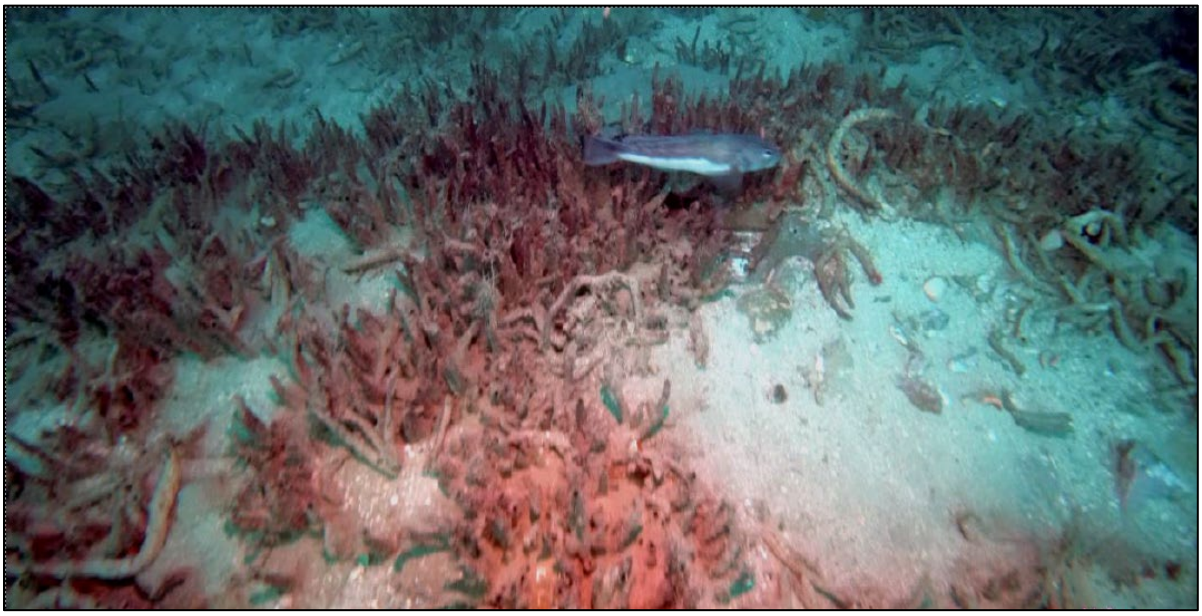
Background information on the parchment worm *Chaetopterus* sp.



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Cover picture: A bed of *Chaetopterus* sp. in the soft sediment habitat of East Bay, Marlborough Sounds, 2023. (Photo credit: Thomas Scott-Simmonds and Rob Davidson)

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THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

EXECUTIVE SUMMARY

The cryptogenic parchment worm *Chaetopterus* sp. was first discovered in New Zealand in 1966. *Chaetopterus* sp. populations remained limited across the country until the mid-1990s, when they experienced a sudden surge in abundance within the Hauraki Gulf. These worms began inhabiting rock crevices and formed extensive dense mats, covering sheltered seafloor areas. During this time, *Chaetopterus* sp. caused problems for scallop dredge fishers, and raised concerns about the exclusion of other benthic species. A recent surge in the population of *Chaetopterus* sp. in Marlborough's Queen Charlotte Sound, with subsequent expansion into the broader Top of the South area, has prompted similar concerns among local authorities, industry, and the public.

The University of Waikato was commissioned by the Marlborough District Council (MDC) under the Ministry of Science and Innovation's Envirolink small advice scheme to conduct a desktop assessment of key technical information related to *Chaetopterus* sp. This assessment aimed to identify potential impacts on local marine ecosystems and industry, explore possible establishment pathways, and highlight gaps in current knowledge. The purpose of synthesising the information was to deepen our understanding of the species in a broad context, aid in decision-making, better inform the public, and identify future research directions.

The key findings of this review on the biology and ecology of the genus *Chaetopterus* were:

Habitat

- *Chaetopterus* are found in temperate to tropical waters, occupying diverse habitats from intertidal zones to the deep sea.
- Higher concentrations of *Chaetopterus* are observed in calm waters with soft sediments, such as sheltered bays and harbours. Stable salinity levels are also crucial for their physiological functions.
- In the Marlborough Sounds, dense aggregations are typically found shallower and in a broader range of habitat types compared to the northeastern regions of New Zealand.

Life history

- *Chaetopterus* can be classified into infaunal species with U-shaped tubes buried in the substrate and epifaunal species with irregular tubes attached to solid structures.
- *Chaetopterus* inhabits the tube throughout its life, which it can quickly repair. These tubes can be up to 50 cm long, with vertical arms reaching up to 22 cm above the seafloor.

- *Chaetopterus* can regenerate all body segments from a single segment, even forming two individuals if the body is cut into two pieces.
- Spawning is triggered by environmental cues and varies by location. In temperate regions, spawning typically occurs in early summer, with rapid growth to adulthood by the season's end. *Chaetopterus* primarily disperses through planktonic larvae, which can remain in the water column for over three months.
- Life habits can vary in response to environmental changes, especially in scallop grounds affected by benthic trawling.
- Various fish species in New Zealand, including blue cod and snapper, feed on *Chaetopterus*.

Impacts

- *Chaetopterus* enhances species richness and diversity by providing refugia and influencing larval settlement. However, their colonisation can also negatively impact native fauna.
- The species plays a crucial role in carbon, nutrient, and energy flow in the subtidal benthic community.
- Dense mats stabilise sediments and can potentially alter sediment dynamics and species composition.
- There is the potential for human-mediated spread through hull fouling, fishing disturbance and transfer of aquaculture stock and equipment.
- *Chaetopterus* can attach to and persist on mussel farm infrastructure, posing risks to young mussels during their early growth stages.
- *Chaetopterus* and their commensals have shown to accumulate trace and major elements, making their symbiotic relationships valuable for monitoring metal distribution and contamination in marine environments.

Research priorities*:*

- Mapping and monitoring of both *Chaetopterus* species in New Zealand to determine extent and population trends.
- Investigations into the impacts of *Chaetopterus*, focusing on their community dynamics and interactions with benthic fauna.
- Research into their impacts on seafloor functioning, including effects on the physical and chemical properties of the benthos.
- Studies on *Chaetopterus* growth rates and reproductive cycles to better understand their population dynamics and dispersal traits.
- Establishing the influence of fishing practices in facilitating the colonisation and spread of *Chaetopterus*.
- Monitoring of mussel farm infrastructure to assess the risk and extent of biofouling impacts to the aquaculture industry.

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INTRODUCTION

The significance of cryptogenic species in marine environments is often overlooked, partly because their unknown origins make it difficult to categorise them as either non-indigenous (NIS) or native species. This ambiguity can lead to challenges in management and conservation strategies, as cryptogenic species may play critical roles in ecosystem dynamics but do not fit neatly into existing frameworks for addressing invasive species or protecting native biodiversity. In New Zealand, marine NIS hold the status of a 'National Indicator,' serving as a measure of the condition of New Zealand's marine environments. However, cryptogenic species or those with uncertain biosecurity status in New Zealand are not incorporated into these standard assessments (Seaward & Inglis, 2018).

The cryptogenic parchment worm, *Chaetopterus* sp. (herein *Chaetopterus* unless specified otherwise), was first discovered in New Zealand in 1966 when three specimens were found by a university student at the Leigh Marine Laboratory. Initially, its populations remained sparse across the country until a sudden increase in abundance occurred in the mid-1990s within the Hauraki Gulf. The worms began inhabiting rock crevices and formed extensive, dense mats on sheltered seafloor areas. During this period, *Chaetopterus* posed problems for scallop dredge fishers and raised concerns about the displacement of other benthic species. Recently, a similar surge in the *Chaetopterus* population in Marlborough's Queen Charlotte Sound, and its subsequent expansion into the broader Top of the South area, has raised similar concerns among local authorities, industry, and the public.

Understanding the biology and characteristics of cryptogenic species such *Chaetopterus* is crucial for marine ecosystem management in New Zealand. Tubeworms can significantly impact ecological interactions, nutrient cycling, and habitat structures; however, limited research within the New Zealand context makes it difficult to accurately predict these effects. Therefore, it is essential to first understand the broader biology and characteristics of *Chaetopterus*, using international studies as a guide. This will enable the development of targeted management practices and provide a better understanding of their influence on local marine ecosystem dynamics. Moreover, because *Chaetopterus* is not currently acknowledged as native or endemic to New Zealand, the species lacks recognised ecological value, and no conservation initiatives are currently in effect.

Conducting a literature review on *Chaetopterus* is crucial due to the concerns regarding their increased populations within the Marlborough Sounds and surrounding regions. While it is possible that this species is endemic, the rapid spread of *Chaetopterus* suggests it may be a recent and invasive marine species. This review aims to consolidate existing information, investigate establishment pathways, and address concerns about broader ecological impacts. Additionally, it will identify knowledge gaps and suggest future research directions.

This summary of technical information on *Chaetopterus* primarily utilises New Zealand sources when available, supplemented by international data as necessary. Given the limited information on *Chaetopterus* in New Zealand, most research on key ecological characteristics is based on studies conducted overseas. Additional information in New Zealand is sourced from personal communications from experts, commercial trawl survey reports, biosecurity surveillance reports, and notes from various ecological studies.

TECHNICAL INFORMATION ON *CHAETOPTERUS*

Identification history and related species

The Chaetopteridae family (also referred to as parchment worms) presents an ongoing challenge in the field of taxonomy and systematics. A comprehensive revision of this family has yet to be undertaken, leading to ongoing uncertainty and confusion regarding the number of accepted species. A dissertation and world review of the genus *Chaetopterus* based on phylogenetic and morphological evidence was undertaken by Moore (2019). However, this research remains largely unpublished. This lack of a thorough taxonomic update has contributed to the persistence of ambiguities in the classification and identification of Chaetopterid species (Osborn et al., 2007; Helm et al., 2022). Recent developments include the reclassification of Chaetopterids as part of the clade Chaetopteriformia, along with Apistobranchidae and Psammodrilidae (Helm et al., 2018).

Historically, *Chaetopterus* was considered a single, morphologically diverse, cosmopolitan species, identified as *Chaetopterus variopedatus* (Fauvel, 1919). The genus's taxonomy underwent partial revision for Pacific species (Nishi, 2001), but significant further revision is needed to assess the identities of both the species used as model organisms and those described from non-Pacific regions (Moore, 2019). Currently, Chaetopteridae comprises four accepted genera: *Chaetopterus* Cuvier, *Spiochaetopterus* Sars, *Phyllochaetopterus* Grube, and *Mesochaetopterus* Potts, with 75 valid species, including several cryptic species complexes (Martin et al., 2022).

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 et al., 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 (Sumida & Case, 1982; Jorgensen et al., 1984; Riisgärd, 1989; Cresson et al., 2016), nervous system (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 & Dehyn, 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).

New Zealand distribution and background studies

Very few studies have predominantly focused on *Chaetopterus* within New Zealand. The two main pieces of literature are an MSc thesis (Acosta, 2001) and a report by Tricklebank et al. (2001). Acosta (2001) explored the taxonomic identity and reasons behind the rapid spread of *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) builds 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 of *Chaetopterus chaetopterus-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; MBP, 2024; MacGibbon et al., 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 2019; 2020; 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:

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 species description, which meets the requirements of the Zoological Code of Nomenclature, has yet to be published for either *Chaetopterus* species, consequently, both species lack full Latin binomial names. Although there has been limited genome sequencing conducted regarding New Zealand *Chaetopterus*, more recent genetic studies have been carried out, and publications on this research are currently in preparation (G. Read, pers. comms. 2023).

Chaetopterus chaetopterus-A

Chaetopterus chaetopterus-A, unlike *C. chaetopterus-B*, 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 poor preservation of museum specimens and holotypes has made it challenging to conduct 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 and those newly described species exhibiting invasive behaviour in New Zealand but for which there are no known records outside the New Zealand region" (MAF, 2008).

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). It prefers shallow areas less than approximately 16 m and substrates with a mix of sand and broken shells (R. Davidson, pers. comms, 2024). Notably, it does not seem to colonise areas with glutinous mud (R. Davidson, pers.

comms, 2024). Records show that *C. Chaetopterus-B* is widespread in the top of the south region with large populations scattered throughout Queen Charlotte and Pelorus Sound (S. Cunningham, pers. comm, 2023, Davidson et al. 2022; MBP, 2024). *Chaetopterus Chaetopterus-B* is classified as a ‘Category 2’ cryptogenic species which refers to “newly discovered species for which there is insufficient information to determine whether New Zealand lies within their native distribution” (MAF 2008).

History of invasion in New Zealand

There are few historical records of *Chaetopterus* in New Zealand. The first documented records date back to 1966 when three specimens were found by a university student at the Leigh Marine Laboratory (Whitely, 1966). They were 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

Populations across the country remained limited until the mid-1990s. 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; https://www.seafriends.org.nz/indepth/invasion.htm). 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. Although, 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 individuals/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 at the Poor Knights Islands 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; NIWA, 2007; 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 in New Zealand (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 Queen Charlotte Sound (QCS) in 1989-90. 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, pers. obs., Davidson et al., 2020).

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, pers. comms, 2024). The appearance of these populations was notably different from the beds found in central Pelorus Sound (R. Davidson, pers. comms, 2024). 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 goes further (R. Davidson, pers. comms, 2024).

While concerns about a sudden population surge in *Chaetopterus* were raised earlier, the first empirical evidence of increased *Chaetopterus* abundances was noted in 2019 during surveys (Fig. 1; Williams et al., 2021) conducted to assess scallop populations in the Marlborough Sounds. These surveys included the quantification of *Chaetopterus* sp. due to their growing prevalence within the fishing grounds. In 2019, the unidentified *Chaetopterus* was found in the catch at 35 out of 120 survey stations, representing a 29% presence. Its distribution included areas of Pelorus Sound (Horseshoe Bay, Waitata Bank, Ketu Bay, Guards Bay) and QCS (Ship Cove). In 2020, *Chaetopterus* was found extending to new ranges (e.g., Chetwodes, Bay of Many Coves, Croisilles Harbour)

(Williams et al., 2019). Shortly before the 2019 scallop survey, a local diver reported a substantial presence of tubeworms, believed to be *Chaetopterus*, in an area of QCS. Samples from this location confirmed that the tubeworms were *C. chaetopterus-B* (Williams et al., 2021).

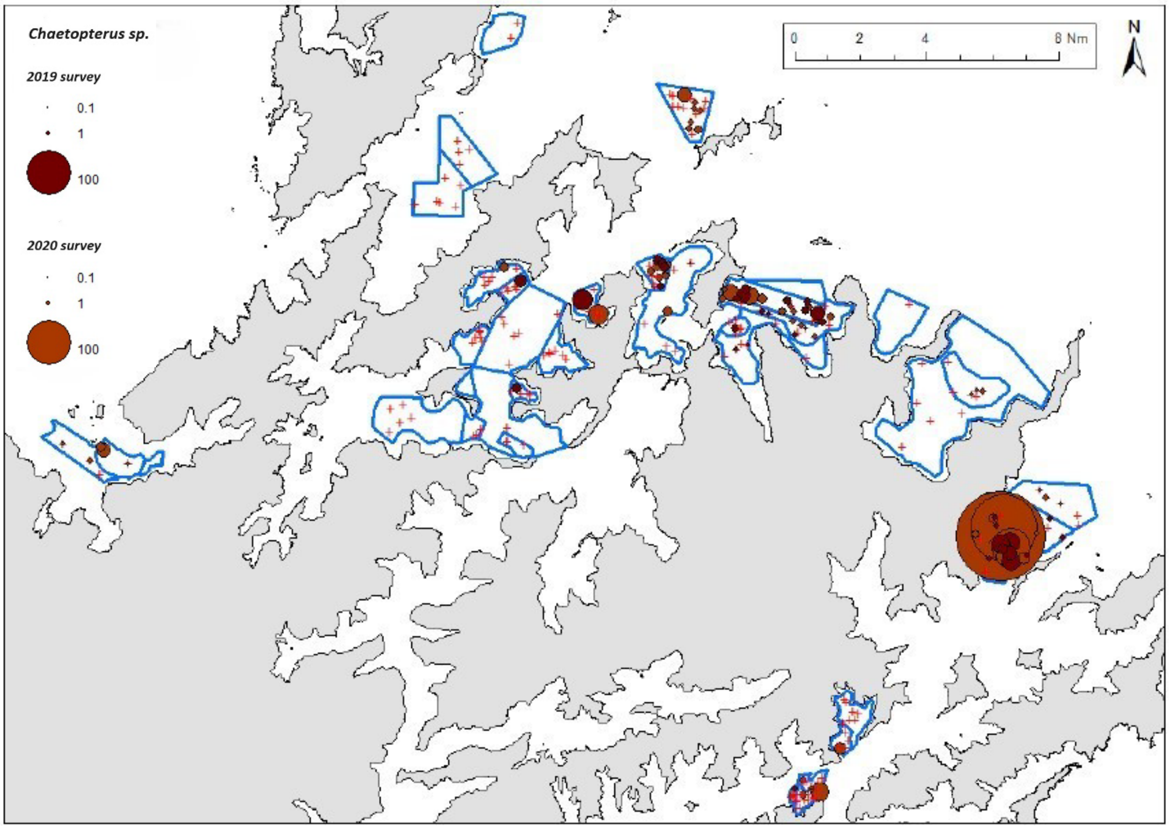

Figure 1. *Chaetopterus* sp. catch per standard tow, Marlborough Sounds dredge surveys, May 2019 (dark brown circles) and May 2020 (light brown circles). Circle area is proportional to the estimated volume (L) caught per standard distance towed (0.4 n. miles). Values are uncorrected for dredge efficiency. Polygons denote survey strata boundaries. (*Adapted from Williams et al., 2021*)

Since 2019, several ecological reports have noted the presence of *Chaetopterus* within areas highlighted as significant marine habitats in the Marlborough Sounds. A survey by Davidson et al. (2020) confirmed the high abundance of *Chaetopterus* at Long Island 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. 2021). 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*. Consequently, a range extension was made by the Ministry of Primary Industries (MPI) (O. Wade, pers. comms, 2022).

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 scallop restoration (Oliver Wade, pers. comm., 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.

BIOLOGY OF *CHAETOPTERUS*

General description

Chaetopteridae is a small family within the phylum Annelida, characterised by species that inhabit self-secreted membranous tubes. The lengths of these tubes and the sizes of the animals can vary significantly among different species and populations (Tricklebank et al., 2001). These species are commonly found in a variety of habitats, ranging from the intertidal zone to the deep sea (Shah et al., 2014; Moore et al., 2017).

Among Chaetopterids, *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.

While most species of *Chaetopterus* are infaunal, some attach their tubes to hard surfaces (Rouse & Pleijel, 2001). This unique characteristic is exhibited by both *Chaetopterus* species within New Zealand (Acosta, 2001; Tricklebank et al., 2001; Davidson et al., 2022). Subsequently, *Chaetopterus* can be categorised into two groups based on ecological and morphological differences: infaunal species, which have U-shaped tubes partially buried in the substrate, and epifaunal species, which have irregular tubes attached to solid three-dimensional structures (Tricklebank et al., 2001). Other chaetopterids are less morphologically specialised than *Chaetopterus* (Moore et al., 2017).

Sexually mature males and females can be easily distinguished by the colour of the gonads (Enders, 1909). The gonadal parapodium of fertile males appears milky-to-yellowish white, while the females have yellow ovaries (Eckberg & Hill, 1996). The sex of immature or young specimens cannot be distinguished (Enders, 1909).

A well-detailed morphological description of *C. chaetopterus-A* is published in Tricklebank et al., (2001). No formal description of *C. chaetopterus-B* is currently available.

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).

Figure 2. Typical example of an adult *Chaetopterus* tube from East Bay, Queen Charlotte Sound.

The tube is typically U-shaped (Fig. 2; Fig. 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 & Martindale, 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).

Figure 3. A dense aggregation of *Chaetopterus* from East Bay, Queen Charlotte Sound, 2023.

The genus *Chaetopterus* comprises several species that exhibit variation in overall tube length (Irvine & Martindale, 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). Although, the length of the tube constructed by *Chaetopterus* species does not strongly correlate with the size of the worm. Instead, studies suggest 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 within the Marlborough Sound 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).

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 (Fig. 4; pers. obs. 2023).

Chaetopterus is renowned for its highly specialised filter-feeding mechanism (Osborn et al., 2007). Their bodies can be divided into three distinct regions (Fig. 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).

Tricklebank et al. (2001) provide a comprehensive description of the body structure of *C. chaetopterus-A*, detailed in Appendix A. The following summary includes information from this study, supplemented by findings from other international research:

Region A comprises a morphologically fused prostomium and peristomium with 9 chaetigers, with the ninth bearing an uncinal torus, or, less commonly, 10 chaetigers.

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. 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).

Figure 4. Body of *Chaetopterus* sp. collected in East Bay, Queen Charlotte Sound, 2023. Note: Measuring board is in 2cm increments.

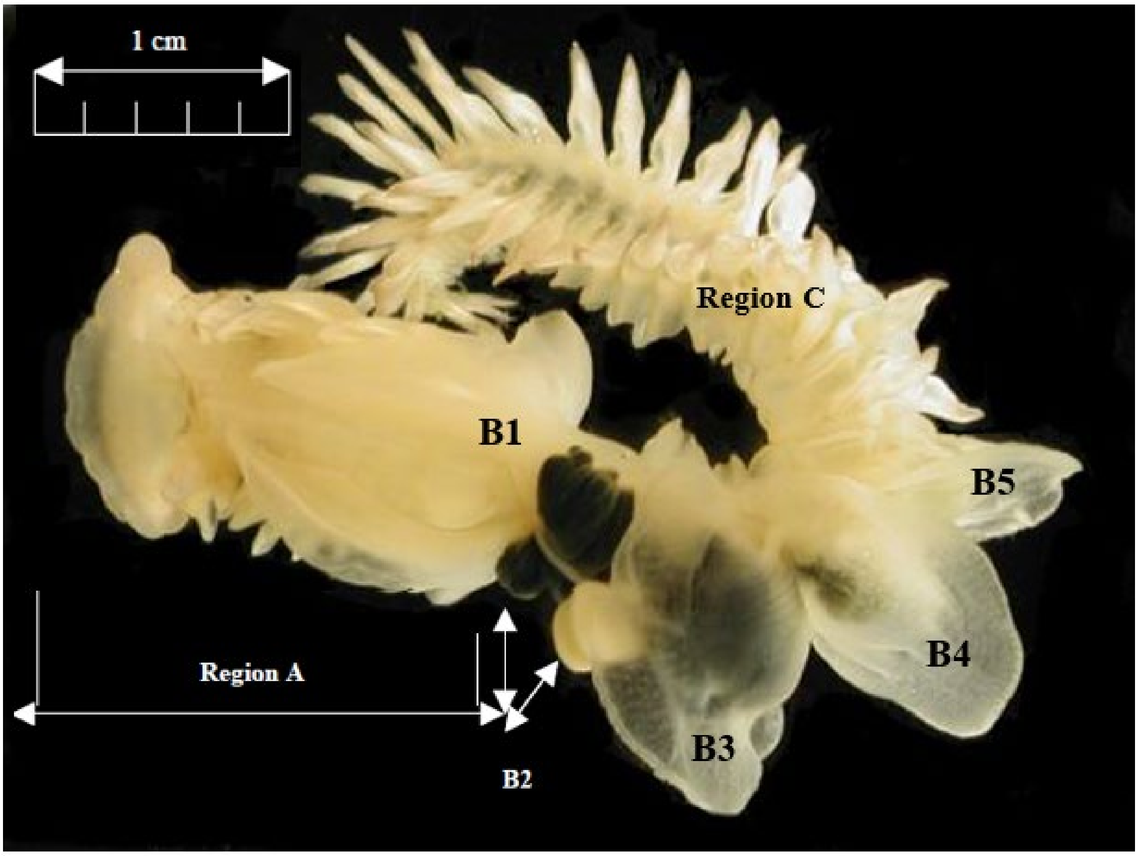

Figure 5. Adult *Chaetopterus* (now known as *C. chaetopterus-A*) from northeastern New Zealand after removal from the tube. Regions A, B (segments B1 – B5) and region C are shown. (*from Tricklebank et al., 2001*).

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).

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 (Berill, 1928; 1952; Faulkner, 1932; Hill, 1972; Eckberg & Hill, 1996). More detailed investigations into the regenerative capabilities of *Chaetopterus* include: (Acosta, 2001; 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 and 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 (Berill 1928). Furthermore, each somite in *Chaetopterus* retains its own identity and is directly replaced during the regeneration process (Eckberg & Hill, 1996).

In New Zealand, experiments with *C. chaetopterus-A* demonstrated a similar pattern to that reported for other *Chaetopterus* species, showing the ability to regenerate both posterior and anterior segments (Acosta, 2001). When the body was cut into two pieces, each piece developed into a separate individual (Acosta, 2001). The time required for regeneration depends on the size of the original segment lost, with larger missing sections taking longer to regenerate. Regeneration was observed to be quicker in juveniles compared to adults (Acosta, 2001). Under laboratory conditions, adult *Chaetopterus* removed from their tubes were able to fully regenerate sections within 30 to 120 days (Acosta, 2001).

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, 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" (Fig. 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-Medioni, 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).

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).

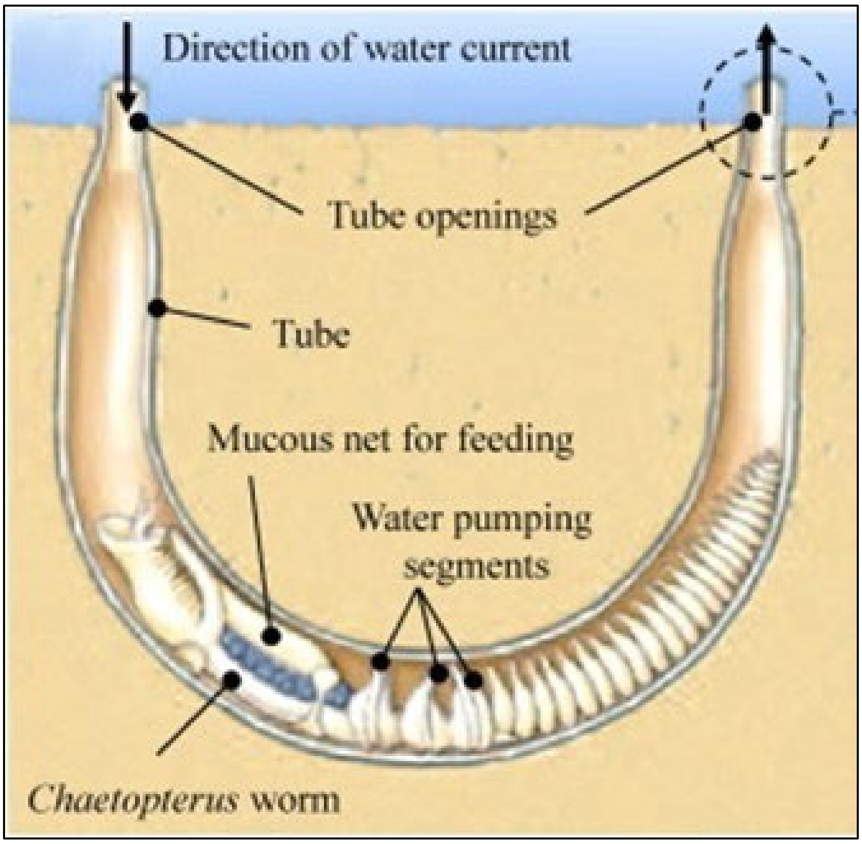

Figure 6. Schematic, adapted from Hickman et al. (2001), of a *Chaetopterus* worm pumping water within its tube for feeding using an elongated mucous net.

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).

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 (Pease, 1940; Carroll & Eckberg, 1983; Sato et al., 1985; Eckberg & Palazzo, 1992; Eckberg & Szuts, 1993; Eckberg & Miller, 1995; Eckberg et al., 1996; Swalla et al., 1985; Thomas, 2000; Wiliams, 2005; Yin, 2007), embryogenesis and early cleavage (Fry, 1932; Eckberg & Anderson, 1996; Yang, 2003; Yang, 2004; Yin & Eckberg, 2009), parthenogenesis (Loeb, 1901), and early development (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). The following has been summarised from these studies.

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 (Fig. 7; Irvine et al., 1999).

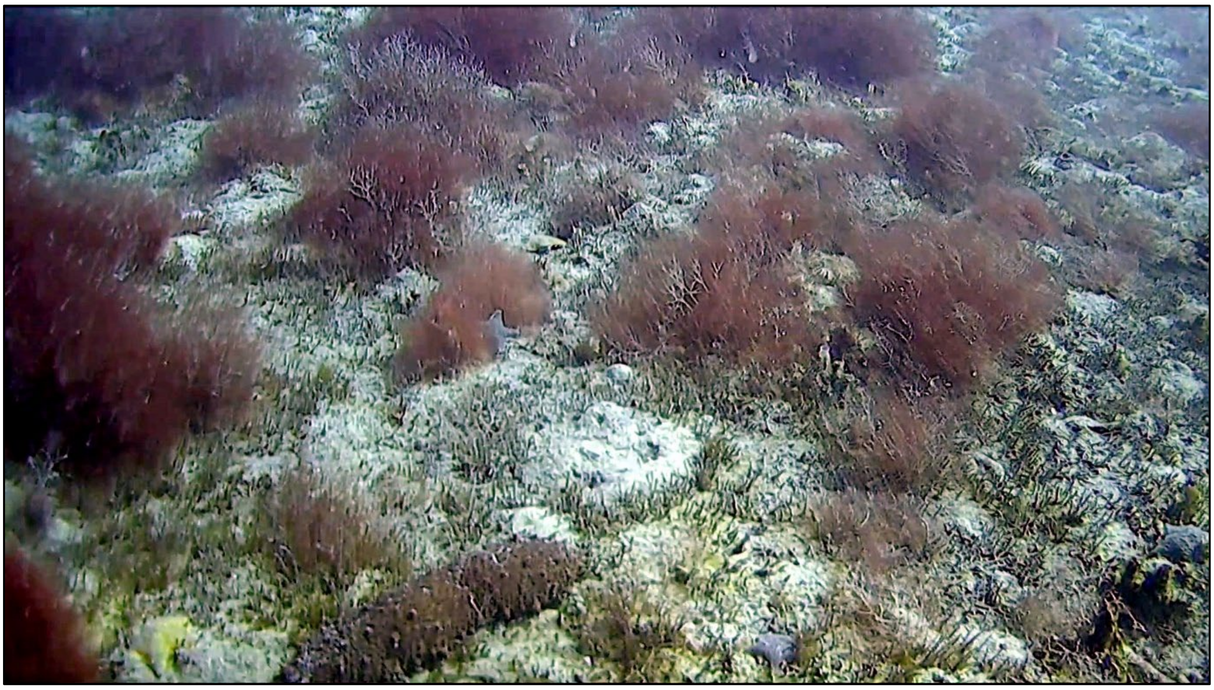

Figure 7. Juvenile *Chaetopterus* sp. in East Bay, Queen Chalotte Sound, 2023.

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 (Fig. 8; Harvey, 1926; Branchini et al., 2013; 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., 2013; Purtov et al., 2021), 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., 2013). 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, 2006; Mirza et al., 2020; Purtov et al., 2021). However, experiments on *C. Chaetopterus-A* demonstrated that induced bioluminescence is confined to segment B1 and region C (Acosta, 2001).

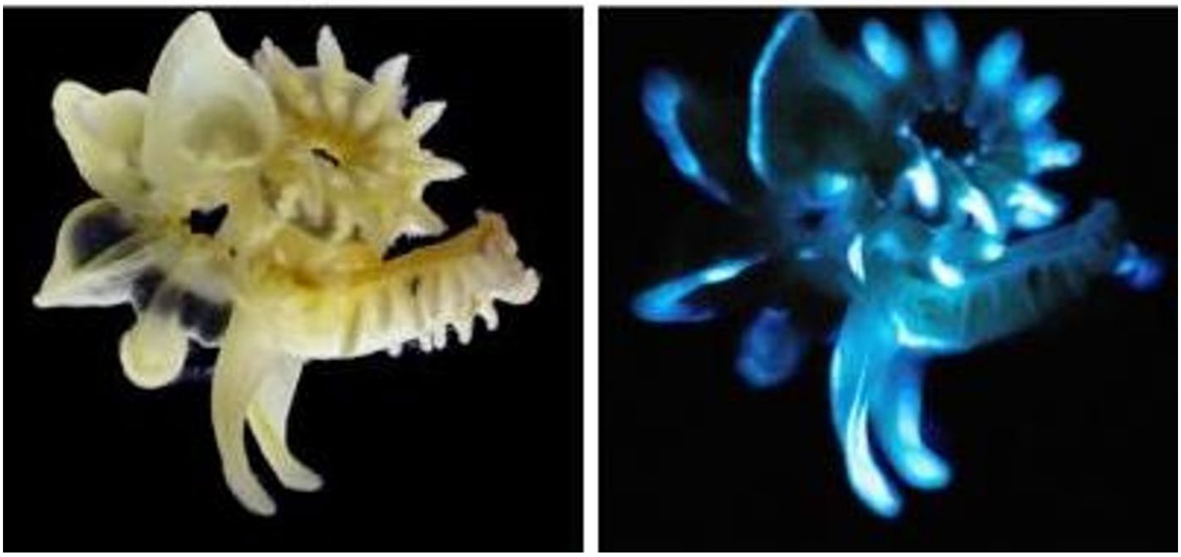

Figure 8. *Chaetopterus* under natural light (left), and in the dark (right) showing blue bioluminescent slime it produces. Photo credit: David Liittschwager

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., 2013). 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; Martin & Anctil, 1984; Sumida & Case, 2009; Mirza et al., 2020). Early studies (e.g., Enders, 1909; Berril, 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 (Joyeux-Laffuie, 1890; Mirza et al., 2020). Further research is needed to understand the purpose of bioluminescence in *Chaetopterus*, including identifying natural predators to validate these theories.

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 (Britayev & Martin, 2016). 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* within Vietnam.

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 2006; Werding & Hiller, 2019; Soto & Martin, 2017). 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.

Habitat 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, 1992; Enders, 1909; Thompson & Schaffner, 2001; Tricklebank et al., 2001; Sun & Qui, 2014). 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). Furthermore, 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 the North Island of 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; Petersen, pers. comm.). *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) investigated the associations of *C. chaetopterus-A* (including epifaunal, infaunal and mats) with environmental variables such as depth, exposure, and sediment type. The findings from this research showed exposure level to be an insignificant factor but identified a significant association between the presence of live *Chaetopterus* and sediment type, particularly noting dense aggregations on coarse substrates (such as sand, sand-gravel, and shell-gravel). While the mean percent cover of *Chaetopterus* mats did not differ significantly among sediment types, they observed the widest range in percent cover on sandy substrates. Depth was also significantly correlated with the presence of all live *Chaetopterus*, with mats predominantly concentrated at depths between 20 and 34 m. However, mats were found across all surveyed depth ranges, from shallow areas (<10 m) to depths exceeding 40 m (Tricklebank et al. 2001).

Though Tricklebank et al. (2001) provides 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 Top of the South 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 Queen Charlotte Sound (Davidson et al., 2019). Dense mats of tube worms are located in shallow soft sediments (>15 m) in East Bay and scattered throughout the bays of the inner and mid Queen Charlotte Sound (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).

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, Virginia where large populations of *C. variopedatus* are present (e.g., Schaffner, 1990; Thompson & Schaffner 2000; 2001).

Global examples

The study by Thompson and Schaffner (2001) investigating the population biology and secondary production of *C. variopedatus* highlighted the worms' role as a significant component of estuarine ecosystems. Worm densities varied seasonally, peaking after summer recruitment periods and ranging from 30 to 1000 individuals/m^2. Recruitment success showed notable variation between monitoring years, with a two-cohort model (juveniles and adults) best describing population dynamics. High secondary production was driven by rapid growth and tube production of new recruits in summer. Interannual differences in production correlated with recruitment success variations. The study underscores *Chaetopterus'* role in carbon, nutrient, and energy flow within the ecosystem, emphasising its temporal influence on benthic suspension feeder effects.

Schaffner (1990) explored the distribution of small-scale organisms and species diversity patterns in estuarine benthic communities of Chesapeake Bay, highlighting positive interactions. The research showed that associations involving *C. variopedatus* and other species, especially epifauna, enhance species richness and diversity in these communities. This emphasises that alterations in habitat quality or availability are shaped more by the presence or absence of organisms, such as *Chaetopterus*, rather than by specific environmental features.

Like *C. variopedatus, Chaetopterus pergamentaceus* plays a crucial ecological role in the soft sediment subtidal benthic community of lower Chesapeake Bay (Thompson & Schaffner, 2000). This research revealed temporal variations in population dynamics that significantly influence the relative importance of benthic suspension feeder effects on ecosystem function. A notable finding was a strong negative correlation between growth rates and total density among juveniles during periods of fluctuating recruitment. This highlights the importance of considering *Chaetopterus* in models of carbon, nutrient, and energy flow within benthic ecosystems.

Lastly, Enders (1909) noted that both male and female individuals of *C. variopedatus* inhabit the same shoals, typically spaced one to three meters apart, with females predominating and comprising sixty percent of collected individuals.

New Zealand

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 (Fig. 9; pers. obs., 2023). 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 *Lannice 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). 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).

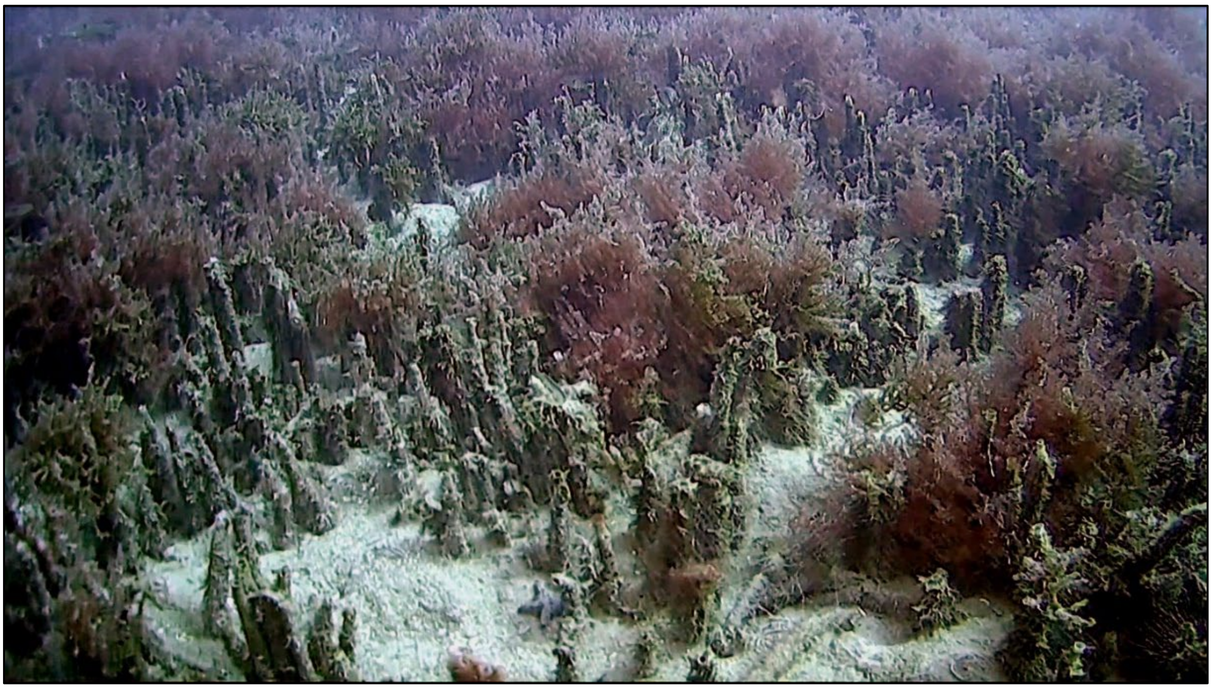

Figure 9. Dense *Chaetopterus* mats within East Bay, Queen Charlotte Sound, 2024.

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.

Predators

Marine biogenic structures, characterised by tubeworm mats that extend several centimetres into the water column, exert significant ecological influence on marine ecosystems (Salomidi et al., 2012). These habitats support a diverse array of taxa, including post-settlement juveniles of commercially important fish species (Watling & Norse, 1998). However, 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 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 (Hugget, 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, 1987).

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*) and blue moki (*Latridopsis ciliaris*) are commonly found among *Chaetopterus* beds and have been observed preying on *Chaetopterus* within QCS (C. Rayes, pers. comm., 2021) (Fig. 10). Additionally, schools of snapper (*Pagrus auratus*) have been observed feeding on newly recruited populations of *Chaetopterus* at Goat Island (Acosta 2001, Shears, pers. comm.). 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, Denny, pers. comm.).

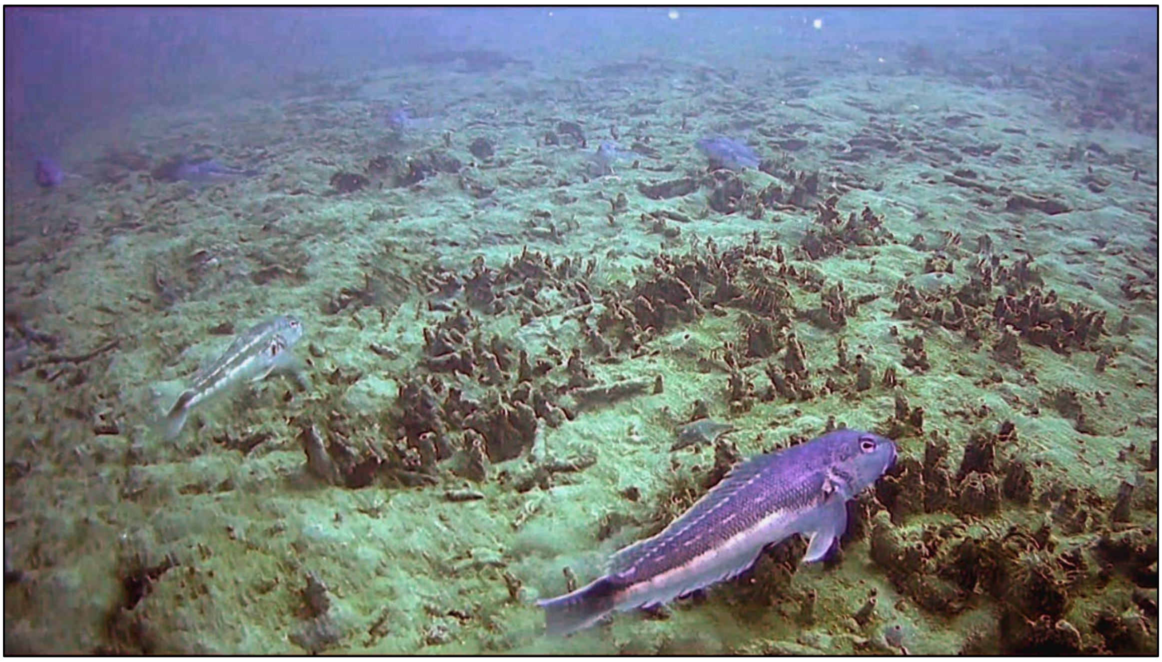

Figure 10. Blue cod within *Chaetopterus* habitat in East Bay, Queen Charlotte Sound, 2023.

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 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 according to the University of San Diego (2017). Ferritin is a critical protein in nearly all living organisms, balancing iron levels in the body by storing and releasing it as needed.

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 (Shah et al., 2014).

The symbiotic relationships involving *Chaetopterus* have significant potential for biomonitoring applications. For instance, the presence of symbionts such *as Polyonyx gibbesi* within *C. variopedatus* tubes enhances the monitoring and study of environmental contaminants across various benthic compartments. Both the polychaete and its commensals accumulate trace and major elements, providing a comprehensive understanding of metal distribution and contamination in marine environments (Eca et al., 2013). Utilising this relationship has significant advantages over bivalves, which typically do not accumulate metals such as Al and Mg at high levels (Eca et al., 2013).

PATHWAYS OF SPREAD

Natural dispersal

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, as noted by Ruiz and Carlton (2003) and Drake and Lodge (2007). In New Zealand, records from the Marine Biosecurity Porthole (MBP 2024, https://www.marinebiosecurity.org.nz/) highlight the ability of *C. chaetopterus-A* to attach to vessel hulls. However, studies focusing specifically on these traits would be required to 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 (Tricklebank et al., 2001, Rintoul, pers. comm.). 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.

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 specimens/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 (Hugget, 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

Biosecurity risk

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 (NMHRSS) 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, 1976). 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 between scallops and *Chaetopterus*.

Between 1999 and 2003, the Coromandel scallop fishery in New Zealand (SCA CS) 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., 2021; MacGibbon et al., 2024).

In 2019, a commercial diver reported to Fisheries New Zealand a sudden proliferation of *Chaetopterus* in Queen Charlotte Sound, coinciding with observations of dead and dying *P. novaezelandiae* ("Scallop mortality in Queen Charlotte Sound", 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.

As previously mentioned, a study by Bremec and Schejter (2019) observed a significant relationship between the *C.s 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 (Fig. 11; S. Cunningham, pers. comm., 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, pers. comm., 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). Further research is needed to understand the risk and extent of these impacts within New Zealand.

Figure 11. Before (left) and after (right) showing *Chaetopterus* sp. 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 (MAF, 2008; MAF) 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.

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 requirements, 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.

Research priorities for New Zealand *Chaetopterus:*

- Mapping and monitoring of both *Chaetopterus* species to determine extent and population trends within the Top of the South region.
- Investigations into the impacts of *Chaetopterus*, focusing on their community dynamics and interactions with benthic fauna.
- Research into their impacts on seafloor functioning, including effects on the physical and chemical properties of the benthos.

- Studies on *Chaetopterus* growth rates and reproductive cycles to better understand their population dynamics and dispersal traits.
- Studies regarding the influence of fishing practices in facilitating the colonisation and spread of *Chaetopterus*.
- Monitoring of mussel farm infrastructure to assess the risk and extent of impacts to the local aquaculture industry.

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

The following section has been taken from (Tricklebank et al., p14, 2001):

"**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.”