)	15699	6.5433	**0.001**	0.120
Mud (% grains < 63 µm)	9016.2	3.5518	**0.001**	0.069
%Afdw	10129	4.027	**0.001**	0.077

Part B: *Chaetopterus* habitats

Variable	SS(trace)	Pseudo-F	P	Prop.
Depth (m)	9252.3	4.7285	**0.001**	0.090
MGS (µm)	3678	1.7744	**0.043**	0.036
%Afdw	7703.3	3.873	**0.001**	0.075
Chae. Abund.	9777.5	5.025	**0.001**	0.095
Chae. Cover (%)	5034.7	2.4625	**0.004**	0.049

2.3.5 Functional group analysis

An nMDS plot (Figure 2.7) illustrates clear differences in functional group (FG) community structure between control and *Chaetopterus* habitats. The stress value of 0.16 indicates that the 2D representation adequately reflects the multidimensional relationships among samples. *Chaetopterus* sites clustered tightly, suggesting greater uniformity in FG composition. In contrast, control sites were more dispersed and positioned distinctly from the *Chaetopterus* grouping, indicating higher variability in functional structure within control habitats.

This clustering of *Chaetopterus* sites aligns with environmental drivers identified in the previous section, such as higher organic matter content and finer sediments, which are likely to favour specific functional traits. Conversely, the broader variability in control sites reflects less structured environmental conditions and greater heterogeneity in community composition.

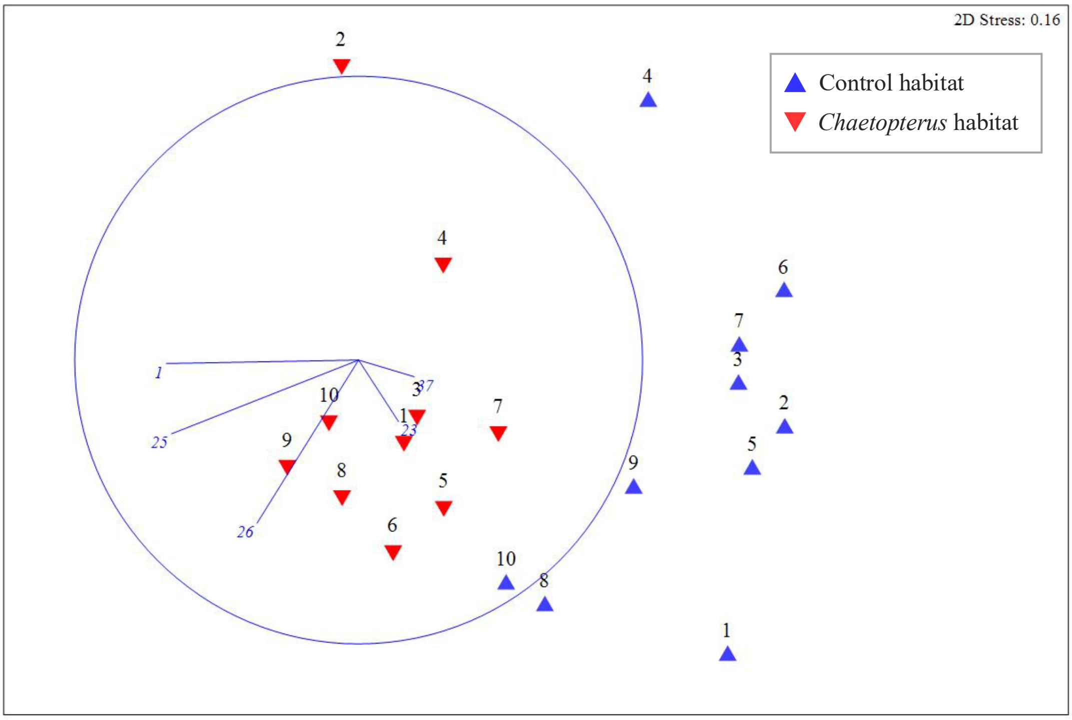


Figure 2.7. *Non-metric multidimensional scaling (nMDS) ordination plot illustrating macroinvertebrate functional group structure differences between control sites (blue triangles with site numbers) and* Chaetopterus *sites (red triangles). Vectors represent five key functional groups (FG1, FG23, FG25, FG26, and FG37) that primarily contribute to community composition variance, with vector length indicating correlation strength. Symbol positions are based on Bray-Curtis similarities of square-root transformed functional group data from five replicate cores per site. Distances between samples reflect relative similarity, with axes being unitless.*

The BEST analysis identified five functional groups (FG1, FG23, FG25, FG26, and FG37) as the primary drivers of differences in FG composition, achieving a correlation of 0.794. These groups, characterised by distinct traits, such as deposit-feeding, scavenging, and predation, were overlaid onto the nMDS plot to visualise their influence on community structure (Figure 2.7). The dominance of groups like FG26 (deposit/grazer/predator) and FG25 (predator/scavenger) in *Chaetopterus* habitats highlights a functional divergence from control sites.

PERMANOVA results demonstrated significant differences in functional group (FG) composition across habitat (p = 0.01), site (p = 0.01), and the habitat × site interaction (p = 0.01). These findings indicate that the influence of habitat on FG composition was context-dependent and varied among sites.

The SIMPER analysis (Table 2.10) further quantified differences, showing that *Chaetopterus* habitats exhibited higher internal similarity (66.93%) compared to control sites (61.58%), consistent with the tighter clustering observed in the nMDS plot. PERMDISP results confirmed significantly lower dispersion in *Chaetopterus* habitats (mean distance to centroid: 33.873 ± 1.039 SE) compared to control sites (37.911 ± 1.208 SE, p = 0.016), suggesting a more homogenised FG composition in *Chaetopterus* habitats.

***Table 2.10**. SIMPER analysis results showing key functional groups contributing to the 44.4% dissimilarity between control and* Chaetopterus *habitats. Abbreviations: Av. Abund = average abundance (per core), Av. Diss = average dissimilarity, Diss/SD = dissimilarity-to-standard deviation ratio, Contrib. % = contribution percentage, Cum. % = cumulative contribution percentage.*

FG number	**Control Av.Abund**	***Chaet.* Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
26	1.94	3.1	3.86	1.43	8.68	8.68
1	0.81	1.83	2.23	1.24	5.03	13.71
25	0.41	1.56	2.22	1.84	5	18.71
22	1.88	1.11	2.01	1.49	4.52	23.24
29	0.2	1.2	2	1.34	4.49	27.73
36	0.59	1.58	1.94	1.6	4.36	32.09
24	2.32	2.48	1.87	1.35	4.21	36.31
10	0.92	1.02	1.81	1.36	4.06	40.37
34	2.41	1.9	1.76	1.8	3.96	44.33
27	2.08	2.05	1.75	1.23	3.94	48.27
28	0.81	1.05	1.62	1.64	3.65	51.93
4	0.74	1.47	1.6	1.44	3.6	55.53
19	0.49	0.98	1.53	1.48	3.44	58.96
20	1.06	0.8	1.33	1.26	2.99	61.95
35	0.85	0.22	1.32	1.37	2.96	64.91
30	0.04	0.66	1.3	0.95	2.93	67.84
11	0.13	0.74	1.27	1.16	2.87	70.71

2.4 Discussion

This study was undertaken to address gaps in the scientific literature concerning the ecological impact of *Chaetopterus* tubeworm beds on sediment properties and macroinvertebrate community composition within New Zealand's coastal ecosystems. Despite the growing significance of other habitat-modifying species in benthic environments, there has been limited research on how *Chaetopterus* might influence sediment characteristics and community dynamics in soft-sediment habitats, particularly within the Marlborough region.

The findings from this study indicate that *Chaetopterus* significantly modifies sediment properties, which in turn appear to drive shifts in macroinvertebrate community composition. Higher diversity, species richness and altered functional group distributions were observed in sites where *Chaetopterus* was present, suggesting that this species plays a substantial role in shaping benthic diversity and habitat complexity. This section will summarise the key findings and discuss the broader ecological implications of *Chaetopterus* as a habitat-modifying species. Finally, recommendations for future research and management approaches will be outlined, followed by concluding remarks on the study's contribution to understanding *Chaetopterus'* role in benthic ecosystem functioning.

2.4.1 Role of *Chaetopterus* in modifying sediment properties

2.4.1.1 Chaetopterus characteristics in East Bay

The distribution and characteristics of *Chaetopterus* in East Bay, underscore its role as a significant habitat modifier and its contribution to enhancing heterogeneity in soft-sediment environments. Spatial variability in tube cover and live individual densities revealed a distinctly patchy distribution, with some sites exhibiting high tube cover despite low densities of live individuals. This pattern reflects the resilience of *Chaetopterus* tubes, which persist and continue to influence the environment even after the occupants have vacated. The durability of these structures, as observed in *Chaetopterus variopedatus* by Shah et al. (2014), enables them to resist degradation and maintain their structural integrity over time.

The heterogeneity created by *Chaetopterus* is likely driven by a combination of environmental and biological factors. Variability in sediment properties, such as grain size and organic matter content, has been shown to influence settlement and tube construction in *Chaetopterus variopedatus* and other tube-building species (Thompson & Schaffner, 2001; Rabaut et al., 2009). Hydrodynamic conditions also play a role, affecting sediment deposition and the retention of fine particles around tube fields (Osborn et al., 2007). Additionally, larval settlement may favour areas with existing tube structures, a behaviour observed in *C. variopedatus* (Osborn et al., 2007) and other species such as *Lanice conchilega* (Rabaut et al., 2009). These combined processes not only drive patchiness in distribution but also enhance habitat complexity, promoting biodiversity and ecological resilience in soft-sediment environments.

In East Bay, *Chaetopterus* was primarily associated with fine to medium sands but also occurred in very fine sands near the sand-mud boundary. This distribution reflects its adaptability to diverse sediment types and its ability to influence local substrate properties, reducing the specificity of its association with particular sediment categories. While earlier studies in New Zealand linked *Chaetopterus* to sandy, sandy-gravel, and shell-gravel substrates (Acosta, 2001; Tricklebank et al., 2001), the findings from East Bay demonstrate its capacity to establish in a broader range of substrata. This adaptability, combined with its habitat-modifying behaviours, supports its role in stabilising sediments and creating organic-rich microenvironments. The specific sedimentary conditions associated with *Chaetopterus* are likely influenced by local environmental factors and resource availability (Enders, 1909; Thompson & Schaffner, 2001; Osborn et al., 2007).

Depth strongly influenced the distribution of *Chaetopterus*, with dense aggregations observed at shallower depths (<14 m) in East Bay, including populations as shallow as 2 m. This contrasts with previous studies in northeastern New Zealand, where *Chaetopterus* mats were predominantly recorded at depths greater than 15 m, with peak frequencies between 25–34 m (Acosta, 2001; Tricklebank et al., 2001). The absence of *Chaetopterus* at high-exposure sites with bottom drag velocities exceeding 0.37 m/s (Acosta, 2001) suggests that hydrodynamic forces play a key role in structuring their distribution. In the Hauraki Gulf, *Chaetopterus* populations were often restricted to deeper sandy and gravelly substrates, where stronger currents may have displaced shallower populations. In contrast, East Bay's sheltered conditions likely allow *Chaetopterus* to persist in shallower depths where reduced hydrodynamic stress provides a stable environment for tube mat formation. These findings highlight the importance of local hydrodynamic regimes in shaping regional differences in *Chaetopterus* depth distributions.

The distribution of *Chaetopterus* across a range of sediment types and depths in East Bay underscores its adaptability and its critical role in structuring benthic habitats. Its ability to form dense, persistent aggregations, coupled with the resilience of its tube structures, establishes the foundation for its impact on sediment properties and ecosystem dynamics, which are explored in the following sections.

2.4.1.2 Influence on sediment properties

This study demonstrates that *Chaetopterus* significantly influences sediment properties in relatively sheltered soft-sediment habitats, particularly by increasing organic matter content and promoting mud accumulation. Sediments within *Chaetopterus* habitats exhibited significantly higher organic matter levels and mud content compared to nearby areas without *Chaetopterus*. Organic matter content showed a positive correlation with *Chaetopterus* density, highlighting the species' role in organic enrichment. This is consistent with previous research on *C. variopedatus*, which facilitates organic matter deposition through filter-feeding, trapping suspended particles in its mucous bag, and depositing faecal material around its tubes (Bailey-Brock, 1979; Wright et al., 1987; Thompson & Schaffner, 2001). These processes not only enrich local sediments but also strengthen bentho-pelagic coupling, similar to the effects observed in other polychaetes, such as *Sabella spallanzanii* (Atalah et al., 2019).

Mud content, used as a proxy for fine particle concentration and sediment stability, was significantly higher in *Chaetopterus* habitats (19.8%) compared to control areas (7.7%). Although no significant correlation was observed between *Chaetopterus* density and mud content, the consistently elevated mud content in *Chaetopterus* habitats suggests that both active and abandoned tubes contribute to sediment stability. The durable structure of *Chaetopterus* tubes allows them to remain intact long after being vacated, maintaining their capacity to trap fine particles and influence sediment composition.

Despite the increased mud content, median grain size (MGS) did not differ significantly between *Chaetopterus* and control habitats. This suggests that *Chaetopterus* primarily influences the finer sediment fractions without significantly altering the overall grain size distribution. Mud content, therefore, emerges as a more sensitive indicator of *Chaetopterus*-driven sediment modification. Localised retention of fine particles around *Chaetopterus* tubes, likely facilitated by reduced near-bottom flow velocities (Eckman et al., 1981; Rabaut et al., 2007), enhances sediment stability within these habitats.

The capacity of *Chaetopterus* to modify sediment properties is influenced by both population density and species-specific traits, such as worm size and tube morphology. For example, the larger size of *Chaetopterus* individuals compared to smaller polychaetes, such as *Lanice conchilega*, allows it to exert stabilising effects at relatively lower densities (Thompson & Schaffner, 2001). In this study, *Chaetopterus* densities ranged from 285 - 1,465 individuals per m^2 (scaled based on core data), within the range associated with significant sediment stabilisation in similar systems (Thompson & Schaffner, 2001). Combined with the tall, protruding nature of *Chaetopterus* tubes, these densities likely enhance fine particle retention and organic matter accumulation.

Correlation analysis highlights the interconnectedness of sediment variables within *Chaetopterus* habitats. Organic matter enrichment and increased mud content were closely associated with the presence and density of *Chaetopterus*, emphasising its role as both a biological and physical modifier of sediment composition. The observed similarity in depth between *Chaetopterus* and control habitats, further isolates *Chaetopterus* activity as the primary driver of these sedimentary changes, independent of depth-related influences.

In summary, *Chaetopterus* alters sediment characteristics through a combination of physical and biological processes, including sediment trapping, organic enrichment, and fine particle retention. The persistent effects of its tube structures, even in the absence of live individuals, reinforce its role in shaping sediment profiles. These findings emphasise the importance of considering multiple sediment variables when evaluating the ecological impacts of *Chaetopterus*, with organic matter and mud content emerging as the most responsive indicators of its influence.

2.4.2 Biodiversity and community structure influences of *Chaetopterus*

The presence of *Chaetopterus* tube mats significantly influenced benthic community structure, as reflected by patterns in abundance (N), species richness (S), Shannon-Wiener diversity (H′), and evenness (J′). Although N was higher in *Chaetopterus* habitats compared to control sites, this difference was not statistically significant. This suggests that the benefits conferred by these habitats are selective, favouring species adapted to stabilised, nutrient-rich sediments rather than universally enhancing population densities. Such selective responses are consistent with findings in other tube-building polychaete systems, such as *Lanice conchilega*, where habitat modifications support certain ecological traits without dramatically increasing overall abundance (Van Hoey et al., 2008; Rabaut, 2009).

By contrast, both S and H′ were significantly higher in *Chaetopterus* habitats. Mean richness was 20.0 species per core in *Chaetopterus* sites, significantly exceeding the 14.5 species recorded in control sites. Similarly, H′ was higher in habitats with *Chaetopterus*, driven by increased S and the structural complexity provided by tube mats. These findings align with Schaffner's (1990) assertion that *C. variopedatus* tubes function as habitat structures that enhance biodiversity by providing refuges, stabilising sediments, and reducing physical disturbances.

The structural complexity provided by *Chaetopterus* tube mats, fosters heterogeneous habitats that support a wide range of ecological niches. By stabilising sediments, these mats likely reduce sediment resuspension and enhance localised nutrient retention, creating conditions that allow species with diverse ecological requirements to coexist. Such findings align with Thrush et al. (2001), who highlighted the positive relationship between habitat complexity and biodiversity in soft-sediment environments. Comparable mechanisms have been observed in other polychaete-dominated systems, such as *Lanice conchilega* aggregations, which enhance species richness and create niches for associated fauna (Van Hoey et al., 2008; Rabaut, 2009). The physical presence of *Chaetopterus* tube mats further amplifies habitat heterogeneity, facilitating the coexistence of diverse species (Schaffner, 1990; Pacheco et al., 2011).

The trophic relationships within *Chaetopterus* habitats likely differ from control sites due to changes in predation and competition dynamics. The structural complexity of tube mats may reduce predation pressure by providing refuges for smaller, vulnerable species, as observed in other biogenic habitats (Romero et al., 2015). These refuges can stabilise trophic interactions by supporting the persistence of prey populations and mitigating the intensity of predator-prey dynamics.

Additionally, the enrichment of surface sediments with organic material in *Chaetopterus* habitats was reflected in the FG analysis, which showed higher abundances of surface-associated deposit feeders (e.g., Amphipoda), scavengers (e.g., *Halicarcinus cookii*), and tube-dwelling suspension feeders (e.g., *Polydora* spp.). This was accompanied by a relative decline in deeper-burrowing deposit feeders such as *Prionospio multicristata* and *Barantolla lepte*, as well as bioturbators like *Tawera spissa* and *Filhollianassa filholi*. These shifts in functional composition suggest a restructuring of trophic pathways, with greater reliance on detrital food sources and a potential shift towards lower trophic levels. Such changes could drive cascading effects on the broader benthic food web and nutrient cycling.

Evenness, which reflects the proportional representation of species within a community, did not differ significantly between *Chaetopterus* and control sites. This indicates that the increased S and H′ observed in *Chaetopterus* habitats were not driven by a disproportionate dominance of certain species. Instead, these habitats supported a broader array of species while maintaining community balance. Similar patterns have been observed in other polychaete systems, where increased S and H′ are accompanied by consistent J′ values (Rabaut et al., 2007).

Control sites, by contrast, exhibited lower S and H′, reflecting dynamic sedimentary conditions characterised by coarser grain sizes, reduced organic matter, and limited structural complexity. Such environments favour opportunistic species adapted to high sediment turnover and reduced habitat stability (Thrush et al., 2001). These findings underscore the importance of *Chaetopterus* in stabilising sediments and enriching surface resources, thereby promoting biodiversity.

Synthesising across variables, the role of *Chaetopterus* in shaping benthic communities is multifaceted. It enhances richness and diversity through habitat modification while maintaining consistent evenness, indicating balanced community responses. By modifying sediment structure and organic matter availability, *Chaetopterus* likely influences trophic relationships by favouring specific feeding groups and reducing predation pressures. These findings highlight the ecological importance of *Chaetopterus* as a habitat-forming species and its potential role in maintaining biodiversity, ecosystem functioning, and trophic stability in soft-sediment environments.

2.4.3 Macroinvertebrate community composition and ecosystem functionality in *Chaetopterus* habitats

This study reveals significant differences in macroinvertebrate community composition between *Chaetopterus* habitats and control sites, as demonstrated by PERMANOVA and SIMPER analyses. PERMANOVA indicated significant effects of habitat, site, and their interaction on community composition. These results highlight that differences were driven not only by the presence of *Chaetopterus,* but also by spatial variability among sites. The significant habitat-by-site interaction suggests that *Chaetopterus*'s influence on community composition is context-dependent, potentially shaped by local environmental factors such as hydrodynamic conditions, sediment grain size, and nutrient availability.

SIMPER analysis identified a 71% overall dissimilarity between *Chaetopterus* habitats and control sites, driven by variations in species abundance and dominance. These differences are closely linked to the environmental modifications created by *Chaetopterus* tube mats. The introduction of three-dimensional complexity, sediment stabilisation, and organic enrichment by these tube mats fosters conditions that promote the establishment and persistence of taxa adapted to stabilised, nutrient-rich sediments. In contrast, the coarser and more dynamic sediment conditions in control sites support a broader range of opportunistic species, reflecting greater variability in community composition.

Environmental drivers underpinning these differences include sediment stabilisation and organic enrichment in *Chaetopterus* habitats. Stabilised sediments supported more homogeneous communities, as evidenced by tighter clustering in the nMDS plot and higher within-group similarity compared to control sites. These conditions favoured specialist taxa such as detritivores and deposit feeders. Conversely, control sites, characterised by dynamic sediment turnover and reduced organic content, supported a more variable community composition dominated by opportunistic species that thrive in heterogeneous substrates.

Key taxa driving dissimilarity further illustrate these patterns. Amphipods, particularly detritivorous species, were significantly more abundant in *Chaetopterus* habitats. These stabilised environments provided ideal burrowing conditions and reduced sediment resuspension (Rabaut et al., 2007), while organic-rich microhabitats supported species reliant on organic-rich sediments (Marsden & Rainbow, 2004). Anecdotal observations of epiphytic algae on *Chaetopterus* tubes suggest potential additional trophic resources for herbivorous amphipods (Duffy, 1990). Similarly, Davidson and Duffy (1992) documented red algae in a muddy sand habitat dominated by *Chaetopterus* with algal cover attached to the worm tubes exceeding 15%.

In contrast, taxa such as Phoxocephalidae amphipods and the polychaete *Prionospio multicristata* were more prevalent in control sites, reflecting their adaptability to coarser, less stable sediments. Phoxocephalidae thrive in mixed sediment environments where sediment turnover creates feeding opportunities (DeWitt, 1988; Conlan, 1994), while *P. multicristata* exploits disturbed habitats characterised by fluctuating sedimentation rates (Pearson &

Rosenberg, 1977). These patterns reflect the dynamic nature of control sites and their capacity to support taxa with broad ecological tolerances.

The interplay between sediment stabilisation in *Chaetopterus* habitats and variability in control sites drives clear differences in community composition. *Chaetopterus* habitats foster specialised, homogeneous communities, while control sites exhibit greater variability due to their dynamic sedimentary conditions. These findings emphasise the importance of sediment modification in shaping macroinvertebrate communities and highlight the broader ecological role of *Chaetopterus* in soft-sediment ecosystems.

The distinct community compositions observed in this study have important implications for ecosystem function. By stabilising sediments, enriching organic matter, and creating structurally complex habitats, *Chaetopterus* promotes biodiversity and supports taxa with specific adaptations to organic-rich environments. Control sites, in contrast, favour generalist and opportunistic species that thrive in less stable, dynamic conditions. This contrast underscores the ecological importance of *Chaetopterus* as a habitat-forming species and its contribution to ecosystem stability and resilience.

2.4.3.1 Functional group shifts in Chaetopterus-modified habitats

The findings demonstrate that *Chaetopterus* tube mats significantly influence functional group (FG) composition within benthic communities, as indicated by PERMANOVA results (p = 0.001 for habitat, site, and habitat × site interaction). This highlights the role of *Chaetopterus* as a habitat-modifying species, with its effects on FG composition shaped by habitat alterations and local environmental factors, including sediment grain size, organic content, and tube mat density. These results suggest that *Chaetopterus* not only modifies physical habitat structure but also influences broader ecological processes, potentially affecting species interactions and ecosystem function.

The functional group composition in *Chaetopterus* habitats was dominated by surface-oriented groups, including FG26 (soft-bodied, deposit/grazer/predator, sediment depth $\leq$3 cm, freely mobile, burrower, small/medium-bodied) and FG36 (rigid, predator/scavenger, sediment depth $\leq$3 cm, freely mobile, medium-bodied). FG26 species, such as Amphipoda sp., exploit stabilised sediments enriched with organic matter, benefiting from traits like deposit feeding, grazing on biofilms, and opportunistic predation (Marsden & Rainbow, 2004). FG36 species, such as *Halicarcinus cookii*, thrive within the structural complexity of tube mats, where stabilised sediments provide refuges, reduced predation risk, and enhanced prey availability

(McLay, 1988). These traits align closely with the enriched, low-energy microhabitats created by *Chaetopterus* tube mats.

In contrast, control sites exhibited greater FG variability, reflecting the dynamic sedimentary conditions of these habitats. Dominant groups included FG22 (soft-bodied, deposit feeders, burrowers) and FG34 (rigid, suspension feeders, sedentary). FG22 species, such as *P. multicristata*, are well-adapted to coarser sediments with high turnover, where burrowing enables access to redistributed organic material (Pearson & Rosenberg, 1977). FG34 species, such as *Nebalia* sp., rely on sediment resuspension to sustain nutrient delivery, a process less prevalent in stabilised *Chaetopterus* habitats (Kristensen, 2000). These groups highlight the functional diversity promoted by dynamic sediment conditions in control sites.

The shift in FG composition reflects the trade-offs inherent in *Chaetopterus*-modified habitats. Stabilisation of surface sediments promotes surface-oriented FGs that enhance organic matter turnover and nutrient cycling but suppresses deeper sedimentary processes such as mixing and resuspension. These findings align with studies on other habitat-forming species, such as *Lanice conchilega*, where structural complexity enhances surface functions at the expense of deeper sedimentary diversity (Rabaut et al., 2007; Van Hoey et al., 2008).

The broader ecological implications of these functional group shifts include enhanced redundancy among surface-oriented groups in *Chaetopterus* habitats, which supports ecosystem resilience to environmental stress. However, reduced diversity in sediment-mixing and suspension-feeding processes may hinder key ecosystem functions, such as nutrient flux and benthic-pelagic coupling (De la Torriente et al., 2020). Predator/scavenger groups like FG36 (e.g., *H. cookii*) likely play a pivotal role in trophic dynamics by regulating prey populations and indirectly influencing sediment properties and nutrient cycling. These trophic interactions underscore the cascading effects of *Chaetopterus* on ecosystem functioning.

Finally, the significant habitat × site interaction highlights the context-specific nature of *Chaetopterus*' ecological impacts. Differences in sediment properties, organic content, and tube mat density across sites mediate the responses of functional groups to habitat modification. Similar findings in other biogenic habitats emphasise the importance of site-level variability in shaping ecosystem functions (Thomsen et al., 2011). These results demonstrate the critical role of *Chaetopterus* in reshaping benthic ecosystems and highlight the need for site-specific management strategies to balance surface-oriented benefits with the preservation of deeper sedimentary functions.

2.4.4 Limitations and future research opportunities

2.4.4.1 Study limitations

This study provides valuable insights into the ecological impacts of *Chaetopterus* on benthic community composition and ecosystem functioning, though several limitations must be acknowledged. First, while functional traits were used as proxies to infer ecosystem processes, direct measurements of biogeochemical parameters such as nutrient concentrations, sediment oxygen demand, and microbial interactions were not undertaken. These factors are critical for validating assumptions about nutrient cycling and organic matter turnover, which underpin the ecosystem functions associated with *Chaetopterus* tube mats (Villnäs et al., 2013; Mäkelin et al., 2024). Including such measurements could provide a more robust understanding of the ecological mechanisms at play.

The temporal scope of this study was also limited, potentially overlooking seasonal variations in *Chaetopterus* activity and its effects on benthic communities. Changes in environmental conditions across seasons, such as sediment dynamics (Urlich, 2020) and organic matter availability (Canuel & Martens, 1993; Bright & Mager, 2017), are likely to influence both *Chaetopterus* and the associated fauna. Similarly, the study's geographical focus was constrained to a single area, meaning the findings may not fully represent the broader impacts of *Chaetopterus* across different sedimentary environments. Regional variations in sediment grain size, hydrodynamics, and organic content could alter the ecological effects observed here, as has been reported for other habitat-forming species like *Lanice conchilega* (Van Hoey et al., 2008; Thomsen et al., 2011). Furthermore, the study's depth range was limited by the operational constraints of SCUBA, potentially excluding deeper habitats where the population dynamics and impacts of *Chaetopterus* may differ.

Another limitation lies in the taxonomic resolution of the species identified. The exclusion of certain functional groups due to insufficient taxonomic differentiation may have underestimated their contributions to the observed community dynamics. This limitation emphasises the need for enhanced taxonomic resources and more comprehensive identification protocols. Additionally, species accumulation curves suggest that increased sampling could reveal further species, particularly rarer taxa, underscoring the importance of sampling effort in fully characterising benthic communities.

Lastly, while traits were used as proxies for ecosystem functions in this study, their direct relationship with ecosystem processes was not validated through mechanistic experiments, as also noted by Greenfield (2013). Traits such as feeding mode or sediment position may shift across environmental gradients, potentially altering their functional roles. For example, the caprellid amphipod *Caprella mutica* demonstrates remarkable feeding adaptability, shifting between grazing, scavenging, filter feeding, and predation in response to environmental conditions (Sara, 1986). Additionally, functional redundancy does not guarantee ecological equivalence, as species with similar traits might differ in their efficiency or impact on key ecosystem processes. This limitation underscores the need for targeted experiments to confirm trait–function relationships, particularly in complex and variable soft-sediment environments (Snelgrove et al., 2014).

Despite these limitations, this study provides a foundational understanding of the ecological role of *Chaetopterus* as a habitat engineer. Future research, addressing these gaps, will enable a more detailed exploration of its impacts, offering a comprehensive understanding of how *Chaetopterus* shapes benthic ecosystems across spatial and temporal scales. Such insights are critical for balancing the ecological benefits of habitat-forming species with the preservation of broader ecosystem functionality. Additionally, the uncertain origins of *Chaetopterus* species in New Zealand highlight the need for further investigation to clarify its ecological role and inform potential management strategies.

2.4.4.2 Recommendations for future research

To address the limitations of this study and deepen our understanding of *Chaetopterus'* role in benthic ecosystems, future research should adopt a multifaceted and nuanced approach. While *Chaetopterus* enhances local biodiversity through habitat modification, its potential to reduce spatial heterogeneity and exclude economically valuable species, such as scallops, warrants closer examination.

Long-term studies are needed to capture temporal variability in *Chaetopterus'* impacts, including seasonal and inter-annual fluctuations. This would help clarify whether the observed effects on community composition and ecosystem processes are consistent over time or vary with changes in environmental conditions, such as recruitment dynamics or organic matter availability. Such studies could also assess the resilience of benthic ecosystems to *Chaetopterus* expansion and the implications for ecosystem functioning.

Further research should explore the processes underpinning nutrient cycling and sediment biogeochemistry in *Chaetopterus* habitats. Quantifying sediment organic carbon, nitrogen, and key nutrient concentrations (e.g., ammonium, nitrate, phosphate) around tube mats would illuminate patterns of nutrient enrichment. Complementing these measurements with sediment oxygen demand and redox potential would provide insights into organic matter degradation and sediment stability. Advanced techniques such as stable isotope analysis and microbial community profiling could trace the pathways of nutrient cycling and identify the contributions of microbial interactions to ecosystem processes. To directly assess bentho-pelagic coupling, deploying benthic flux chambers would quantify nutrient exchanges between sediments and the water column.

Expanding the spatial scale of research is crucial for understanding the generalisability of *Chaetopterus'* impacts. By examining multiple regions across New Zealand's coastline with varying sediment types, organic content, and hydrodynamic conditions, future studies could determine how environmental context modulates *Chaetopterus'* ecological effects. Such regional comparisons would also reveal how habitat modification by *Chaetopterus* interacts with other benthic processes and species, providing valuable insights into its role within broader ecosystem dynamics.

Identifying the density thresholds at which *Chaetopterus* tube mats significantly influence community composition, sediment stabilisation, and functional redundancy would provide critical insights for management. Research should assess how these thresholds vary across different sediment types and hydrodynamic regimes, helping to predict the impacts of *Chaetopterus* in unstudied regions. Additionally, investigating whether *Chaetopterus* competes with or facilitates other habitat-forming species, such as seagrass beds or other polychaetes, would shed light on its broader ecological implications. This would help clarify whether *Chaetopterus* promotes ecosystem diversity or contributes to homogenisation at larger spatial scales.

Beyond its effects on macrofaunal communities, *Chaetopterus* tube mats may also influence higher trophic levels, including larger, mobile species such as demersal fish. Biogenic structures have been shown to enhance fish abundance and diversity by providing shelter, prey resources, and altered hydrodynamic conditions (Zalmon, 2011; Ryer et al., 2007). However, the role of *Chaetopterus* as a fish habitat in New Zealand's coastal ecosystems remains poorly understood. Future studies should examine fish assemblages associated with *Chaetopterus* habitats compared to unmodified soft sediments, using methods such as baited remote underwater video stations (BRUVS) or diver-based surveys. Understanding these interactions would provide a more holistic perspective on the ecological significance of *Chaetopterus* and its role in supporting broader food web dynamics.

The observed reduction in spatial heterogeneity within *Chaetopterus* habitats, highlights the importance of understanding the trade-offs associated with its habitat modification. While local species richness and diversity may increase, the potential loss of regional-scale diversity poses challenges for ecosystem management. Investigating how *Chaetopterus* influences habitat heterogeneity, biodiversity, and ecosystem resilience across sedimentary contexts would provide critical insights into its dual role as a biodiversity enhancer and suppressor of deeper sediment processes. These findings would inform conservation strategies aimed at balancing the benefits of enhanced surface processes with the preservation of sediment mixing and regional-scale diversity.

Incorporating these research directions would not only address key gaps in our understanding of *Chaetopterus'* ecological impacts but also provide valuable guidance for managing soft-sediment ecosystems. By recognising the trade-offs between local and regional diversity and accounting for site-specific variability, future research could ensure a balanced approach to conserving benthic habitats shaped by this habitat-forming species.

2.4.5 Conclusion

This study highlights the transformative role of *Chaetopterus* as an ecosystem engineer, reshaping benthic habitats by enhancing stability, increasing structural complexity, and altering sediment properties. As defined by Jones et al. (1994), ecosystem engineers are organisms that "directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials." *Chaetopterus* exemplifies this definition by modifying, maintaining, and creating habitats. Its dual role as an autogenic engineer is evident in the physical structure of its tubes, which provide stabilised environments that enhance biodiversity and functional diversity. Simultaneously, as an allogenic engineer, it transforms sediment properties—such as grain size distribution and organic content—through mechanical stabilisation and sediment consolidation, further altering habitat conditions and fostering ecological diversity.

The impacts of *Chaetopterus* extend beyond sediment modification. In predominantly featureless soft-bottom habitats, the physical presence of *Chaetopterus* tubes introduces critical ecological complexity, effectively transforming the seafloor into a mosaic of microhabitats. These structures create stabilised and enriched surface sediments, providing ecological niches for a variety of benthic organisms that might otherwise struggle to thrive in the relatively uniform conditions of soft-sediment environments. For instance, the tubes offer surfaces for biofilm development and refuge for small invertebrates, reducing predation risks and enhancing resource availability. This structural complexity supports a diverse range of functional groups, from deposit feeders exploiting detritus-rich sediments to predators taking advantage of increased prey abundance. By fostering such trophic interactions and habitat heterogeneity, *Chaetopterus* amplifies species richness and functional diversity within benthic environments.

Recognising the habitat-modifying influence of *Chaetopterus* is essential for marine conservation and management. As pressures on benthic ecosystems mount, understanding the ecological roles of such species provides critical insights for maintaining biodiversity, ecosystem functioning, and the services they underpin. A notable outcome of this research is the identification of context-dependent effects, with variations in macroinvertebrate community composition linked to site-specific factors such as sediment grain size, organic content, and *Chaetopterus* density. These findings highlight the importance of local environmental conditions in modulating the ecological impacts of *Chaetopterus*, underscoring the need for broader spatial studies to understand its role across diverse habitats.

This study also contributes valuable insights into the largely unexplored role of *Chaetopterus* within New Zealand's marine ecosystems. Despite its widespread occurrence, research into its ecological functions and origins in this region remains scarce. By demonstrating how *Chaetopterus* influences sedimentary habitats and benthic community composition, this study helps fill critical knowledge gaps and provides a foundation for future research into its ecological significance. Understanding the origin of *Chaetopterus* is particularly important for guiding conservation and management strategies. If this species is confirmed to be native, its habitat-engineering role highlights the importance of prioritising the protection of these unique ecosystems. Conversely, if identified as an invasive species, strategic management decisions will be required to mitigate potential ecological impacts while considering its influence on local biodiversity and ecosystem functioning.

In conclusion, *Chaetopterus* plays a key role in shaping benthic communities, supporting biodiversity, and influencing ecosystem functions through its habitat-engineering activities, regardless of its origin. While enhancing surface-oriented processes such as organic matter turnover and nutrient cycling, its presence may also constrain deeper sediment dynamics and bioturbation, highlighting the trade-offs associated with habitat modification. These findings contribute to a broader understanding of habitat-forming species in marine ecosystems and provide valuable insights for the conservation and management of New Zealand's soft-sediment habitats amid increasing environmental change.

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Appendices

Appendix A: Description of *C. chaetopterus-A*

Excerpt from Tricklebank et al. (2001, p. 14):

“**Colour**: Live colour overall is very pale yellow, slightly more intense on the ventral plastron and notopodia of region A, and the dorsal cupule of B2. Surface pigmentation is only prominent on the anterior 'funnel' of the mouth and peristomium and their margins, consisting of densely scattered reddish points. Palps are pale or variably tinged reddish. Notopodial lobes of region C have some pigment on extremities and mid-dorsal surface, enough to tinge with reddish colour, not visible in gravid worms. Black eye pigment is present as a ribbon-shaped area in the crease between the peristomial lateral flap and A1/palp insertion, thus partly obscured in adults, with only the ribbon edge exposed. The ribbon often appears staple-shaped (bend outermost) in the posterior view. On B2, the expanded dorsal folds and pouching of the prominent intestinal surface are a very dark green (typical of *Chaetopterus*), and the dark colouration of the intestine continues to be visible beneath the paddles of B3-B4, although the intestine narrows beyond B3. (Specimens become paler and have little noticeable surface pigment if maintained in aquaria without an added food supply.

Dimensions and meristics: Maximum preserved length 79 mm, mean mature adult length 62.7 mm (sample of 9 sexually mature adults, relaxed before fixation). Region A of 9 chaetigers with the 9th with an uncinal torus. Uncommonly, region A has 10 chaetigers without an uncinal torus on the last chaetiger (13%, n62), or 9 chaetigers without an uncinal torus on the last chaetiger (1 specimen). This variation is attributed to the side effect of regeneration of region A following partial predation or damage. All juveniles examined had 9 chaetigers in region A. Maximum number of C chaetigers is 28 (mean 23, n19). Region A maximum length is 14 mm (mean 10.3, n24). In specimens relaxed before fixation, region A is slightly narrower than long (mean 0.86, n19). However, in contracted bulk-fixed specimens, region A is wider than long. Region B is slightly shorter than region C (mean 0.83, n17). In life, region A is distinctly narrower than long, and region B is distinctly shorter than region C.

General morphology: The anterior ventral lip surrounding the mouth is a spade-shaped round-edged wedge, in life neatly matching the inner curve of the tube. The prostomium is not distinct but the dorsal lip is slightly raised near the midline, and a small mound of tissue anterior to the anterior termination of the dorsal food groove probably represents the prostomium. Grooved palps are about as long as the width of the anterior end. The notopodial lobe of A4 is shorter than the others; in side view, the length of the chaetal fascicle is noticeably shorter. A clear blister-like swelling ('bulla') at the base of region A notopodial lobes is usually visible in life on all chaetigers except A1, largest around A5-6. Notochaetae of region A are typical of the genus, having slender shafts embedded in notopodial lobes and terminating in leaf-like tips (lanceolate chaetae) exposed along the lobe's outer (ventral) edge, with the distalmost chaetae having the slenderest tips. Lanceolate chaetae are largest on about A5, with up to 40 per fascicle, in middle A parapodia sometimes overlapping as if in 2 rows, then slenderer and in single rows in posterior A chaetigers. A4 has 5-12 heavy, reddish-brown to dark brown spines with chisel-like tips, with the dorsalmost 2-3 spines paler and more slender. Spine tip has a rounded anterior edge, concave medially, and rises to a pointed posterior edge.

Region B morphology is typical for the genus, with 5 segments as follows: B1 with dorsal aliform notopodia and ventral sucker; B2 with dorsal green digestive organ, dorsal cupule, and ventral sucker; B3-5 with dorsal bell-shaped paddle-pistons and ventral suckers. B1 dorsal notopodial lobes' outer and inner edges are curved for most of their length, with distal inner edges straight and vertical, slightly concave, forming a contact/mating surface that in life adheres by suction, forming a complete ring. On the inner surface of the ‘ring,’ a thin flange of epidermis occurs anterior to a deep groove and anterior to the distal contact/mating surface. B1 notopodia have embedded slender needle-like spines.

B1 sucker has uncinal lines on the anterior and posterior margins but not meeting laterally, with anterior left and right lines overlapping where they meet midventrally. Anterior and posterior uncinal bands are in a wide irregular row, with uncini not uniformly in line, rather randomly non-overlapping so that the uncinal band width is double or triple the length of individual uncini, especially towards the midline. B2 sucker is unique with a double rim on its anterior edge. An uncinal line is present on the posterior rim, but this rim continues anteriorly without uncini. This rim edge overlaps a part of the sucker which has an anterior line of uncini. In live animals, this morphological feature is clearly apparent but less so in preserved specimens. B3 sucker has an uncinal line posteriorly only. Uncinal bands of B2–3 are in wide irregular rows as in B1. B4 and B5 suckers also have an uncinal line posteriorly only, and B4-5 sucker shape and size are very similar to B3. Uncinal bands of B4–5 are less wide, approximating a single row. A very small unicinal group occurs on the lateral edge of B3–5 paddles.

Each region C chaetiger has a ventral neuropodial flap/torus divided medially into two lobes. C1 flap is much wider than those following, and transitional between the post edge of B5 and C2 flap. All C chaetigers also have a lateral flap/torus with an uncinal band, and a weakly-developed neuropodial dorsal cirrus, most apparent on the first few C lateral tori. Region C region uncini usually have 7 teeth per uncinus. While there are not actually two separate rows of uncini, the position of each uncinus only partly overlaps its neighbour so that again there is an appearance of irregular 2 rows, especially on the lateral neuropodial torus. Region C notopodial lobes are slender with weakly clavate bases, with embedded slender needle-like spines, about 6 per fascicle.

Uncini morphology: All uncini have tendons embedded in the parapodial torus. At the top of the uncinus (uncinus oriented with teeth curved down, 'top' towards the outer edge of the torus it is embedded in) a short tendon projects at right angles. At the bottom, a much longer thicker tendon is present. The top tendon is more easily detached, and its presence is more difficult to detect.

A9 uncinal band, viewed in entirety, appears to consist of a single row of uncini at each end, broadening to an irregular band at least 2 uncinal lengths wide in the mid-band. Under greater magnification, densely-packed uncini are seen not to be in separate rows but rather overlapping at random distances. Uncini furthest from the torus edge are more embedded and may be replacements still growing. Uncini have 5 free teeth (topmost much smaller). A9 uncini are about 90 µm in length, 45 µm in width, and are the largest uncini on the body.

B1 anterior and posterior rows have uncini with 6 free teeth present. Uncini are about 70 µm in length, 35 µm in width. The upper tendon is slightly shorter than the uncinus, the lower tendon is about 2.5 times the uncinus length. The B5-paddle lateral group is a compact group of about 50 uncini. 9-11 free teeth are present. Uncini are about 45 µm in length, 20 µm in width, and are the smallest on the body. The upper tendon is very short, and the lower tendon is about the same length as the uncinus. Lateral uncini of C1 have 6 teeth (7 + non-free) 75 µm long, 35 µm wide. C1 ventral uncini are in a near-uniform row. Uncini have 8-9 free teeth (9-10th not yet free) and are about 55 µm long, 25 µm wide.

Tube: Tube wall is thin, pale, parchment-like, easily torn, consisting of several adhering translucent layers (laminations), with the outer layer lightly encrusted with a 'camouflage' of local sediment and available coarser particles. Dried-out tubes have a papery, 'dry leaf' fragility. Tube maximum diameter is 10 – 15 mm in adults, tapering to narrower openings at both ends, with more pronounced taper over the last 2 to 4 mm. Tube length is variable but 150 mm or more in large adults. Tube active ends are paler than the rest of the tube, more or less uncoated, sometimes with reinforcing rings' of prior tube endings. Worms rebuild damaged tube ends, shaping direction of opening to suit, and seal off unwanted openings so that more than one 'opening' at an end may be present."

Appendix B: Descriptions of drop camera stations

Table A1. *Summary of drop camera stations from the initial survey in East Bay, Queen Charlotte Sound, detailing station number, depth, geographic coordinates (NZTM), substratum type, and the relative abundance of* Chaetopterus *and associated fauna. Relative abundance categories include descriptions of life stages (e.g., juveniles or adults) and notable features such as dead or empty tubes.*

No.	Depth (m)	Coordinates (NZTM)	Substratum	Relative abundance
1	1, 1.9m	1709988.7,5440979.1	silt & clay,	abundant,
2	2, 2.8m	1710029.4,5440971.6	silt & clay,	occasional (adults)
3	3, 1.8m	1710182.4,5440805.4	silt & clay,	abundant (juveniles) occasional (adults)
4	4, 1.7m	1711120.6,5440849.8	silt & clay,	
5	5, 2.9m	1710977.1,5440840.1	silt & clay,	abundant (juv), common (common)
6	6, 3.2m	1710905.2,5440856.0	silt & clay,f sand,	
7	7, 3.6m	1711132.4,5440917.2	silt & clay,	occasional (juveniles)
8	8, 6.4m	1712095.2,5440776.2	silt & clay,cobble,	horse mussel, very occ adults
9	9, 3m	1712157.2,5440752.8	silt & clay,	abundant,
10	10, 4.8m	1712222.5,5440831.5	cobble,silt & clay,	abundant,
11	11, 10.9m	1712130.5,5440854.8	silt & clay,	common,
12	12, 6.3m	1712289.8,5440816.2	silt & clay,	abundant,
13	13, 8.4m	1712372.5,5440871.5	silt & clay,	common, but also bare patches
14	14, 6.7m	1712456.5,5440916.8	silt & clay,f sand,	abundant,
15	15, 7.4m	1712933.0,5442304.5	silt & clay,nat. shell,f sand,	occasional and patchy
16	16, 9.4m	1712623.5,5442337.9	silt & clay,nat. shell,cobble (occ)	common,
17	17, 8.8m	1712704.8,5442315.2	silt & clay,f sand,nat. shell,	abundant,
18	18, 2.5m	1714444.5,5443085.3	silt & clay, nat. shell, red algae bed	occasional,
19	19, 7.5m	1714411.1,5443143.7	silt & clay,f sand,nat. shell,	abundant (dead and alive)
20	20, 6m	1714431.1,5443174.4	silt & clay,f sand,nat. shell,	dead tubes, large bare patches
21	21, 7.7m	1714417.8,5443255.4	silt & clay,cobble (occ)f sand,nat. shell,	dense patches
22	22, 4.7m	1715077.6,5444509.0	silt & clay,f sand,	nothing
23	23, 5.6m	1715119.5,5444549.4	cobble,boulder,	common,
24	24, 10.4m	1715105.8,5444555.2	silt & clay,f sand,	common, lots of dead tubes
25	25, 11.6m	1715121.0,5444625.5	f sand,silt, rock outcrops,	occasional patches
26	26, 9.1m	1715221.3,5444952.1	f sand,nat. shell,silt,cobble,	occasional,
27	27, 4.9m	1715340.8,5445001.5	f sand,nat. shell,silt & clay,	occasional,
28	28, 3.9m	1715431.3,5445926.7	f sand,silt,nat. shell,	occ juveniles
29	29, 10.9m	1715298.9,5446009.7	f sand,silt & clay,nat. shell,	common,
30	30, 14m	1715117.1,5446095.6	f sand,silt & clay,nat. shell,	common,
31	31, 6.2m	1715152.4,5446275.8	f sand,nat. shell,	abundant,
32	32, 4m	1715096.2,5446377.7	f sand,nat. shell,	occasional,
33	33, 2,7m	1715073.9,5446430.4	f sand,nat. shell,	occasional,
34	34, 3.8m	1714686.1,5446075.7	f sand,cobble,	abundant patches
35	35, 6.3m	1714685.4,5446011.3	f sand,silt,nat. shell,	abundant,
36	36, 8.4m	1714654.5,5445919.6	f sand,silt,nat. shell,	abundant,
37	37, 6.4m	1713693.6,5445041.1	silt & clay,	common, abundant patches
38	38, 4.2m	1713572.0,5445042.0	silt & clay,	common, abundant patches
39	39, 6.9m	1713551.5,5444948.6	silt & clay,f sand,	abundant stunted tubes
40	40, 9m	1712705.6,5444228.9	f sand,nat. shell,silt & clay,	occasional, dead tubes
41	41, 6.1m	1712587.7,5444257.8	f sand,silt & clay,nat. shell,	nothing
42	42, 7.8m	1712467.4,5444107.0	cobble,f sand,silt,nat. shell,	common,
43	43, 3.2m	1711330.1,5445410.9	cobble,f sand,	common,
44	44, 5m	1711390.1,5445548.0	f sand,nat. shell,silt,	nothing
45	45, 4.9m	1711421.4,5445631.8	pebbles,nat. shell,	abundant,
46	46, 8.5m	1711388.1,5445662.2	pebbles,sand,nat. shell,	common,
47	47, 13m	1711345.1,5445645.0	sand,nat. shell,silt & clay,	abundant in patches
48	48, 10.5m	1709501.6,5442191.7	cobble,silt & clay,	common,
49	49, 7.4m	1709546.5,5442161.6	silt & clay,cobble (occ)	abundant patches
50	50, 7.6m	1709608.6,5442172.0	f sand,silt & clay,nat. shell,	nothing
51	51, 10m	1709679.4,5442191.4	f sand,nat. shell,silt & clay,	abundant patches, empty tubes

Appendix C: Variables, *Chaetopterus* properties, and diversity indices across all sites

Table A2. *Mean (SE) values for environmental variables,* Chaetopterus *properties, and key diversity indices for each habitat site (n = 5). Variables include depth, median grain size (MGS), mud content, silt, number of* Chaetopterus *individuals and* Chaetopterus *cover, number of species (S), number of individuals (N), Shannon-Wiener diversity index (H'), and Pielou's evenness index (J'). Control and* Chaetopterus *sites are presented for comparison across these parameters.*

Site	**Habitat**	**Depth (m)**	**Organic content (%afdw)**	**Median Grain Size (µm)**	**Mud content (% < 63 µm)**	**Silt content (% < 2 µm)**	**Number of *Chae.* (# 0.02m^2)**	**Number of *Chae.* (# m^2)**	***Chae.* cover (% m^2)**	**S**	**N**	**H'**	**J'**
1	Control	8.9 (0.5)	3.0 (0.2)	206 (29)	10.9 (2.9)	1 (0.4)	-	-	-	9.6 (4.4)	31 (15)	1.69 (0.48)	0.8 (0.2)
	Chaetopterus	9.5 (0.9)	3.9 (0.2)	114 (33)	36.5 (8.9)	7 (2.1)	16.4 (10.2)	577 (432)	62 (16)	22.8 (5.4)	62 (18)	2.67 (0.30)	0.9 (0.03)
2	Control	2.3 (0.4)	2.1 (0.1)	150 (8)	10.5 (2.1)	1 (0.6)	-	-	-	14.6 (3.3)	41 (10)	2.21 (0.30)	0.8 (0.1)
	Chaetopterus	2.2 (0.3)	2.8 (0.9)	174 (5)	9.4 (2.2)	2 (0.4)	6.0 (1.9)	285 (104)	83 (10)	12.8 (2.2)	21 (4)	2.38 (0.23)	0.9 (0.03)
3	Control	2.8 (0.1)	2.3 (0.2)	172 (5)	10.8 (2.4)	1 (0.1)	-	-	-	18.0 (1.9)	55 (8)	2.27 (0.29)	0.8 (0.1)
	Chaetopterus	2.8 (0.3)	2.1 (0.1)	212 (9)	9.4 (2.2)	2 (0.4)	14.8 (4.5)	517 (270)	59 (21)	17.0 (3.3)	70 (26)	2.00 (0.31)	0.7 (0.1)
4	Control	6.3 (0.6)	1.7 (0.1)	191 (27)	11.9 (3.8)	1 (0.6)	-	-	-	11.0 (2.9)	22 (6)	1.99 (0.27)	0.8 (0.1)
	Chaetopterus	7.0 (0.4)	2.7 (0.1)	181 (38)	25.5 (7.0)	4 (1.4)	6.8 (3.7)	328 (185)	86 (12)	15.6 (3.5)	36 (9)	2.34 (0.23)	0.9 (0.02)
5	Control	7.7 (1.2)	1.9 (0.04)	198 (9)	9.1 (2.1)	1 (0.2)	-	-	-	13.0 (3.1)	35 (10)	2.15 (0.42)	0.8 (0.1)
	Chaetopterus	7.9 (1.0)	2.9 (0.1)	154 (29)	16.9 (3.1)	3 (0.7)	14.6 (11.4)	467 (357)	56 (7)	20.6 (5.4)	69 (29)	2.47 (0.11)	0.8 (0.1)
6	Control	5.0 (0.1)	1.3 (0.03)	185 (9)	5.1 (1.0)	1 (0.2)	-	-	-	10.2 (2.9)	26 (9)	1.98 (0.38)	0.9 (0.1)
	Chaetopterus	6.6 (0.5)	2.0 (0.1)	231 (13)	11.5 (4.1)	2 (0.9)	11.2 (4.3)	304 (113)	48 (3)	17.4 (2.7)	45 (18)	2.26 (0.46)	0.8 (0.2)
7	Control	4.2 (0.3)	1.5 (0.1)	230 (7)	4.1 (1.5)	1 (0.2)	-	-	-	13.8 (2.2)	26 (9)	2.44 (0.13)	0.9 (0.03)
	Chaetopterus	5.5 (0.2)	2.1 (0.1)	236 (11)	8.6 (1.0)	2 (0.3)	10.6 (7.6)	475 (323)	81 (10)	18.8 (6.5)	66 (51)	2.26 (0.34)	0.8 (0.1)
8	Control	6.5 (0.7)	2.4 (0.1)	534 (84)	4.5 (0.6)	0.4 (0.1)	-	-	-	20.4 (2.5)	89 (26)	2.37 (0.11)	0.8 (0.03)
	Chaetopterus	5.6 (0.2)	3.1 (0.03)	469 (29)	9.3 (0.4)	2 (0.1)	34.0 (10.2)	1465 (301)	78 (9)	25.4 (5.6)	83 (25)	2.59 (0.39)	0.8 (0.1)
9	Control	8.2 (0.4)	1.7 (0.1)	226 (8)	4.4 (0.9)	1 (0.3)	-	-	-	20.0 (7.1)	57 (32)	2.59 (0.26)	0.9 (0.1)
	Chaetopterus	8.4 (0.6)	4.1 (0.1)	322 (75)	20.3 (3.0)	5 (0.8)	28.6 (8.4)	638 (166)	42 (13)	23.2 (3.0)	48 (11)	2.87 (0.16)	0.9 (0.03)
10	Control	13.0 (0.2)	2.9 (0.05)	356 (39)	5.3 (1.4)	1 (0.2)	-	-	-	14.0 (4.5)	44 (9)	1.94 (0.59)	0.7 (0.1)
	Chaetopterus	12.5 (0.6)	5.3 (0.5)	65 (28)	50.6 (6.4)	9 (2.4)	24.6 (10.2)	790 (341)	57 (4)	26.2 (1.9)	62 (19)	2.94 (0.21)	0.9 (0.1)

Appendix D: Summed abundance data from each habitat type

Table A3. *Summed abundance data from each habitat type (control and* Chaetopterus*) including taxa name and group.*

		Habitat group	
Taxa	***Group***	Control	*Chaetopterus*
Sponge Unid.	Porifera	0	2
Arachnanthus sp.	Anthozoa	3	0
Edwardsia sp.	Anthozoa	2	2
Nemertea	Nemertea	17	16
Phascolosoma annulatum	Sipuncula	3	34
Phascolosoma sp.	Sipuncula	0	17
Leptochiton inquinatus	Polyplacophora	1	4
Amalda mucronata	Gastropoda	1	0
Berthella sp.	Gastropoda	0	2
Cominella adspersa	Gastropoda	1	0
Turbo Smaragada	Gastropoda	0	2
Zeacolpus sp.	Gastropoda	0	1
Philine auriformis	Opisthobranchia	7	0
Philine powelli	Opisthobranchia	2	0
Bivalvia Unid.	Bivalvia	2	0
Arthritica bifurca	Bivalvia	1	1
Thracia sp.	Bivalvia	1	0
Bassina yatei	Bivalvia	3	0
Borniola reniformis	Bivalvia	0	9
Cardita aoteana	Bivalvia	0	2
Corbula zelandica	Bivalvia	27	35
Divalucina cumingi	Bivalvia	1	0
Dosinia lambata	Bivalvia	5	0
Dosinia subrosea	Bivalvia	5	1
Gari (psammobia) convexa	Bivalvia	22	0
Gari sp.	Bivalvia	0	1
Gari stangeri	Bivalvia	49	0
Gonimyrtea concinna	Bivalvia	0	1
Hiatella arctica	Bivalvia	0	1
Hiatula silequens	Bivalvia	1	0
Hunkydora novozelandica	Bivalvia	1	0
Leptomya retiaria retiaria	Bivalvia	14	146
Limaria orientalis	Bivalvia	0	1
Macomona liliana	Bivalvia	23	8
Melliteryx parva	Bivalvia	0	1
Modiolus areolatus	Bivalvia	0	1
Musculus impactus	Bivalvia	0	4
Myadora striata	Bivalvia	2	0
Nucula hartvigiana	Bivalvia	27	37
Purpurocardia purpurata	Bivalvia	0	3
Ruditapes largillierti	Bivalvia	1	5
Scalpomactra scalpellum	Bivalvia	2	5
Scintillona zelandica	Bivalvia	2	36
Serratina charlottae	Bivalvia	0	2
Tawera spissa	Bivalvia	39	4
Tellinota edgari	Bivalvia	2	0
Theora lubrica	Bivalvia	1	0
Zemysina sp.	Bivalvia	7	48
Oligochaeta	Oligochaeta	3	0
Polychaeta Indet.	Polychaeta:	0	1
Amphinomidae	Polychaeta: Amphinomidae	0	1
Ceratonereis sp.	Polychaeta: Nereididae	0	8
Nereis falcaria	Polychaeta: Nereidae	0	4
Orbinia papillosa	Polychaeta: Orbiniidae	25	0
Scoloplos cylindrifer	Polychaeta: Orbiniidae	1	1

Taxa	***Group***	Control	*Chaetopterus*
Paraonidae	Polychaeta: Paraonidae	4	0
Boccardia sp.	Polychaeta: Spionidae	1	0
Paraprionospio pinnata	Polychaeta: Spionidae	7	0
Polydora sp.	Polychaeta: Spionidae	93	6
Prionospio aucklandica	Polychaeta: Spionidae	31	3
Prionospio multicristata	Polychaeta: Spionidae	147	15
Prionospio yuriel	Polychaeta: Spionidae	1	0
Spio readi	Polychaeta: Spionidae	3	0
Spiophanes modestus	Polychaeta: Spionidae	1	0
Magelona dakini	Polychaeta: Magelonidae	4	0
Phyllochaetopterus socialis	Polychaeta: Chaetopteridae	5	1
Barantolla lepte	Polychaeta: Capitellidae	281	174
Capitella sp.	Polychaeta: Capitellidae	1	0
Notomastus zeylanicus	Polychaeta: Capitellidae	28	157
Maldanidae	Polychaeta: Maldanidae	90	37
Armandia maculata	Polychaeta: Opheliidae	25	51
Travisia olens	Polychaeta: Opheliidae	0	1
Scalibregma inflatum	Polychaeta: Scalibregmidae	0	6
Phyllodocidae	Polychaeta: Phyllodocidae	3	13
Polynoidae	Polychaeta: Polynoidae	1	15
Hesionidae	Polychaeta: Hesionidae	17	75
Syllidae	Polychaeta: Syllidae	20	34
Exogoninae	Polychaeta: Syllidae	7	1
Nereidae (juvenile)	Polychaeta: Nereidae	6	31
Platynereis australis	Polychaeta: Nereidae	0	7
Glyceridae	Polychaeta: Glyceridae	24	76
Goniadidae	Polychaeta: Goniadidae	174	1
Aglaophamus sp.	Polychaeta: Nephtyidae	11	0
Nephtyidae	Polychaeta: Nephtyidae	1	0
Eunicidae	Polychaeta: Eunicidae	2	20
Lysidice ninetta	Polychaeta: Eunicidae	0	6
Marphysa sp.	Polychaeta: Eunicidae	0	3
Lumbrineridae	Polychaeta: Lumbrineridae	41	104
Dorvilleidae	Polychaeta: Dorvilleidae	2	67
Myriochele sp.	Polychaeta: Oweniidae	1	0
Ampharetidae	Polychaeta: Ampharetidae	1	4
Cirratulidae	Polychaeta: Cirratulidae	15	42
Flabelligeridae	Polychaeta: Flabelligeridae	1	1
Lagis australis	Polychaeta: Pectinariidae	1	3
Terebellidae	Polychaeta: Terebellidae	3	60
Sabellidae	Polychaeta: Sabellidae	0	5
Euchone pallida	Polychaeta: Sabellidae	10	6
Galeolaria hystrix	Polychaeta: Serpulidae	0	2
Nebalia sp.	Crustacea	0	15
Mysidacea	Mysidacea	13	13
Cumacea	Cumacea	10	0
Tanaidacea	Tanaidacea	8	108
Anthuridea	Isopoda	27	18
Eurylana arcuata	Isopoda	2	0
Natatolana sp.	Isopoda	4	0
Ampelisca sp.	Amphipoda	2	0
Lysianassidae	Amphipoda	61	7
Oedicerotidae	Amphipoda	26	0
Phoxocephalidae	Amphipoda	201	44
Urothoidae	Amphipoda	12	0
Amphipoda Unid.	Amphipoda	247	650
Paguridae	Decapoda	10	1
Alpheus novaezealandiae	Decapoda	0	10
Austrohelice crassa	Decapoda	0	1
Callianassa filholi	Decapoda	15	3

Taxa	***Group***	Control	*Chaetopterus*
Halicarcinus cookii	Decapoda	12	106
Hemiplax hirtipes	Decapoda	9	14
Liocarcinus corrugatus	Decapoda	0	1
Nectocarcinus benetti	Decapoda	1	2
Nepinnotheres novaezelandiae	Decapoda	0	3
Notomithrax minor	Decapoda	1	8
Ogyrides sp	Decapoda	1	0
Palaemon affinis	Decapoda	0	80
Petrolisthes novaezelandiae	Decapoda	1	38
Philocheras australis	Decapoda	11	17
Upogebia danai	Decapoda	0	2
Shrimp Unid.	Decapoda	0	1
Cypridinoides sp.	Ostracoda	1	0
Diasterope grisea	Ostracoda	29	8
Leuroleberis zealandica	Ostracoda	4	0
Parasterope quadrata	Ostracoda	9	1
Scleroconcha sp.	Ostracoda	5	0
Phoronus sp.	Phoronida	7	6
Waltonia inconspicua	Brachiopoda	0	1
Echinocardium cordatum	Echinoidea	12	5
Hemichordata	Hemichordata	0	2
Cocinasteras muricata	Asteroidea	0	1
Patiriella regularis	Asteroidea	0	25
Ophiuroidea	Ophiuroidea	3	80
Ophionereis fasciata	Ophiuroidea	0	1
Chiridota nigra	Holothuroidea	1	21
Rynkatorpa uncinata	Holothuroidea	2	2
Trochodota sp.	Holothuroidea	8	17
Asterocarpa humilis	Ascidiacea	0	1
Cnemidocarpa bicornuta	Ascidiacea	1	8
Cnemidocarpa nisiotis	Ascidiacea	0	7
Pyura dopelgangera	Ascidiacea	0	2
Pyura rugata	Ascidiacea	0	2
Pyura sp.	Ascidiacea	0	5
Epigonichthys hectori	Cephalocordata	7	1
TOTAL number of individuals		**2130**	**2812**

Appendix E: Dominant species in each habitat group

Table A4. *Dominant species contributing to 70% of the total abundance within each habitat type, including their average abundance per core (0.02 m²), percentage contribution to total abundance (% Contrib.), and cumulative percentage of total abundance (% Cum.). Species marked with an asterisk (*) were found in both habitat types.*

Control habitat

Species name	Common Name	Group	Avg. abund.	Contrib.%	Cum.%
*Barantolla lepte**	Polychaete worm	Polychaeta: Capitellidae	5.62	13.19	13.19
*Amphipoda sp.**	Amphipod	Amphipoda	4.94	11.60	24.79
Phoxocephalidae	Amphipod (family)	Amphipoda	4.02	9.44	34.23
Goniadidae	Polychaete worm	Polychaeta: Goniadidae	3.48	8.17	42.39
Prionospio multicristata	Polychaete worm	Polychaeta: Spionidae	2.94	6.90	49.30
Polydora sp.	Polychaete worm	Polychaeta: Spionidae	1.86	4.37	53.66
Maldanidae	Bamboo Worms	Polychaeta: Maldanidae	1.8	4.23	57.89
Lysianassidae	Amphipod (family)	Amphipoda	1.22	2.86	60.75
Gari stangeri	Sunset shell	Bivalvia	0.98	2.30	63.05
Lumbrineridae*	Polychaete worm	Polychaeta: Lumbrineridae	0.82	1.92	64.98
Tawera spissa	Morning Star	Bivalvia	0.78	1.83	66.81
Prionospio aucklandica	Polychaete worm	Polychaeta: Spionidae	0.62	1.46	68.26
Diasterope grisea	Ostracod	Ostracoda	0.58	1.36	69.62
*Notomastus zeylanicus**	Polychaete worm	Polychaeta: Capitellidae	0.56	1.31	70.94

***Chaetopterus* habitat**

Species name	Common Name	Group	Avg. abund.	Contrib.%	Cum.%
*Amphipoda sp.**	Amphipod	Amphipoda	13	23.12	23.12
*Barantolla lepte**	Polychaete worm	Polychaeta: Capitellidae	3.48	6.19	29.30
*Notomastus zeylanicus**	Polychaete worm	Polychaeta: Capitellidae	3.14	5.58	34.89
Leptomya retiaria retiaria	Small bivalve	Bivalvia	2.92	5.19	40.08
Tanaidacea	Tanaid shrimp	Tanaidacea	2.16	3.84	43.92
Halicarcinus cookii	Pill-box Crab	Decapoda	2.12	3.77	47.69
Lumbrineridae*	Polychaete worm	Polychaeta: Lumbrineridae	2.08	3.70	51.39
Ophiuroidea	Brittle stars	Ophiuroidea	1.6	2.84	54.23
Palaemon affinis	Estuarine Prawn	Decapoda	1.6	2.84	57.08
Glyceridae	Polychaete worm	Polychaeta: Glyceridae	1.52	2.70	59.78
Hesionidae	Polychaete Worm	Polychaeta: Hesionidae	1.5	2.67	62.45
Dorvilleidae	Polychaete worm	Polychaeta: Dorvilleidae	1.34	2.38	64.83
Terebellidae	Polychaete worm	Polychaeta: Terebellidae	1.2	2.13	66.96
Armandia maculata	Polychaete worm	Polychaeta: Opheliidae	1.02	1.81	68.78
Zemysina sp.	Bivalve	Bivalvia	0.96	1.71	70.48