



# Polychaetes as aquaculture feed: feeding experiments and nutritional value analysis of *Eurythoe* spp.

Arne Valentin Heydtmann<sup>1,2</sup> · Constanze von Waldthausen<sup>2</sup> · Sabine Keuter<sup>2,3</sup> · Andreas Kunzmann<sup>2</sup> · Lara Stuthmann<sup>2</sup>

Received: 9 October 2025 / Accepted: 8 December 2025  
© The Author(s) 2025

## Abstract

Aquaculture needs more environmentally friendly alternatives to fishmeal-based feed. Polychaetes could be part of a solution, since they are comparatively easy to cultivate. *Eurythoe* sp. and especially the species complex *Eurythoe complanata* is widely distributed across tropical coasts and aquaria. However, studies on the biology, needed for a targeted cultivation, are rare. In order to evaluate the species' potential as an aquaculture species, an understanding especially of their feeding preferences and proximate composition, namely lipid, carbohydrate and protein content, is essential. Here, we present a—to the best of our knowledge—first adapted protocol to quantify lipid, carbohydrate and protein content in *Eurythoe* spp., as well as a comparison of female and male individuals of two species of the genus, referred to as *spec. 1* (*Eurythoe cf. complanata*) and *spec. 2* (*Eurythoe* sp.). Overall, the values of the lipid content ranged between 7 and 13% of the dry weight (DW) with the male polychaetes of *spec. 1* showing lower lipid concentrations compared to the other species. Additionally, the male polychaetes showed higher carbohydrate levels than females or individuals of the other species. Carbohydrate concentrations between 3 and 10% DW were measured. The protein content of all specimens was between 27 and 37% DW. A 90-day feeding experiment revealed highest specific growth rates (SGR) of the group fed with a control of pellets, compared to algae commercially available as fish feed and spinach. Spontaneous fragmentation, known as a form of asexual reproduction among annelids, occurred over the experimental run. Despite the revealed high potential as a feed source for aquaculture purposes, more detailed investigations are necessary, especially regarding the targeted feeding and potential complications due to their venom.

**Keywords** Polychaetes · Proximate composition · Aquaculture feed · Feeding preferences

---

Handling Editor: Ercument Genc

---

✉ Arne Valentin Heydtmann  
arne.heydtmann@leibniz-zmt.de

<sup>1</sup> University of Bremen, Bibliothekstraße 1, 28359 Bremen, Germany

<sup>2</sup> Leibniz Centre for Tropical Marine Research (ZMT) Bremen, Fahrenheitstraße 6, 28359 Bremen, Germany

<sup>3</sup> Helmholtz Centre Hereon, Max-Planck-Straße 1, 21502 Geesthacht, Germany

## Introduction

Aquaculture is becoming increasingly important for the global food supply. However, for a sustainable growth of the sector more environmentally friendly and reliable alternatives to fishmeal-based feed are needed. Polychaetes could be part of a solution due to their high content of proteins, essential amino acids and polyunsaturated fatty acids (Wang et al. 2019a; Jerónimo et al. 2021; Pan et al. 2021), as well as their relatively easy (co-)cultivability (Brown et al. 2011; Nederlof 2022). Besides, deposit feeding polychaetes can retain wasted essential fatty acids, like EPA and DHA, and turn waste material in general in high-quality proteins and lipids making them an interesting species for integration in integrated-multi trophic systems (Jerónimo et al. 2021). Hence, a further introduction of polychaetes in the aquaculture sector could become key for environmentally sustainable feed stuff, as well as a driver towards circular principles (Panteli et al. 2025). Polychaetes are already used as a nutritional resource for crustaceans broodstocks (Wang et al. 2025; Panteli et al. 2025) and their use as supplements for other species has been investigated (Díaz-Castañeda and Reish 2009; Dorgham et al. 2015; Panteli et al. 2025). However, the majority are harvested from the wild with only a few species being cultivated (Cole et al. 2018; Wang et al. 2025).

Species of the genus *Eurythoe* are distributed in all tropical seas (GBIF 2025). *Eurythoe complanata* is a known species of the genus. The existence of *E. complanata* in the Mediterranean was proven and the species complex was divided into the two so-called “morphospecies” *E. complanata*, consisting of two cryptic species, and *E. laevisetis* (Arias et al. 2013). They belong to the family Amphinomidae, which are commonly known as *fireworms*, due to the venom contained in their bristles. In the case of *E. complanata*, it is the neurotoxin complanin (Nakamura et al. 2008). *E. complanata* is bisexual combining sexual and asexual reproduction (Kudenov 1974; Müller et al. 2003). A weakly developed sexual dimorphism has been observed, meaning that male and female individuals only differ in their colouration, with females being pinkish red and males whitish, especially on their dorsolateral surfaces, which has been attributed to the different gametes produced (Kudenov 1974). *E. complanata* reproduces via a combination of sexual reproduction through mating and asexual reproduction by fragmentation with subsequent rapid regeneration. It is one of two species within the amphinomids, where bidirectional regeneration was observed (Kudenov 1974; Yáñez-Rivera and Méndez 2014; Toso et al. 2024). The *ex-novo* production of the anterior body part requires that the fragments rely on their energy reserves. This starvation period can last for at least 50 days with a notable depletion of energy reserves compared to the beginning of the regeneration (Yáñez-Rivera and Méndez 2014; Toso et al. 2024). While fragmentation appears to occur spontaneously (Pardo and Amaral 2005), the exact triggers remain unknown. Hence, fragmentation and following regeneration could have a notable impact on yields in case of a targeted aquaculture of these species, making an understanding of factors causing fragmentation essential.

The nocturnal or crepuscular worms are usually found in shallow waters and the intertidal zone, where they are hiding below stones or in corals (Pardo and Amaral 2005). Although *E. complanata* is relatively well studied, their diet remains controversial (Engel et al. 2023). The species was described as a carnivorous or omnivorous scavenger (Blake et al. 1995, Pardo and Amaral 2005). Laboratory observations of Pardo and Amaral (2005) report feeding on pieces of fish using chemosensory perception, whereas the use of stable isotope and fatty acid markers reveals a low trophic position with a diet mainly consisting of plant material, like algae (Engel et al. 2023, Pérez-Posada et al.

**Table 1** Lipid-, protein- and carbohydrate concentrations standardized as % of the dry weight (DW) of different species of polychaetes

Species	Lipids [% DW]	Proteins	Carbohydrates	Reference
<i>Diopatra neapolitana</i>	26.31	51.87	18.58	Selvam (2021)
<i>Glycera sp.</i>	20.99	50.50	2.04	Bharath et al. (2021)
<i>Hediste diversicolor</i>	11.00	60.00	18.00	Wang et al. (2019a, b)
<i>Halla parthenopeia</i>	25.65	50.06	21.76	Selvam (2021)
<i>Marphysa mossambica</i>	27.98	51.14	17.76	Selvam (2021)
<i>Nereis virens</i>	32.31	49.04	2.67	Bharath et al. (2021)
<i>Perinereis cultrifera</i>	11.99	53.62	17.53	Bharath et al. (2021)
<i>Perinereis quatrefagesi</i>	24.08	49.32	24.61	Selvam (2021)

2025). The authors presume that the species likely ingests sediment without targeting specific compounds (Engel et al. 2023). However, the feeding could also depend on the choices the animals have. An understanding of the feeding ecology is essential when cultivating the organisms for their potential use as feed stuff, since their nutritional composition likely depends on their diet (Asghari et al. 2017; Wibowo et al. 2020). The choice of diet further contributes essentially to the sustainability of the production of the polychaetes. Therefore, we chose plant-based feed options as treatments for the feeding experiments in order to evaluate the potential of *Eurythoe* spp. to upcycle plant-derived nutrients as well as their ability to utilize plant-based feed for growth.

In order to be able to make statements about the utilisation potential of *Eurythoe* spp., the body composition has to be assessed first. Currently, not much is known about the composition of *Eurythoe* in general and the species complex of *E. complanata* especially. However, literature data show that for most polychaete species proteins make up the largest part of the body composition with ~50–60% dry weight (DW), followed by lipids and carbohydrates (Table 1).

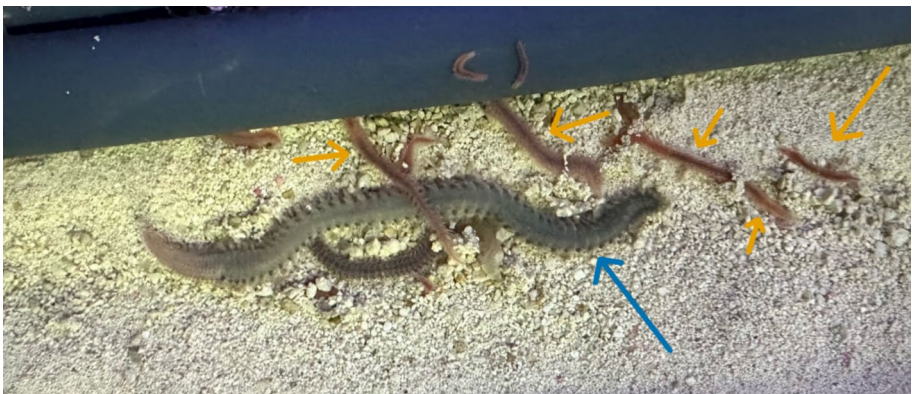
This study aims to analyse the utilisation potential of *Eurythoe* spp. as fish feed in aquaculture, and to provide a basis to link the species' composition with their feeding. Hence, it introduces (1) a reliable and reproducible protocol for measuring lipid, protein and carbohydrate concentrations of polychaetes, adapted for the quantification of *Eurythoe* spp. (2) The method is then applied to the population thriving at the aquaculture facilities of Leibniz Centre for Tropical Marine Research (ZMT) in Bremen for decades. Distinction was made between two kinds of *Eurythoe*, as well as between male and female individuals of the larger group. We hypothesize that the different sexes and sizes will exhibit differences in the proximate composition due to their requirements for gamete production (sexual dimorphism) and potentially different target food sources. (3) In a long-term laboratory experiment, the species' growth and composition were linked with three different food items. Observations regarding fragmentation of the species contribute to a basic understanding for establishment of a potential aquaculture of the organisms. Based on recent studies (Engel et al. 2023, Pérez-Posada et al. 2025), we hypothesize that *E. complanata* will be able to use the plant-derived nutrients for growth, but that commercial pellets, used as a control, will result in higher specific growth rates (SGRs), due to the easier digestibility.

## Materials and methods

### Biomass and cultivation of *Eurythoe* spp.

*Eurythoe* spp. were cultivated in a tank with a sediment layer (5–10 cm) connected to a circulation system containing several other organisms (fish, seaweed, molluscs, crustaceans) in the aquaria facilities of the Leibniz Centre for Tropical Marine Research (ZMT; Marine Experimental Ecology, MAREE). The recirculated water was treated through a skimmer, an ultra-violet (UV) tube and biofilter material with nitrifying bacteria. The experimental aquaria were filled with artificial seawater, which was kept at constant temperature (T), salinity ( $S_A$ ) and pH values ( $T 24.7 \pm 0.3$  °C;  $S_A 34.5 \pm 0.1$ ; pH  $8.1 \pm 0.1$ ) via a heating rod and an automatic refill system. Approximately one third of the system water was replaced weekly. Worms were fed mainly with commercial pellets usually used for herbivores (Marine Grazer mini, Vitalis Aquatic Nutrition, Thorne, UK). The pellets sank to the floor after feeding and worms were observed to flock around and consume them. Hence, these pellets were used as a control in the feeding experiment.

To identify the polychaete species in the aquaria at ZMT, DNA was extracted from a large and a small polychaete specimen using a DNA extraction kit (Monarch Spin gDNA Extraction Kit, New England Biolabs GmbH, Germany). The cytochrome oxidase subunit I (COI) was amplified using polymerase chain reactions (PCR), cleaned using a clean-up kit (Monarch Spin PCR & DNA Cleanup Kit, New England Biolabs GmbH, Germany) and Sanger sequenced. It could also be concluded from sequence analysis that the larger specimen probably belonged to the species complex *Eurythoe complanata*. However, the smaller polychaete showed significant deviations in the COI sequence and could therefore not be assigned to the species complex of *Eurythoe complanata* with certainty. For this reason, in the following the larger species is referred to as *Eurythoe cf. complanata* (*spec. 1*) and the smaller as *Eurythoe* (*spec. 2*) (Fig. 1).



**Fig. 1** Polychaetes in the aquaria at the Leibniz Centre for Tropical Marine Research (ZMT). Depicted is an individual of the bigger species (*Eurythoe spec. 1*, male, blue arrow) and several individuals of the smaller species (*Eurythoe spec. 2*, orange arrows)

## Comparative nutrient analysis of *Eurythoe spec. 1* and *spec. 2*

For determination of potential differences in the lipid, carbohydrate and protein composition of *spec. 1* male and female, as well as *spec. 2* organisms, four polychaetes of each group were isolated in glass jars (1 L) set-up in a constant climate room (25 °C) of the biology lab at ZMT Bremen for two weeks (Fig. 2). The jars were equipped with a bubble stone with aeration, two PVC tubes attached with a cable tie to provide a place for the animals to hide and a cover for the jar. A LED lamp (Aquaillumination, Hydra, Germany, 12:12 dark:light cycle at  $\sim 50 \mu\text{mol photons}^{-2} \text{ s}^{-1}$ ) was positioned above the jars and the overall set-up was covered by a wooden framework with black fabric attached. In accordance with the crepuscular/nocturnal nature of the animals, the light:dark cycle was run contradictory to the sun. This enabled a feeding of the animals during their perceived night time. The animals were fed with pellets (Vitalis Aquatic Nutrition, United Kingdom) until three days before freezing in liquid nitrogen with subsequent storage at  $-80 \text{ }^\circ\text{C}$ . Prior to freezing, the wet weight (WWs) of the worms was taken, after carefully damping them on a tissue. After freezing for at least 24 h, the worms were freeze-dried (Alpha 1–4 LDplus, Martin Christ Gefriertrocknungsanlagen GmbH, Osterode am Harz, Germany). The dry weight (DW) was quantified after the process. The ratio of WW to DW was calculated afterwards. The lipid, protein and carbohydrate measurements were conducted following the protocol described in the “Homogenisation of biomass” to “Total protein content” sections.

### Feeding experiment

The feeding experiment was conducted between February and June 2024 in a similar set-up as described in the “Comparative nutrient analysis of *Eurythoe spec. 1* and *spec. 2*” section. During the experiment three different food items were fed to four replicates, respectively. Fish pellets that were fed to worms during the pre-culture were used as a control (Vitalis Aquatic Nutrition). Besides, purchased algae used as supplement feed for herbivorous fish was used (Green Marine Algae, Ocean Nutrition, Essen, Belgium), referred to as “Algae” in the following. Frozen spinach was used as a plant-based alternative (REWE Bio Blattspinat, REWE Markt GmbH, Köln, Germany), referred to as “Spinach”.



**Fig. 2** Nine of the twelve glass jars used for the isolation of the polychaetes with bubble stones and PVC tubes placed in a constant temperature room

Twelve individuals of *E. spec. I* were chosen from the stock at ZMT (see “Biomass and cultivation of *Eurythoe* spp.”) with an initial weight of  $3.43 \pm 0.86$  g. In this experiment we did not differentiate between sexes. For acclimation, the animals were positioned each in a glass jar on 29.02.24 and kept there until the start of the experiment on 26.03.24, being fed with fish feed pellets (Vitalis Aquatic Nutrition). The worms were starved for six days prior to the start of the experiment. On feeding days, the animals were first weighed (balance: TE214S-OCE, Sartorius AG, Göttingen, Germany) and afterwards fed with one of three respective items, depending on their treatment. Feeding took place ad libitum in a time frame of 4–24 h, by placing the respective food item in the jar. The feeding time differed between days; however, it was kept constant for all the experimental jars. Feeding took place on experiment days 10, 16, 21, 27, 35, 41, 48, 57, 62, 69, 77, 83 and 90. After each feeding period, water was exchanged to remove uneaten feed and faeces.

The specific growth rate (SGR,  $d^{-1}$ ) was calculated based on the wet weight of the individual organisms, following the formula (Wang et al. 2019b):

$$SGR (d^{-1}) = ((\ln (WW_t) - \ln (WW_0)) / t) \quad (1)$$

with  $WW_t$  referring to  $WW$  (g) at the respective experimental day and  $WW_0$  rereferring to the initial  $WW$  (g) at the start if the experiment, so  $t$  refers to the respective experimental day (d).

During the experiment spontaneous fragmentations of the organisms were observed. The SGR was quantified based on the sum of all fragments of the respective replicate. However, when fragmentation happened, the weight and number of the separate fragments was noted. To analyse the mode of fragmentation, the percentage of total weight for each fragment was calculated and the fragments sorted by weight, with 1 being the heaviest and 4 being the lightest (based on  $WW$ ). Percent of total weight (%) was based on the following formula:

$$\text{Percent of total weight (\%)} = (100 / WW_{\text{total}}) * WW_{\text{fragment } x} \quad (2)$$

with  $WW_{\text{total}}$  referring to the wet weight of the whole individual or rather all fragments and  $WW_{\text{fragment}}$  referring to the  $WW$  of the respective fragment. The experiment was conducted over a period of 90 days and on 17.06.24, *E. spec. I* individuals were weighed and frozen for further analysis ( $n=4$ ). Prior to this, worms were starved for seven days in order to ensure that their stomachs had been emptied. The worms'  $WW$  and  $DW$  were taken before freezing ( $-80$  °C) and freeze-drying (Alpha 1–4 LDplus, Martin Christ Gefrier-trocknungsanlagen GmbH, Osterode am Harz, Germany). The ratio of  $WW$  to  $DW$  was quantified using the sum of all fragments per initial replicate, respectively. The worms' compositions were quantified as described in the “Homogenisation of biomass” to “Total protein content” sections.

## Homogenisation of biomass

For the proximate analysis fresh polychaetes were frozen in liquid nitrogen. A Ultra-Turrax (T 10 basic ULTRA-TURRAX, IKA-Werke GmbH & CO. KG, Staufen im Breisgau, Germany) was used for homogenization and a 1:20 dilution (w:v) based on the  $WW$  was prepared using a sodium phosphate buffer (0.1 M  $K_2HPO_4$ ; 0.1 M  $KH_2PO_4$ ; pH 7.5). Homogenization was then carried out 6 times for 20 s each at level 4 of the Ultra-Turrax

on ice. After homogenization aliquots for total lipid, carbohydrate and total protein content measurements were taken and stored at  $-80\text{ }^{\circ}\text{C}$  until further use.

### Total lipid content

The total lipid content was analysed following Bligh and Dyer (1959), with glycerol tri-palmitate in chloroform as a standard (concentrations of 0, 0.05, 0.1, 0.2, 0.4, 0.8, 1.6, 2.4  $\text{mg mL}^{-1}$ ). A total of 300  $\mu\text{L}$  of the homogenate obtained from the polychaetes was diluted with 500  $\mu\text{L}$  chloroform, 500  $\mu\text{L}$  methanol and 250  $\mu\text{L}$  ultrapure water before being centrifuged (10 min, room temperature, 1000 g). The lower phase was transferred and diluted 1:2 with chloroform. 500  $\mu\text{L}$  of sulphuric acid was added to the samples before incubation (200  $^{\circ}\text{C}$ , 20 min). After cooling down, 1.5 mL ultrapure water was added to the samples and absorbance was measured at 375 nm (200  $\mu\text{L}$  of sample).

### Carbohydrate content

Total carbohydrates were measured based on De Coen and Janssen (1997). Glucose in ultrapure water was used as a standard (concentrations of 0, 0.0078, 0.016, 0.032, 0.0625, 0.125, 0.25  $\text{mg mL}^{-1}$ ). Trichloroacetic acid (100  $\mu\text{L}$ , 15%) was added to 300  $\mu\text{L}$  homogenate and incubated at  $-20\text{ }^{\circ}\text{C}$  for 10 min. The samples were then centrifuged (10 min, 4  $^{\circ}\text{C}$ , 1000 g). The remaining pellet was further used for protein analysis (see “Carbohydrate content”). For the measurements, 50  $\mu\text{L}$  phenol and 200  $\mu\text{L}$  sulphuric acid were added to 50  $\mu\text{L}$  of the diluted samples (1:5 with KP buffer) before incubation (30 min., room temperature). Absorbance was measured at 492 nm.

### Total protein content

The determination of the total protein content was based on Bradford (1976). Bovine serum albumin in ultrapure water was used as a standard (concentrations of 0, 0.0155, 0.0313, 0.0625, 0.125, 0.25, 0.5, 0.75, 1.0  $\text{mg mL}^{-1}$ ). The pellet (see “Total lipid content”) was resuspended in 500  $\mu\text{L}$  NaOH (1 M) and incubated (30 min., 60  $^{\circ}\text{C}$ ). pH was adjusted to 6–8 by adding 1.67 N HCl. Afterwards samples were diluted with KP buffer (1:5). After adding 270  $\mu\text{L}$  Bio-Rad Protein Assay Reagent to 30  $\mu\text{L}$  of each sample, they were incubated (30 min, room temperature) in the dark. The absorbance was then measured at 592 nm.

### Statistical analyses

The data were analysed using R Studio (R Core Team 2022, R Studio: Integrated Development for R Studio, PBC, Boston, USA, Version 2022.02.1) and packages tidyverse (Wickham 2019), ggplot2 (Wickham et al. 2019a) and dyplr (Wickham et al. 2019b). Outliers were determined using Grubb’s test ( $\alpha=0.05$ ) in a web-based version of Graph-Pad (<https://www.graphpad.com/quickcalcs/grubbs1/>). For the comparison of males and females of *spec. 1* and individuals of *spec. 2*, as well as of different feeding treatments on a single day in the feeding experiment, WW to DW ratio after the experimental run and percent of total of fragments, a one-way analysis of variance (one-way ANOVA) was performed with a subsequent post hoc test (TukeyHSD, Honest Significant Difference).

Homogeneity and normality assumption were tested using Levene's test and the Shapiro–Wilk test, respectively. When assumptions were not met, a Kruskal–Wallis test and a subsequent post hoc test (Dunn's) were run. Different letters indicate significant differences ( $\alpha=0.05$ ). The data are presented as mean  $\pm$  standard deviation (SD) if not indicated differently. For the composition of the worms, the units mg protein/lipid/carbohydrates mg DW<sup>-1</sup> were used synonymous with % DW. Statistical outputs are presented in Supplements II – XI.

## Results

### Comparative nutrient analysis of *Eurythoe spec. 1* and *spec. 2*

The two different species could be distinguished by their size. Additionally, *spec. 2* showed a slightly different colour pattern. They had a dark line in the middle of their dorsal side, which was missing in the first and last quarters of *spec. 1*. Under the blue lights of the aquaria, the different sexes in *spec. 1* could be distinguished according to Kudenov (1974), with the females showing a pinkish and the males a whitish colouration, especially at the posterior quarter of the body. However, with the lighting that was used for taking photos, the males of *spec. 1* appeared greyer and darker than the females (Fig. 1).

Overall, the values of the lipid, carbohydrates and protein ranged between 7 and 13% of the dry weight (DW), 3 and 10% DW and 27 and 37% DW, respectively.

All sexes of *spec. 1* (female:  $3.85 \pm 0.15$ , male:  $4.25 \pm 0.09$ ), as well as *spec. 2* ( $4.33 \pm 0.91$ ) showed similar ratios of WW to DW ( $\text{Chi}^2(2) = 5.12$ ,  $p = 0.077$ ).

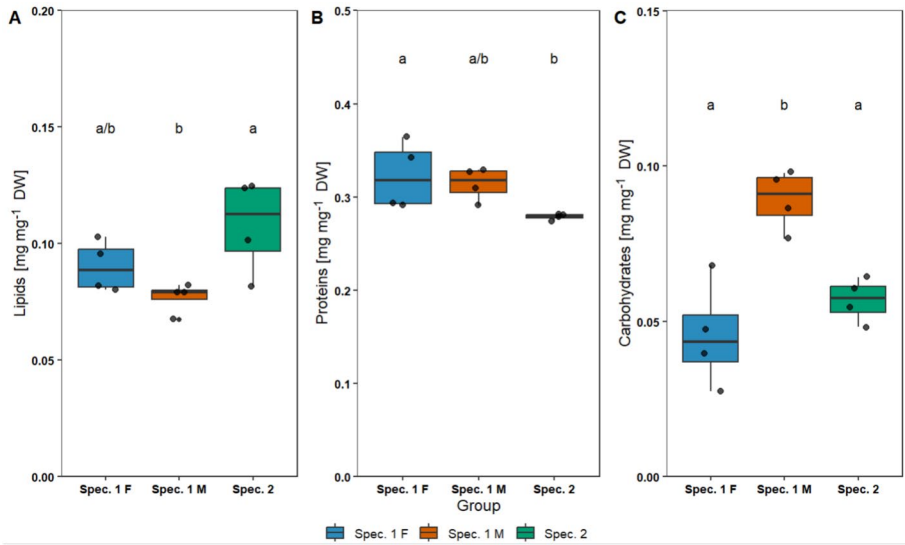
The mean lipid concentration of *spec. 2* ( $0.108 \pm 0.02$  mg lipid mg DW<sup>-1</sup>) was significantly ( $F(9,2) = 4.998$ ,  $p < 0.05$ ) higher compared to the male polychaetes of *spec. 1* ( $0.077 \pm 0.006$  mg lipid mg DW<sup>-1</sup>; Fig. 3A). Even though the sex did not have a significant impact on the lipid content of *spec. 1*, there was a trend of higher values for the females ( $0.09 \pm 0.011$  mg lipid mg DW<sup>-1</sup>, Fig. 3A).

The protein content between the sexes of *spec. 1* was similar (*spec. 1* female:  $0.323 \pm 0.036$  mg protein mg DW<sup>-1</sup> and male:  $0.314 \pm 0.018$  mg protein mg DW<sup>-1</sup>) with significantly ( $\text{Chi}^2(2) = 7.54$ ,  $p < 0.05$ ) lower values for *spec. 2* ( $0.279 \pm 0.003$  mg protein mg DW<sup>-1</sup>, Fig. 3B) compared to the female individuals of *spec. 1*. The average carbohydrate concentration of the male polychaetes of species *spec. 1* ( $0.089 \pm 0.01$  mg carbohydrates mg DW<sup>-1</sup>) was significantly higher ( $F(9,2) = 14.27$ ,  $p < 0.01$ ) compared to the mean of the females ( $0.046 \pm 0.017$  mg carbohydrates mg DW<sup>-1</sup>) and of species *spec. 2* ( $0.057 \pm 0.007$  mg carbohydrates mg DW<sup>-1</sup>).

### Feeding experiment

Polychaetes of all treatments lost weight during the acclimation phase, indicated by negative SGRs at the start of the experiment (Fig. 4A). *E. spec. 1* of the control increased slightly in their growth over 90 days (Fig. 4A), compared to worms fed with spinach and algae that overall lost weight. *Spec. 1* fed with algae showed the significantly lowest SGRs on experimental day 48 ( $F(9,2) = 12.89$ ,  $p < 0.01$ ). However, decreasing SGRs of worms fed with spinach resulted in similar rates with values of algae-fed animals from day 57 onwards (Fig. 4A). At the end of the experiment, the *Control* showed a positive SGR ( $0.0011 \pm 0.0007$  day<sup>-1</sup>) and significantly higher means ( $F(9,2) = 23.56$ ,





**Fig. 3** Lipid (A), protein (B), and carbohydrate (C) concentrations (mg component per mg dry weight (DW)) for females (F) and males (M) of *Eurythoe spec. 1* and *spec. 2*, respectively ( $n=4$ ). Individual values are represented by dots. The horizontal line in the boxplot represents the median and the box the interquartile range, with the upper end of the box at the 3rd quartile and the lower end at the 1st quartile. The vertical lines indicate the range of measured concentrations. A single point outside this range represents an outlier. Significant differences are marked with different letters based on a one-way ANOVA (carbohydrates, lipids) or a Kruskal–Wallis test (protein) ( $\alpha=0.05$ ). To avoid overlap of data points a small amount of noise was added to each point using the jitter function in RStudio

$p < 0.001$ ), than those treatments fed with spinach ( $-0.0040 \pm 0.0007 \text{ d}^{-1}$ ) and algae ( $-0.0052 \pm 0.0022 \text{ d}^{-1}$ ). The ratio of WW to DW was similar across all treatments (*Control*  $3.7 \pm 0.17$ , *Algae*  $3.90 \pm 0.14$ , *Spinach*  $3.92 \pm 0.05$ ;  $F(9,2) = 2.349$ ,  $p = 0.151$ ).

Individuals of *spec. 1* fragmented throughout the experimental run. One specimen of *spec. 1* already fragmented during the acclimation phase explaining the initial fragment size of five instead of four for feeding treatment *Algae* (Fig. 4B). Two individuals of *spec. 1* of the *Control* were found on the 27th experimental day to have fragmented in two and three pieces, respectively, leading to overall seven fragments in this treatment. Worms of treatment *Algae* fragmented on day 69, when one organism separated in two pieces (Fig. 4B).

After 90 days all individuals of *spec. 1* fragmented at least into two pieces, with the exception of one individual of the treatment *Algae* (Fig. 4B). At the end of the experiment *spec. 1* fed with spinach had in sum the highest number of fragments (14), followed by those of treatments *Control* (13) and *Algae* (10). However, the distribution of fragments between replicates showed a different trend, indicated by the means of the respective group (*Spinach*:  $3.50 \pm 0.58$ , *Control*:  $3.25 \pm 1.26$ , *Algae*:  $2.50 \pm 1.29$ ). The first fragmentation into two fragments (5 worms), followed by fragmentation into 3 pieces (3 worms) and four pieces (2 worms, Fig. 5). In case of two pieces, one fragment showed a significantly higher percentage of the total weight with values around 55–75%, compared to the smaller one ( $F(8,1) = 47.89$ ,  $p < 0.001$ , Fig. 5). In case of fragmentation

**Fig. 4** **A** Specific growth rate (SGR,  $d^{-1}$ ) of *Eurythoe cf. complanata* (*spec. 1*) over a feeding experiment of 90 days with treatments *Control* (commercial pellet), *Algae* and *Spinach*. Organisms were fed with the respective feeding treatment on days indicated on *x*-axis with prior acclimation under feeding with fish pellets. SGRs are based on wet weight (WW) of worms at the start of the experiment and the respective measurement day. SGRs of the initial day are based on the start of the acclimation phase. Data are presented as mean  $\pm$  standard deviation with  $n=4$ . Different letters indicate significant differences based on a one-way ANOVA with Tukey's HSD post hoc test ( $\alpha=0.05$ ). The grey dashed line indicates a SGR of 0. **B** Sum of fragments of the similar experiment. Data are presented as sum of the fragments with an initial count of one worm per replicate per treatment. The grey dashed line indicates the initial of four fragments, with one individual of treatment *Algae* already fragmented during the acclimation period

into three pieces, one fragment showed a significantly larger weight, relative to the other two (Fig. 5,  $F(6,2) = 119.9$ ,  $p < 0.001$ , Fig. 5).

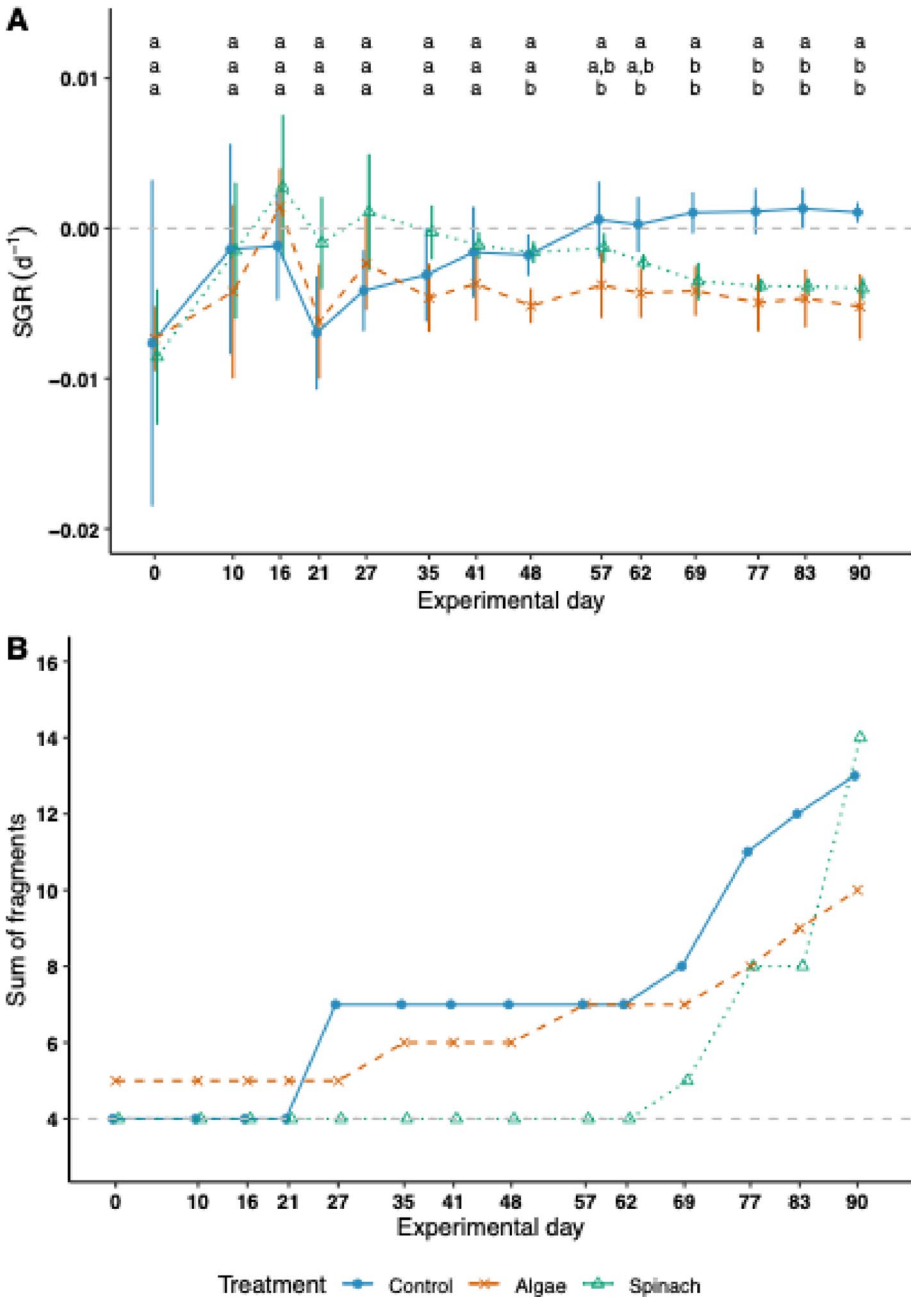
The lipid and protein content of *E. spec. 1* was similar between different feeding treatments (*Control*:  $0.086 \pm 0.019$ ; *Algae*:  $0.061 \pm 0.015$ , *Spinach*:  $0.076 \pm 0.012$  mg lipid  $mg^{-1}$  DW; *Control*:  $0.318 \pm 0.022$ , *Algae*:  $0.278 \pm 0.094$ , *Spinach*:  $0.311 \pm 0.071$  mg protein  $mg^{-1}$  DW, Fig. 6A, B). The treatment *Control* showed significantly ( $F(9,2) = 12.13$ ,  $p < 0.001$ , Fig. 6C) higher values of carbohydrates ( $0.045 \pm 0.008$  mg carbohydrates  $mg^{-1}$  DW), compared to means of the other treatments (*Algae*:  $0.021 \pm 0.011$ , *Spinach*:  $0.020 \pm 0.004$  mg carbohydrates  $mg^{-1}$  DW).

## Discussion

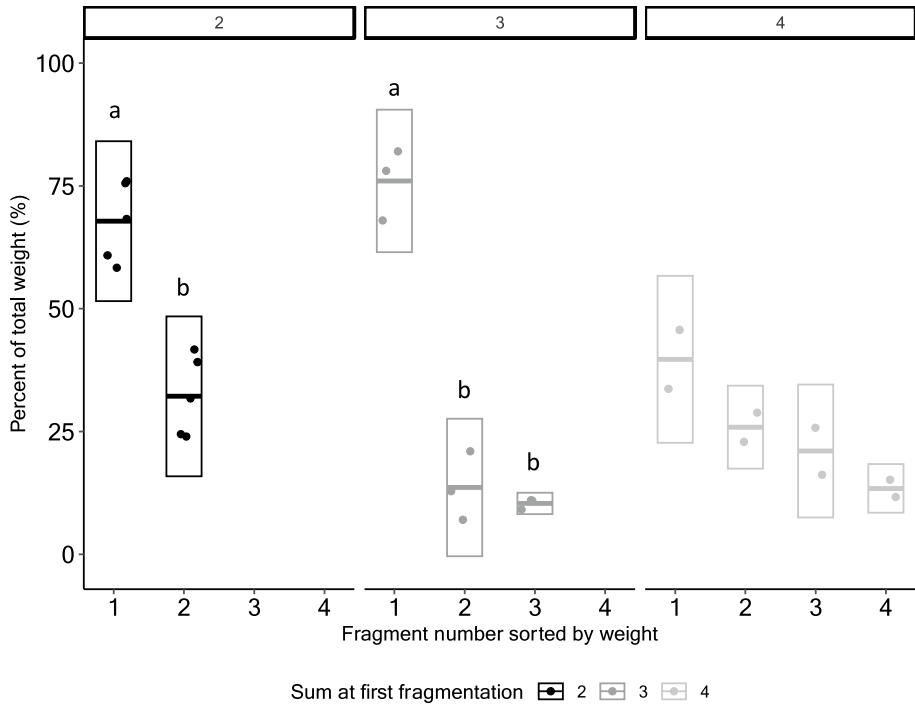
The aim of this research was to link the species' composition with their feeding patterns in order to provide a basis for the species' targeted cultivation and their use in the context of aquaculture. Overall, the quantified compositions of *E. cf. complanata* (*spec. 1*) and *Eurythoe spec. 2* were at the lower range of other polychaete species following the typical pattern of macronutrient composition (Wang et al. 2019b; Selvam 2021; Bharath et al. 2021, Table 1). However, protein concentrations quantified in this study were considerably below the reported range for other polychaetes and only a smaller proportion of the DW could be broken down in this study compared to the previously cited studies (Table 1). This might be explained by variations between protocols, as well as *Eurythoes'* high proportion of inorganic material due to its particularly large number of bristles, which are mainly made up of calcium carbonate and apatite clusters (Righi et al. 2021).

## Comparative nutrient analysis of *Eurythoe spec. 1* and *spec. 2*

The results confirmed the hypothesis that the species composition differs between sexes and between *spec. 1* and *spec. 2*. The sexes of the species *spec. 1* were differentiated based on Kudenov (1974) using the described different colourations. In contrast to Kudenov (1974), who reported that mainly the dorsolateral, interramal and ventral sides should be coloured—in both male and female polychaetes—the clearest colourations were found on the dorsal side of the posterior quarter. In general, colour differences between the sexes are known in some polychaete species. Male polychaetes are usually whitish and the females pink to reddish in colour (Simon 1967; Pernet 2000; Chatelain et al. 2008), which is due to the different gametes developed in the tissue of the coelom and gut. While Chatelain et al. (2008) also observed reddish-coloured female individuals, the male polychaetes of the species *N. virens* were dark-coloured, similarly to the observations in this study.

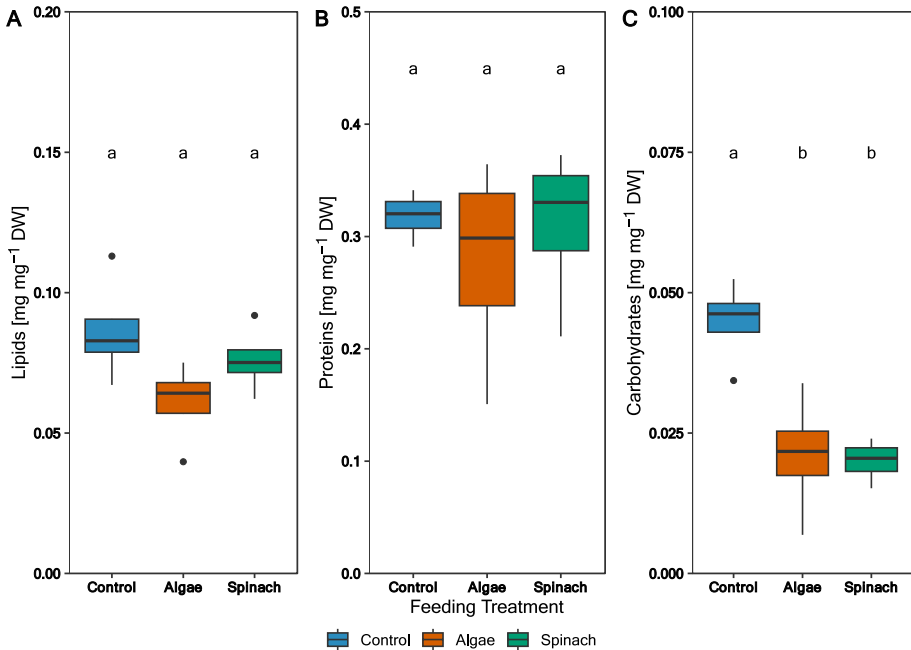


To the best of our knowledge, this study investigated the compositional differences between the sexes in polychaetes for the first time. Aligning with our expectations we found some form of sexual dimorphism regarding the proximate composition in *spec. 1*, which might be explained by behavioural differences or more likely by the different



**Fig. 5** Percent of total weight (%) of fragments (sorted by wet weight, WW) at first fragmentation of *Eurythoe cf. complanata* (*spec. 1*) independently of experimental day. The groups are differentiated by the number of fragments that worms were found to have after first fragmentation. Data are presented as mean  $\pm$  standard deviation, SD ( $n=2-5$ ). Different letters indicate significant differences based on one-way ANOVA with Tukey's HSD post hoc test ( $\alpha=0.05$ ). For one group no statistical test was conducted, because of the low number of replicates ( $n=2$ ). To avoid overlap of data points a small amount of noise was added to each point using the jitter function in RStudio

requirements of gamete production. Female individuals often require lipids for oocyte production and therefore have correspondingly higher lipid reserves (Giese 1966; Pocock et al. 1971; Kudenov 1974). In addition, the highest lipid concentrations within polychaetes have been found in oocytes (Giese 1966; Pocock et al. 1971; Lee et al. 2005; Schenk et al. 2006), which could relate to the trend of higher lipid concentrations in females of *spec. 1*, compared to the males. Additionally, we were also able to show the hypothesized different proximate composition of *spec. 2*, probably as a result of different feeding habits. *Spec. 2* could naturally be subject to higher predation pressure due to its smaller size, potentially resulting in a higher stress level and lipid accumulation for adequate energy reserves. The largest proportion of protein mass is accounted for by proteins that form muscles and perform structural functions (Adams 1978; Hooper and Thuma 2005; Righi et al. 2021). Therefore, the protein concentration appears to be biologically robust, which explains similar concentrations between sexes of *spec. 1*. The trend of higher carbohydrate and lower protein concentrations in *spec. 2* could be due to different feeding habits or energy storage mechanisms. Besides, significantly highest carbohydrate concentrations of male polychaetes of species *spec. 1* could be explained by different feeding strategies or the need for quickly available energy for possible fights or general competitive advantages. This kind of



**Fig. 6** Lipid (A), protein (B) and carbohydrate (C) concentrations (mg component mg<sup>-1</sup> dry weight (DW)) of *Eurythoe cf. complanata (spec. I)* fed over 90 days with different feeding treatments (*Control, Algae, Spinach*, n=4). Individual values are represented by dots. The horizontal line in the boxplot represents the median and the box the interquartile range, with the upper end of the box at the 3rd quartile and the lower end at the 1st quartile. The vertical lines indicate the range of measured concentrations. A single point outside this range represents an outlier. Significant differences are marked with different letters based on a one-way ANOVA (alpha=0.05). To avoid overlap of data points a small amount of noise was added to each point using the jitter function in RStudio

competition among males has already been demonstrated for some species of polychaetes (Premoli and Sella 1995). Further studies could be conducted to verify the reported differences between the sexes and further link them to the hypothesised biological functions. Additionally, future assessments of detailed fatty acid and amino acid profiles could refine the understanding of those nutritional differences and support a more complete evaluation of their suitability as feed protein resources.

### Feeding experiment

The long-term laboratory experiment was designed to increase the understanding of the basic feeding ecology and biology of *E. cf. complanata (spec. I)* and to draw conclusions for the practical application of targeted cultivation. The hypothesis that *spec. I* will be able to use the plant-derived nutrients for growth, but that pellets will result in higher specific growth rates (SGRs), can be partially confirmed. The SGRs in this experiment were considerably lower than those reported, e.g. from polychaete *H. diversicolor*, ranging from 0.0025 to 0.058 d<sup>-1</sup> (Bischoff 2007; Pajand et al. 2017; Wang et al. 2019b). Significantly higher SGRs of *spec. I* from the *Control* treatment compared to those fed with spinach and algae might have occurred, because the diets were not designed isoenergetic and pellets

containing fish and fish by-products are energy-denser than plant-based *Algae* and *Spinach* feed (Supplements XII). The different feed was offered for at least four hours, which should have been enough time for polychaetes to prey on the items, considering that Pardo and Amaral (2005) found the species to detect fish pieces within 5 min. However, the absence of sediment in the experimental set-up could have influenced the feeding choices of the worms, considering that Engel et al. (2023) reported fatty acid and isotopic markers indicating a predominately herbivorous or omnivorous diet that polychaetes might have ingested dominantly non-selectively through the sediment (Engel et al. 2023). Future experiments could consider the effect of the surrounding on the feeding strategies of *E. complanata*. Even though the observed spontaneous fragmentation throughout the experiment seems to be typical behaviour for the species complex (Pardo and Amaral 2005), the effect on the nutrient uptake of the species is likely immense. After fragmentation one piece of the worm relies on the energy reserves until the anterior part is regenerated (Yáñez-Rivera and Méndez 2014; Toso et al. 2024). Therefore, the fragmentation rate could have led to the low or rather negative growth rates in the experiment. Interestingly, the size of the individual fragments, expressed as percent of total weight (%) seemed to be depending on the number of fragments that the worm disintegrated into (Fig. 5). There could be a connection between the size of the fragment and whether this was the anterior or posterior piece, bearing important information for utilisation in aquaculture. However, since the animals were not checked daily for potential new fragmentations, it cannot be ruled out, that the animals were fragmenting in several steps.

## Implications for the aquaculture sector

Polychaetes have great potential as an alternative to fish meal in fish feed. The high protein content of up to 37% DW of both *Eurythoe* species demonstrated in this study makes them a promising option for this purpose. Compared to other promising alternative sources for fish feed, *Eurythoe* spp. fall in the lower range of resources like microalgae (3–80% protein, Ahmad et al. 2022) or the black soldier fly (32–53% protein, Lu et al. 2022) regarding their protein content. Even though, direct comparisons should be taken with care, since the composition of macronutrients depends on several factors. However, this highlights the huge utilisation potential of efficiently producing high-quality protein using low-cost feed. Since the highest protein concentrations were found in polychaetes of the species *Eurythoe spec. 1*, those seem to be the best option. However, additional analyses of the fatty acid and amino acid composition would be necessary for further recommendations. *E. cf. complanata* could be a particularly suitable candidate due to the easy cultivation already observed at ZMT. Both the fact that *E. cf. complanata* is omnivorous and its high habitat diversity could be an additional advantage, as it is well known that the composition of polychaetes, especially that of the fatty acids, can be manipulated by the feed and the substrate on which they are kept (Asghari et al. 2017; Pajand et al. 2020; Wibowo et al. 2020). Accordingly, the respective components could be adjusted depending on the intended area of application. In addition, the significant differences observed between the feeding groups (Fig. 4A) could be utilized to tailor the feed composition according to specific applications. The fragmentation of *E. cf. complanata* in the context of aquaculture could lead to decreases in biomass accumulation, since one fragment is unable to feed until the development of a new anterior. Therefore, triggers for fragmentation need to be investigated further in order to keep the fragmentation rates low. On the other hand, this behaviour could make

reproductive efforts during cultivation obsolete. In order to decide for the most efficient strategy, further research is required.

Besides, the polychaetes could be used to upcycle waste or low-value feed. For example, Nederlof et al. (2019) were able to detect high concentrations of polyunsaturated fatty acids in polychaetes that were fed with feed only containing low concentrations of these. In addition, synthesis pathways for valuable fatty acids in polychaetes are known (Olive et al. 2009; Pairohakul et al. 2021, Villena-Rodríguez et al. 2025). Furthermore, Anglade et al. (2024) were able to retrace the nutrient uptake of *Hediste diversicolor* fed smolt sludge and found that the polychaetes could efficiently take up nutrients for growth, validating similar previous results (Wang et al. 2019a; Anglade et al. 2023). An integrated aquaculture approach promises efficient biomass production of polychaetes that can later be used as a high-value aquaculture feed resource, hence contributing to an increase in aquaculture (or production) income. In case of *E. cf. complanata*, a fast accumulation of biomass in an integrated multi-trophic aquaculture system (IMTA) could already be observed at ZMT.

However, there are still hurdles in the use of polychaetes as animal feed. First of all, polychaetes are known to accumulate harmful substances (Méndez and Páez-Osuna 1998; Roveta et al. 2021; Watson et al. 2024), which is why a controlled rearing of the animals would be essential. In addition, due to the presence of complanin the bristles of *E. cf. complanata* would have to be removed before further processing. In future studies, controlled feeding trials with aquaculture species could investigate how the inclusion of *E. complanata* in formulated diets affects growth performance, feed efficiency, and overall animal health, thereby clarifying its practical role as a feed ingredient. Once both the practical and biological aspects are better understood, polychaetes could be a valuable source of protein not only in aquaculture, but also in livestock feed. In case of *Eurythoe*, some further research focusing on different sexes and the two different (sub)species will have to be carried out before then, for which an important foundation was laid with this study.

## Conclusion

The proximate composition of *Eurythoe* spp., as well as the comparably easy cultivation and the promising application in multi-trophic set-ups support the high potential of these organisms for the aquaculture feed sector. Two species of *Eurythoe* spp. were identified visually distinguishable by their size. Male organisms of the larger sized species *E. cf. complanata* showed significantly higher content of carbohydrates, compared to the females. The differences in composition between the sexes of the larger species suggest that organisms can be chosen based on the needs for the specific feed. The feeding experiment run with *E. cf. complanata* showed that feeding with commercially available pellets led to higher SGR, compared to spinach and algae. However, a deeper understanding of the fragmentation and feeding behaviour of the species is required in order to reliably cultivate the worms in a controlled environment on a larger scale and with sustainable feedstuff. Additionally, further validations of our results as well as additional studies investigating the species detailed composition as well as their application potential are warranted. The presented adapted protocol to quantify protein, lipid and carbohydrate content of *Eurythoe* spp. will support further research in this regard.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10499-025-02407-9>.

**Acknowledgements** The authors were happy to receive financial support from the core budget of ZMT (inhouse funding Recycling 8907). The authors thank PD Dr. Ekin Tilic (Senckenberg Research Institute and Natural History Museum, Head of Section—Marine Invertebrates II) for the support with the interpretation of the sequence data of *Eurythoe* spp.

**Author contributions** Arne Valentin Heydtmann: conceptualization, methodology, formal analysis, investigation, data curation, writing—original draft, visualisation; Constanze von Waldthausen: conceptualization, methodology, investigation, resources, writing—review and editing; Sabine Keuter: methodology, investigation, writing—review and editing; Andreas Kunzmann: conceptualization, writing—review and editing, supervision, project administration, funding acquisition; Lara Stuthmann: conceptualization, methodology, formal analysis, investigation, data curation, writing—original draft, visualisation, supervision

**Funding** Open Access funding enabled and organized by Projekt DEAL.

**Data availability** The data were uploaded to Open Science Framework and can be accessed via the website at <https://doi.org/https://doi.org/10.17605/OSF.IO/S4ANG>.

## Declarations

**Competing interests** The authors declare no competing interests.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Adams E (1978) Invertebrate collagens: marked differences from vertebrate collagens appear in only a few invertebrate groups. *Science* 202(4368):591–598. <https://doi.org/10.1126/science.212833>
- Ahmad A, Hassan SW, Banat F (2022) An overview of microalgae biomass as a sustainable aquaculture feed ingredient: food security and circular economy. *Bioengineered* 13(4):9521–9547. <https://doi.org/10.1080/21655979.2022.2061148>
- Anglade I, Dahl TH, Kristensen BSB, Hagemann A, Malzahn AM, Reitan KI (2023) Biochemical composition of *Hediste diversicolor* (OF Müller 1776) (Annelida: Nereidae) reared on different types of aquaculture sludge. *Front Mar Sci* 10:1197052. <https://doi.org/10.3389/fmars.2023.1197052>
- Anglade I, Sæther HOE, Hagemann A, Reitan KI, Malzahn AM (2024) Nutrient upcycling and flows of carbon, nitrogen, and phosphorus in *Hediste diversicolor* (OF Müller, 1776) (Annelida: Nereidae) fed aquaculture sludge. *Front Mar Sci* 11:1458426. <https://doi.org/10.3389/fmars.2024.1458426>
- Arias A, Barroso R, Anadón N, Paiva PC (2013) On the occurrence of the fireworm *Eurythoe complanata* complex (Annelida, Amphinomididae) in the Mediterranean Sea with an updated revision of the alien Mediterranean amphinomids. *ZooKeys* 337:19–33. <https://doi.org/10.3897/zookeys.337.5811>
- Asghari S, Salarzadeh AR, Rohani K, Yahyavi M, Mohammadzadeh F (2017) Fatty acid profile of wild and farmed sandworms, *Perinereis nuntia*, in the Coast of Bandar Abbas, Iran. *Turk J Fish Aquat Sci* 17:1049–1053. <https://doi.org/10.4194/1303-2712-v17>



- Bharath J, Priya A, Stella C (2021) A comparative study on the nutritional value of three polychaete species used in shrimp aquaculture. *Sustain Agri Food Env Res* 9(4). <https://doi.org/10.7770/safer-v0n0-art2188>
- Bischoff, AA (2007) Solid waste reduction of closed recirculated aquaculture systems by secondary culture of detritivorous organisms. PhD-Thesis at the Leibniz-Institute of Marine Sciences, Kiel, Germany, p 26
- Brown N, Eddy S, Plaud S (2011) Utilization of waste from a marine recirculating fish culture system as a feed source for the polychaete worm, *Nereis virens*. *Aquaculture* 322:177–183. <https://doi.org/10.1016/j.aquaculture.2011.09.017>
- Chatelain ÉH, Breton S, Lemieux H, Blier PU (2008) Epitoky in *Nereis (Neanthes) virens* (Polychaeta: Nereididae): a story about sex and death. *Comp Biochem Physiol B Biochem Mol Biol* 149(1):202–208. <https://doi.org/10.1016/j.cbpb.2007.09.006>
- Cole VJ, Chick RC, Hutchings PA (2018) A review of global fisheries for polychaete worms as a resource for recreational fishers: diversity, sustainability and research needs. *Rev Fish Biol Fish* 28:543–565. <https://doi.org/10.1007/s11160-018-9523-4>
- Engel et al. 2023: Engel N, Aguado MT, Maraun M (2023) Trophic ecology of three marine polychaete species: Evidence from laboratory experiments using stable isotope ( $^{15}\text{N}$ ,  $^{13}\text{C}$ ), fatty acid (NLFA) analyses, and C and N stoichiometry. *Marine Environmental Research*, 185, 105878. <https://doi.org/10.1016/j.marenvres.2023.105878>
- Díaz-Castañeda V, Reish D (2009) Polychaetes in environmental studies. *Annelids in Modern Biology* 7:203–227. <https://doi.org/10.1002/9780470455203.ch11>
- Dorgham MM, Hamdy R, Hassan H, Atta MM (2015) Biochemical composition of the nereidid *Perinereis cultrifera* from the Egyptian Mediterranean Coast. *Rev Biol Mar Oceanogr* 50(3):535–543. <https://doi.org/10.4067/S0718-19572015000400011>
- GBIF.org (27 August 2025) GBIF occurrence download. <https://doi.org/10.15468/dl.5evbfc>
- Giese AC (1966) Lipids in the economy of marine invertebrates. *Physiol Rev* 46(2):244–298. <https://doi.org/10.1152/physrev.1966.46.2.244>
- Hooper SL, Thuma JB (2005) Invertebrate muscles: muscle specific genes and proteins. *Physiol Rev* 85(3):1001–1060. <https://doi.org/10.1152/physrev.00019.2004>
- Jerónimo D, Lillebø AI, Maciel E, Domingues MRM, Cremades J, Calado R (2021) Unravelling the fatty acid profiles of different polychaete species cultured under integrated multi-trophic aquaculture (IMTA). *Sci Rep* 11(1):10812. <https://doi.org/10.1038/s41598-021-90185-8>
- Kudenov JD (1974) The reproductive biology of *Eurythoe complanata* (Pallas, 1766), (Polychaeta: Amphinomidae). PhD thesis, The University of Arizona, Tucson, AZ, USA, 128 pp
- Lee RF, Walker A, Reish DJ (2005) Characterization of lipovitellin in eggs of the polychaete *Neanthes arenaceodentata*. *Comp Biochem Physiol B Biochem Mol Biol* 140(3):381–386. <https://doi.org/10.1016/j.cbpc.2004.11.002>
- Lu S, Taethaisong N, Meethip W, Surakhunthod J, Sinpru B, Sroichak T, Archa P, Thongpea S, Paengkoum S, Purba RAP, Paengkoum P (2022) Nutritional composition of black soldier fly larvae (*Hermetia illucens* L.) and its potential uses as alternative protein sources in animal diets: a review. *Insects* 13(9):831. <https://doi.org/10.3390/insects13090831>
- Méndez N, Páez-Osuna F (1998) Trace metals in two populations of the fireworm *Eurythoe complanata* from Mazatlan Bay: effect of body size on concentrations. *Environ Pollut* 102(2–3):279–285. [https://doi.org/10.1016/S0269-7491\(98\)00061-X](https://doi.org/10.1016/S0269-7491(98)00061-X)
- Müller MC, Berenzen A, Westheide W (2003) Experiments on anterior regeneration in *Eurythoe complanata* (“Polychaeta”, Amphinomidae): reconfiguration of the nervous system and its function for regeneration. *Zoomorphology* 122:95–103. <https://doi.org/10.1007/s00435-003-0073-4>
- Nakamura K, Tachikawa Y, Kitamura M, Ohno O, Suganuma M, Uemura D (2008) Complanine, an inflammation-inducing substance isolated from the marine fireworm *Eurythoe complanata*. *Org Biomol Chem* 6(12):2058–2060. <https://doi.org/10.1039/B803107J>
- Nederlof MA (2022) Integrated multi-trophic aquaculture: nutrient retention efficiency and valorisation of waste nutrients. PhD thesis, Wageningen University and Research, 191 pp. <https://doi.org/10.18174/564056>
- Nederlof MA, Jansen HM, Dahlgren TG, Fang J, Meier S, Ivind Strand A, Sveier H, Verdegem MCI, Smaal AC (2019) Application of polychaetes in (de) coupled integrated aquaculture: production of a high-quality marine resource. *Aquac Environ Interact* 11:221–237. <https://doi.org/10.3354/aei00309>
- Olive PJ, Duangchinda T, Ashforth E, Craig S, Ward AC, Davies SJ (2009) Net gain of long-chain polyunsaturated fatty acids (PUFA) in a lugworm *Arenicola marina* bioturbated mesocosm. *Mar Ecol Prog Ser* 387:223–239. <https://doi.org/10.3354/meps08088>

- Pairohakul S, Olive PJ, Bentley MG, Caldwell GS (2021) Trophic upgrading of long-chain polyunsaturated fatty acids by polychaetes: a stable isotope approach using *Alitta virens*. *Mar Biol* 168:1–13. <https://doi.org/10.1007/s00227-021-03874-3>
- Pajand ZO, Soltani M, Kamali A, Bahmani M (2020) Growth, survival and fatty acids profile of polychaete, *Nereis diversicolor* (Müller, 1776) cultured using waste water of great sturgeon, *Huso huso* (Linnaeus, 1758) at different densities in an integrated farming system. *Iran J Fish Sci* 19(1):234–247. <https://doi.org/10.22092/ijfs.2019.118779>
- Pan YL, Rodrigues MJ, Pereira CG, Engrola S, Colen R, Mansinhos I, Romano A, Andrade PB, Fernandes F, Custódio L (2021) Exploring the biotechnological value of marine invertebrates: a closer look at the biochemical and antioxidant properties of *Sabella spallanzanii* and *microcosmus squamiger*. *Animals* 11(12):3557. <https://doi.org/10.3390/ani11123557>
- Panteli N, Kousoulaki K, Antonopoulou E, Carter CG, Nengas I, Henry M, Karapanagiotidis IT, Mente E (2025) Which novel ingredient should be considered the “holy grail” for sustainable production of fin-fish aquafeeds? *Rev Aquac* 17(1):e12969. <https://doi.org/10.1111/raq.12969>
- Pajand ZO, Soltani M, Bahmani M, Kamali A (2017) The role of polychaete *Nereis diversicolor* in bioremediation of wastewater and its growth performance and fatty acid composition in an integrated culture system with *Huso huso* (Linnaeus, 1758). *Aquaculture Research*, 48(10), 5271–5279. <https://doi.org/10.1111/are.13340>
- Pérez-Posada I, Cabanillas-Terán N, Carrera-Parra LF, Lizcano DJ, Sánchez A (2025) Trophic ecology of Caribbean polychaetes: responses to environmental changes driven by massive *Sargassum* arrivals. *Food Webs*. <https://doi.org/10.1016/j.fooweb.2025.e00411>
- Pernet B (2000) Reproduction and development of three symbiotic scale worms (Polychaeta: Polynoidae). *Invertebr Biol* 119(1):45–57. <https://doi.org/10.1111/j.1744-7410.2000.tb00173.x>
- Pocock DME, Marsden JR, Hamilton JG (1971) Lipids in an intertidal polychaete and their relation to maturation of the worm. *Comp Biochem Physiol A Physiol* 39(4):683–697. [https://doi.org/10.1016/0300-9629\(71\)90192-7](https://doi.org/10.1016/0300-9629(71)90192-7)
- Premoli MC, Sella G (1995) Sex economy in benthic polychaetes. *Ethol Ecol Evol* 7(1):27–48. <https://doi.org/10.1080/08927014.1995.9522968>
- Righi S, Savioli M, Prevedelli D, Simonini R, Malferrari D (2021) Unravelling the ultrastructure and mineralogical composition of fireworm stinging bristles. *Zoology* 144:125851. <https://doi.org/10.1016/j.zool.2020.125851>
- Roveta C, Annibaldi A, Afghan A, Calcinai B, Di Camillo CG, Gregorin C, Illuminati S, Mantas TP, Truzzi C, Puce S (2021) Biomonitoring of heavy metals: the unexplored role of marine sessile taxa. *Appl Sci* 11(2):580. <https://doi.org/10.3390/app11020580>
- Schenk S, Harris JR, Hoeger U (2006) A discoidal lipoprotein from the coelomic fluid of the polychaete *Nereis virens*. *Comp Biochem Physiol B Biochem Mol Biol* 143(2):236–243. <https://doi.org/10.1016/j.cbpb.2005.11.012>
- Selvam SB (2021) Proximate analysis of bait polychaetes from Port Dickson, Malaysia as prospectus replacement for aquaculture feed. *International Journal of Forest, Animal and Fisheries Research* 5(1):25–39. <https://doi.org/10.22161/ijfaf.5.1.4>
- Simon JL (1967) Reproduction and larval development of *Spio setosa* (Spionidae; Polychaeta). *Bull Mar Sci* 17(2):398–431
- Toso A, Mammone M, Rossi S, Piraino S, Giangrande A (2024) Effect of temperature and body size on anterior and posterior regeneration in *Hermodice carunculata* (Polychaeta, Amphinomidae). *Mar Biol* 171(8):152. <https://doi.org/10.1007/s00227-024-04468-5>
- Villena-Rodríguez A, Navarro JC, Hontoria F, Castro LF, Malzahn AM, Hagemann A, Monroig Ó (2025) Biosynthesis of long-chain polyunsaturated fatty acids in the nereid polychaete *Hediste diversicolor*: molecular cloning and functional characterisation of three fatty acyl elongases and two front-end desaturases. *Aquaculture* 595:741497. <https://doi.org/10.1016/j.aquaculture.2024.741497>
- Wang H, Hagemann A, Reitan KI, Ejlertsson J, Wollan H, Handå A, Malzahn AM (2019a) Potential of the polychaete *Hediste diversicolor* fed on aquaculture and biogas side streams as an aquaculture food source. *Aquacult Environ Interact* 11:551–562. <https://doi.org/10.3354/aei00331>
- Wang H, Seekamp I, Malzahn A, Hagemann A, Carvajal AK, Slizyte R, Standal IB, Handå A, Reitan KI (2019b) Growth and nutritional composition of the polychaete *Hediste diversicolor* (OF Müller, 1776) cultivated on waste from land-based salmon smolt aquaculture. *Aquaculture* 502:232–241. <https://doi.org/10.1016/j.aquaculture.2018.12.047>
- Wang X, Sui Z, Xu X, Chai Y, Wang H (2025) Nutritional value and biochemical composition of two new tropical polychaete species: Potential use as feed ingredients. *Journal of the World Aquaculture Society*, 56(1), e13122. <https://doi.org/10.1111/jwas.13122>

- Watson GJ, White S, Gobert S, Lepoint G, Sturaro N, Richir J (2024) Trace element contamination biomonitoring: a comparative study between the polychaetes *Alitta virens* and *Hediste diversicolor*. Environ Pollut 363:125116. <https://doi.org/10.1016/j.envpol.2024.125116>
- Wibowo ES, Yuwono E, Sukardi P, Siregar AS (2020) Survival rate, growth, and chemical content of *Dendronereis pinnaticirris* (Polychaeta, Nereidae) in maintenance with different feeds and substrates. Indones J Mar Sci 25(2):75–84. <https://doi.org/10.14710/ik.ijms.25.2.75-84>
- Wickham H (2019) Tidyverse: easily install and load the 'Tidyverse'. R package version 2.0.0
- Wickham H, Chang W, Henry L, Pedersen TL, Takahashi K, Wilke C, Woo K, Yutani H (2019a) ggplot2: create elegant data visualisations using the grammar of graphics. R package version 3.5.1 <https://doi.org/10.32614/cran.package.ggplot2>
- Wickham H, François R, Henry L, Müller K (2019b) dplyr: a grammar of data manipulation. R package version 3.5.0. <https://doi.org/10.32614/cran.package.dplyr>
- Yáñez-Rivera B, Méndez N (2014) Regeneration in the stinging fireworm *Eurythoe* (Annelida): lipid and triglyceride evaluation. J Exp Mar Biol Ecol 459:137–143. <https://doi.org/10.1016/j.jembe.2014.05.023>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.