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Naked Clams to open a new sector in sustainable nutritious food production

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The global population urgently requires alternative food sources that provide the micronutrient-rich profile of meat and fish but with lower environmental cost. We present a solution in the form of 'Naked Clams' (teredinids/shipworms) - a seldom researched group of bivalves, that feature tiny shells and live in and feed on wood, turning it into protein and essential nutrients. We report the first pilot system for Naked Clam aquaculture, the first nutritional profile and feeding efficacy assessment, and demonstrate value offered by microencapsulated feeds in fortifying Naked Clams. Naked Clams were rich in nutrients including vitamin B_{12} and monounsaturated fatty acids, and shared the high protein content of conventional bivalves such as blue mussels (*Mytilus edulis*). Microencapsulated algal feeds enriched the Naked Clams with essential PUFAs including EPA and DHA, with potential for further tailoring. Additional work is required, but this study represents a gateway to a new form of sustainable food production.

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INTRODUCTION

The United Nations warns that efforts to curb greenhouse-gas emissions and the impacts of global warming will fall significantly short without drastic changes in global land use, agriculture and human diets[1]. Increased adoption of 'Blue Foods', foods sourced from aquatic and marine environments, can make up a vital component of this change[2]. These foods are already important for the economies, livelihoods, and public health of many nations, being nutrient rich[3] and typically with a lower carbon, land, and water footprint than most terrestrial meats[4]. Intensive and controlled or 'urban' aquaculture comprises a lucrative and growing sector, promising faster growth, reduced costs, improved food safety and sustainability[5–7]. Bivalves, species like mussels and clams, are one such 'Blue Food' with outstanding potential[8]. Bivalves are rich in protein, essential fatty acids and key micronutrients as well as having a lower environmental impact than other sources of protein[8–10]. However, conventional bivalve farming has limitations making the sector financially less attractive than other more profitable but less sustainable sectors such as salmon farming[11,12]. These problems include habitat degradation and historical over-exploitation[13], food safety in increasingly polluted open marine environments[9,10], aquaculture and displacement of native species[14], slow growth rates compared with fish[10], infection and disease in both wild-caught and hatchery grown animals[15,16], costly processing, transport and storage[10,12]. Manufacturer, retail and consumer interest in bivalves is also weak compared to finfish and crustacean aquaculture sectors[10,12,17]. Lastly, slow growth rates in some bivalves increases costs therefore limiting commercial viability[10,18,19].

Teredinids are a seldom researched group of bivalves in the context of aquaculture, yet may offer the answer to providing intensive, rapid, and sustainable growth of nutrient-rich bivalve protein[20]. Teredinids are the world's fastest growing bivalves and can grow an order of magnitude faster than other bivalves. For example, *Teredo navalis*, the species of aquaculture potential used in our study, can grow at 1.5–2 mm per day[21,22], far outstripping conventional 'large-shelled' bivalves such as mussels, which typically grow at 0.1–0.2 mm per day[23,24]. Teredinids are unique in that they live in and feed on wood. As such, they do not build large protective shells, but have a tiny, highly-adapted shell for drilling, that only covers the anterior end of the body[20,22]. Their wood-boring nature formed the foundation of sustainable, low environmental impact early 'farming' of teredinids by Australian Aboriginals as a food source[25]. Today teredinids are wild-harvested and consumed in regions of Oceania and Southeast Asia, and are considered a delicacy and renowned for their health benefits[26]. In the Philippines, they are called 'tamilok'[27], harvested from dead mangrove trees, and sold in local markets raw and dipped in salt, chilli and vinegar[20]. In Thailand, they are known as priyang talay, and eaten in curries or braised with fish paste and bananas in a stew[20]. We note that teredinids are commonly referred to as shipworms, due to their historical legacy of destroying unprotected wooden ships[28]. However, in the interest of boosting the public image of this under-utilised seafood species and providing a more appetising name, we refer to all teredinids as 'Naked Clams' based on their tiny shells and exposed bodies. There is a rich precedent for rebranding seafood species for palatability and marketability – for example, 'malabar blood snappers', 'rock crabs' and 'slimeheads', are now marketed as 'scarlet snapper', 'peekytoe crabs' and 'orange roughy' respectively[29].

A Naked Clam aquaculture system could offer a new opportunity for rapid production of sustainable bivalve meat[20]. A production system could effectively turn sustainably grown wood from trees into protein for people to eat, supporting circular economy opportunities using recycled wood or wood destined for landfill[30,31]. Naked Clams could offer reduced processing costs as they do not require shucking[10]. There is also the potential for enclosed production systems in indoor environments with tailored feed that could optimise growth, quality, nutritional profile and

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palatability as well as eliminate water quality and food safety concerns[20]. Further opportunities include installation of production systems alongside other coastal industries such as wind farms, seaweed farms, or located close to the consumers in areas for regeneration and renewal, or even in shipping containers as part of a modular farming system. Moreover, the potential economic opportunity could be great. As one example, UK consumers purchased £8.7 billion of seafood in 2019[32]; hypothetically if a new Naked Clam sector emerged and grew to just 5% the size of this, it would be worth over £400 million. There is already evidence of fast potential Naked Clam animal growth, established markets in Southeast Asia, and purported health benefits. Yet, scaled Naked Clam aquaculture has never yet been attempted.

The underpinning requirement for any form of Naked Clam aquaculture is an understanding of the most effective way to grow and feed them in a scalable aquaculture setting, and critically, an understanding of their nutritional profile. Regarding feeding preferences, the endosymbiotic bacterial microbiome in the gill allows Naked Clams to extract carbohydrates as an energy source and protein for growth from the cellulose, hemicellulose and lignin in wood[30,33,34]. As filter feeders, it is also thought that the Naked Clams can get nitrogen and carbon from suspended organic matter, such as plankton, within water around the wood[35,36]. Yet the relative role and importance of wood versus suspended material (such as plankton or dissolved organic material) remains uncertain, with some studies indicating suspended matter is primary and essential[36], and others that suggest wood alone is sufficient[37]. There is a need to understand whether including suspended feed in aquaculture would add additional value to the Naked Clam biomass and nutrient profile. We note, no formal nutritional or micro-nutritional profile of Naked Clams has ever been published in reputable literature[20]. In the Philippines and Thailand where the clams are consumed, they are renowned for excellent nutritional properties[26,38]. However, the nutritional profile of Naked Clams on measures comparable to other bivalves such as mussels, as well as levels of key fatty acids and micronutrients, remains unknown. Approaches to Naked Clam aquaculture could be misinformed unless knowledge gaps around their nutritional profile and feeding preferences are addressed.

This study aimed to establish a firm research foundation for Naked Clam aquaculture. We provide the first demonstration of a modular Naked Clam aquaculture system, and the first assimilation efficacy of Naked Clams under different dietary regimes – a crucial step in determining whether fortification (i.e. delivery of additional nutrients beneficial to Naked Clam or human health) is possible using a supplemental suspended feed source (i.e. microencapsulated feed). Importantly, our analysis of faecal production under different dietary regimes provides crucial insight into a controversy around the primary source of nutrition for these animals. In addition, we performed the first formal nutritional profile of a Naked Clam, including fatty acid profile, B_{12}, carbohydrate, fat, and protein content across feeding regimes. This analysis was also the first use of a novel B_{12} profiling methodology and second trial of a lipid analysis methodology, both developed specifically for bivalve tissue, with high applicability to the aquaculture sector and food regulatory bodies. Together, these data demonstrate a novel aquaculture system that offers scalable and sustainable opportunities for rapid production of low environmental impact bivalve meat in an enclosed production system that eliminates water quality and food safety concerns.

RESULTS

Feeding efficacy

The pilot Naked Clam modular aquaculture system we developed is shown in Fig. 1, and comprises wooden panels in static (non-circulating) aerated aquaria. It was effective in allowing us to assess the relative assimilation efficacy of different feed types. This included a microencapsulated feed which consisted of an algal formulation surrounded by a waxy coating (see Methods). Faecal count analyses revealed that the mean faecal weight from Naked Clams fed on the wood + microcapsule diet (0.26 ± 0.05 (SE) mg) was significantly greater than that from Naked Clams fed on wood only (0.11 ± 0.01 (SE) mg) or wood + Shellfish Diet 1800 (0.13 ± 0.01 (SE) mg) (ANOVA, $F(2,6) = 6.27$, $p < 0.05$; Tukey's HSD $p < 0.05$) (Fig. 2a). Faecal production rates were also significantly lower in Naked Clams fed on wood + microcapsules (15.0 ± 1.5 pellet individual^{-1} day^{-1}) compared to those fed on wood + Shellfish Diet 1800 (49.0 ± 9.0 pellet individual^{-1} day^{-1}) (ANOVA, $F(2,6) = 10.71$, $p < 0.05$; Tukey's HSD $p < 0.01$) (Fig. 2b). There was however no significant difference in faecal weight per day between the diet types (ANOVA, $F(2,6) = 2.02$, $p > 0.05$) (Fig. 2c). Combined, these three results indicate that whilst there was no overall difference in assimilation rate between diet types (shown by the same faecal weight per day), the retention time for microencapsulated feed in the gut was longer, indicated by the heavier faecal pellet weight and lower production rate from Naked Clams fed on the microencapsulated feed versus those fed on the Shellfish Diet.

The Scanning Electron Microscopy - Energy Dispersive Spectroscopy (SEM-EDS) data shows that Naked Clams supplemented with microcapsules display clear differences in faecal material (frass), both compositionally and elementally, compared with control animals fed on a diet solely composed of wood (Fig. 3). SEM images show animals feeding only on wood produced uniform shredded wood fragments in their waste (Fig. 3a), compared with frass that was larger and clumpier in animals enriched with a microcapsule feed (Fig. 3b). This corroborates the

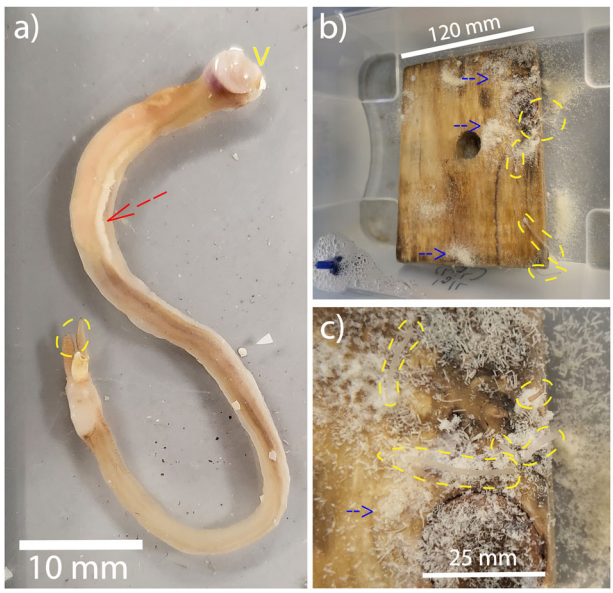

Fig. 1 Naked Clams grown in a simple modular aquaculture system fed only wood. An 82 mm *Teredo navalis* individual, removed from the wood, is shown in (**a**). Most of the white meat extends beyond the valves as indicated by a yellow V in (**a**) – hence the name 'Naked Clams'. Naked Clams can be grown in wood using a simple, modular aquaculture system as shown in (**b**). The siphons of Naked Clams are the only structures that extend beyond the wooden burrows, and are outlined by yellow dashed lines and magnified in (**c**). Note the fragments of waste wood dust (frass) covering the wooden panel, shown by the blue arrows, indicating active feeding and growth on wood. This, together with the ripe gonad shown by the red arrow in (**a**), demonstrates the efficacy of our modular aquaculture system in rearing healthy animals.

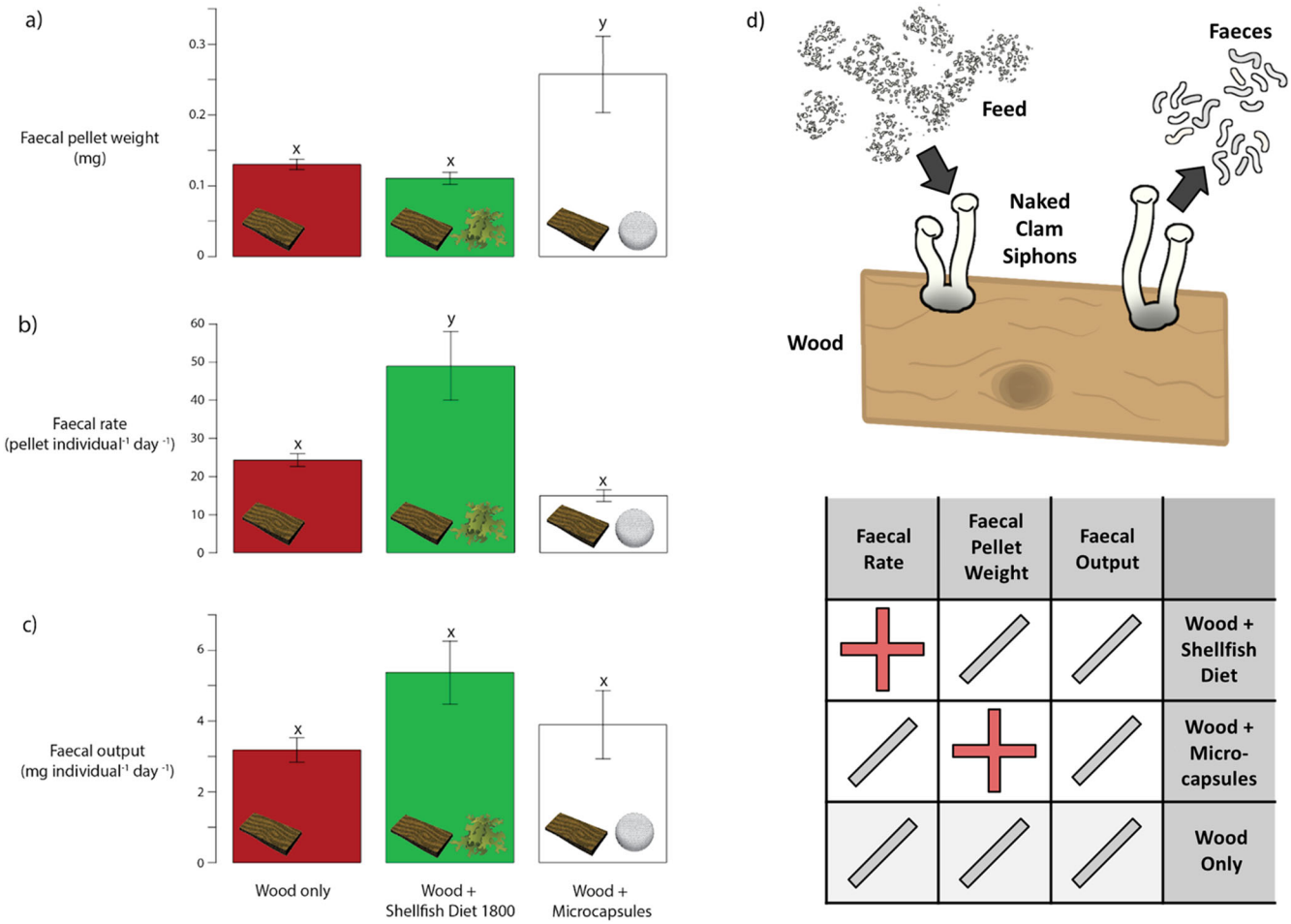

Fig. 2 Feed assimilation efficacy of Naked Clams under different dietary regimes. Faecal pellet weight is shown in (**a**), faecal production rate in (**b**), and faecal output in (**c**). Error bars represent standard error of the mean. Letters x and y indicate post-hoc test outcomes, where shared letters indicate no significant difference between groups. A schematic of the feeding assimilation experimental design and efficacy data is shown in (**d**), with the '+' indicating an increase, and '/' indicating no change.

findings of our feed assimilation efficacy trials, where animals with a microencapsulated supplemented diet produced heavier faecal pellets (Fig. 2a) and no noticeable pseudofaeces. Subsequent EDS analysis of faecal material from these microcapsule supplemented animals displayed approximately 5× the amount of calcium with minor amounts of silica and sulphur also detected (Fig. 3c–f).

Nutritional profile

We were successful in performing the first formal nutritional profile of a Naked Clam (*T. navalis*). The fatty acid profile, carbohydrate, and protein content, as well as the organic micronutrient vitamin B_{12} (hereafter B_{12}), was compared across our three feeding regimes, and also against that of the commercially farmed blue mussel (*Mytlius edulis*, referred to as blue mussels hereon). This analysis was also the first to determine the B_{12} content of Naked Clams, and a second trial of a lipid analysis methodology developed specifically for bivalve tissue (de-coagulation of bivalve tissues prior to lipid extraction).

Basic biochemical composition analyses revealed that Naked Clams had a higher ash content than blue mussels, and hence lower levels of the metabolite groups protein, fat, and carbohydrate (Fig. 4). Proteins were the dominant metabolite group in both Naked Clams and mussels. Importantly, supplementation with the microencapsulated feed led to a significantly greater protein content than feeding on wood alone, with values of 29% and 22.5% per unit dry weight (DW) (ANOVA, $F(1,22) = 14.04$, $p < 0.05$; Tukey–Kramer's HSD, $p < 0.05$). Carbohydrate content ranged between 16–19% w/w, while lipid content was 3.5–3.8% w/w.

Analyses revealed that Naked Clams had significantly higher levels of B_{12} than blue mussels (Fig. 4). The B_{12} content of Naked Clams fed on wood + microcapsules was 142 ± 9 (SE) µg B_{12} per 100 g DW, significantly greater than that of blue mussels at 81 ± 9 (SE) µg per 100 g DW (ANOVA, $F(1,13) = 9.87$, $p < 0.01$; Tukey–Kramer's HSD, $p < 0.01$). There was however no significant difference in B_{12} levels between Naked Clams fed on wood only or wood + microcapsules; supplementation with microencapsulated feed did not positively influence the B_{12} content.

Fatty acid composition assessments revealed that Naked Clams contained a greater content of long chain saturated fatty acids than blue mussels, and that supplementation with microencapsulated feed increases the content of polyunsaturated fatty acids (PUFAs) EPA (Eicosapentaenoic acid, 20:5(n-3)) and DHA (Docosahexaenoic acid, 22:6(n-3)) (Fig. 5). Mass spectrometry revealed that in Naked Clams reared on either wood only or wood + microcapsules, the saturated FAMEs stearic acid (C18:0) and palmitic acid (C16:0) were dominant, followed by the mono-unsaturated FAMEs oleic acid (C18:1) and palmitoleic acid (C16:1) in high abundance (Fig. 5a). Supplementation of the wood only diet with microencapsulated feed appeared to have an impact on the polyunsaturated acid distribution and content (Fig. 5a). Specifically, while EPA only accounted for 0.8% of the total FAMEs and DHA was not detectable in Naked Clams grown solely on

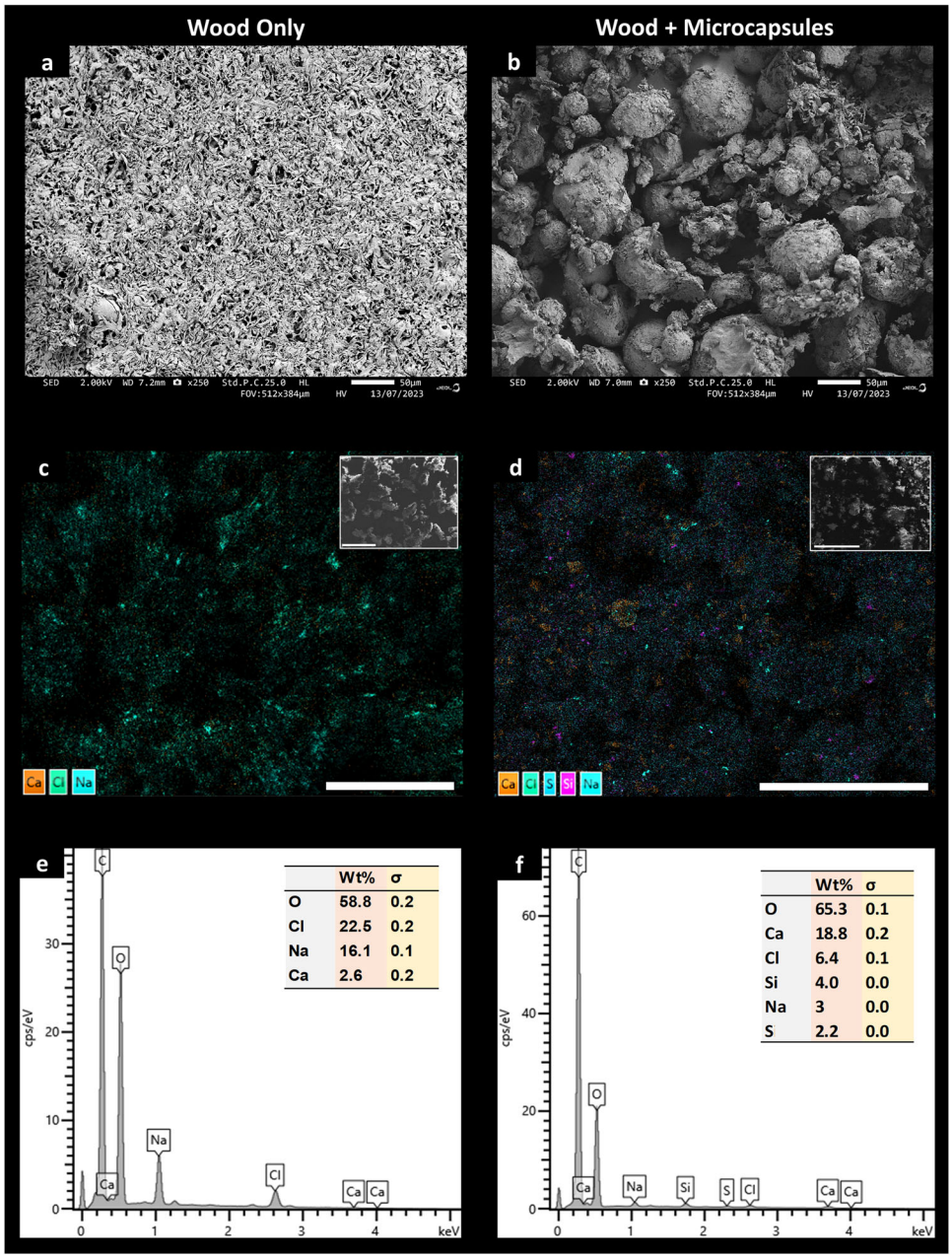

Fig. 3 Scanning Electron Microscopy (SEM) and Energy Dispersive X-ray Spectroscopy (EDS) mapping of Naked Clam faeces. SEM images of Naked Clam faeces at 250× magnification (scale bar = 50 µm) for animal feeding on wood only (**a**) and wood plus microcapsules (**b**). Elemental mapping overlay image of faeces for animal feeding on wood only (**c**) and wood plus microcapsules (**d**), with raw SEM image displayed in the top right corner. EDS elemental spectra from (**c**) and (**d**), shown in (**e**) and (**f**) respectively.

wood, whereas the respective percentages of EPA and DHA in Naked Clams supplemented with microencapsulated were 1.8% and 1.6% (Fig. 5b). Overall, the total polyunsaturated fatty acid content of Naked Clams supplemented with microencapsulated feed was increased by 75.8% compared to wood only feed (ANOVA, $F(1,22) = 6.83$, $p < 0.05$; Tukey–Kramer's HSD, $p < 0.05$). The fatty acid profile of Naked Clams grown in this study differed compared to commercially produced blue mussel tissues tested. The dominant fatty acid of the blue mussel tested was arachidonic acid (C20:4n6, 27%) (Fig. 5a), while EPA, DHA accounted for 1.7% and 10.2% of the total FAMEs, respectively. Although EPA levels were similar to Naked Clams supplemented with microcapsules, DHA and total polyunsaturated FAME content (43.9%) exceeded that of Naked Clams.

DISCUSSION

This study provided the first demonstration of a pilot Naked Clam aquaculture system, and revealed that Naked Clams are naturally rich in nutrients key to human health including protein, vitamin B_{12}, and monounsaturated fats such as oleic acid. We also revealed an important opportunity for nutritional supplementation, demonstrating how Naked Clams can be fortified with additional nutrients using microencapsulated feeds, in this case leading to elevated levels of the essential PUFAs EPA and DHA. The study represents a gateway into a new form of sustainable food production that allows the conversion of wood into a protein and nutrient rich human foodstuff.

We piloted a simple and effective system for the controlled husbandry of Naked Clams in an indoor environment (Fig. 1). The

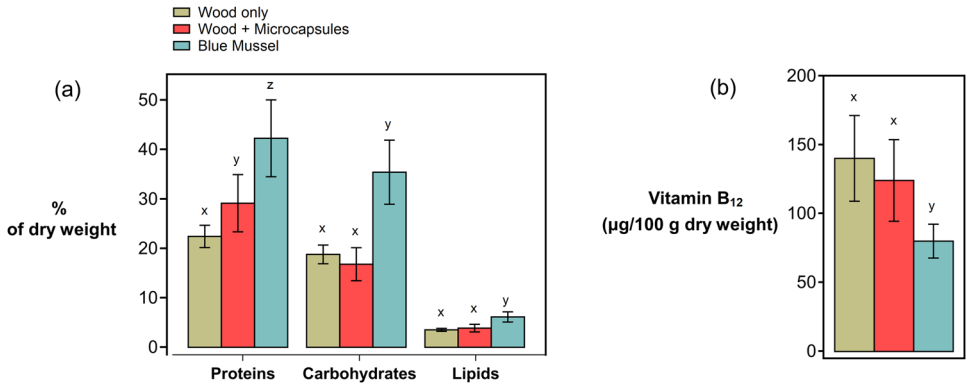

Fig. 4 Biochemical composition of Naked Clams and blue mussels. a Protein, carbohydrate, lipid, and (**b**) vitamin B_{12} content (expressed as a fraction of total dry weight) of Naked Clams fed with wood only (brown), Naked Clams fed with wood + microcapsules (red), and commercially farmed blue mussels (*Mytilus edulis)* (blue). Data are expressed as mean +/− standard deviation (SD) of technical replicates ($n = 12$ for Naked Clams, $n = 4$ for blue mussels). Letters x, y, and z indicate post-hoc test outcomes, where shared letters indicate no significant difference between groups.

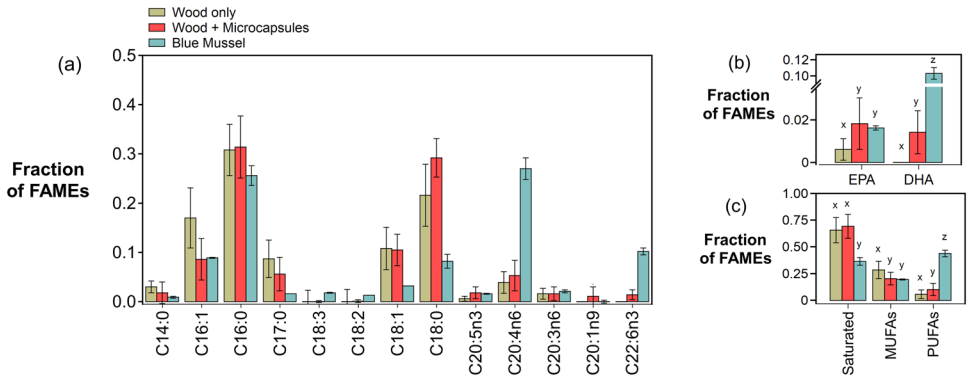

Fig. 5 Fatty acid composition of Naked Clams and blue mussels. a Fatty acid methyl ester (FAME) composition (expressed as a fraction of total FAMEs) of Naked Clams fed with wood only (brown), Naked Clams fed with wood + microcapsules (red), and commercially farmed blue mussels (*Mytilus edulis)* (blue). **b** EPA (Eicosapentaenoic acid, 20:5(n-3)), DHA (Docosahexaenoic acid, 22:6(n-3)), (**c**) total saturated, mono-unsaturated (MUFAs) and poly-unsaturated fatty acids (PUFAs) are highlighted. Data are expressed as mean +/− SD of technical replicates ($n = 12$ for Naked Clams, $n = 3$ for blue mussels). Letters x, y, and z indicate post-hoc test outcomes, where shared letters indicate no significant difference between groups. Full (empirical and chemical) names of fatty acids are shown in Table S1.

system does not require any complex feeding apparatus or flow-through water exchange systems, and supports active growth of healthy Naked Clams. It provides a foundation for the development of a scaled framework for commercial aquaculture, although further research and development will be required to meet this goal. For example, there is the opportunity for additional growth condition optimisation (e.g. salinity, temperature, wood species substrate), and there is potential to alter the mechanism by which supplemental feed such as microcapsules is delivered to Naked Clams in the aquaria to increase feeding efficiency. While we demonstrate the simplicity, efficacy and value of Naked Clam aquaculture, future studies should optimise growth rates and feeding protocols, which are essential for the commercial application of this novel aquaculture system.

The feeding efficacy studies demonstrated that Naked Clams could successfully digest supplemental suspended feeds, and represents the first time that feeding rates between xlyothophy (wood-feeding) and filter-feeding have been formally assessed in these animals (Fig. 2). By demonstrating that *Teredo navalis* could grow solely on a diet of wood (Fig. 1), and that feeding rates do not change significantly between xlyotrophy and filter-feeding, we address a controversy in the literature on the source of nutrition for this species[37] and show that filter-feeding is an important component of the diet but not the primary source as previously suggested[36]. Further studies are required to determine the feeding ratios between xylotrophy and filter-feeding in other Naked Clams species. For example, the rock-eating *Lithoredo abatanica* is likely far more reliant upon filter- feeding[39,40], and the giant *Kuphus polythalamius* (the world's longest bivalve), which inhabits both wood and marine sediments[41], is thought to derive nutrition solely from a chemoautotrophic, sulphur-oxidising symbiosis[42,43]. The longer retention time of the microencapsulated feeds in the Naked Clam gut, relative to liquid algal feed (Shellfish Diet 1800), suggest a greater timeframe for nutrient absorption, indicating that Naked Clams are able to extract more nutrients from microcapsules than from regular algal feed. This is corroborated by the presence of degraded microcapsule matter in the supplement-fed Naked Clam faeces, and the larger, clumpier faecal material that is elementally enriched compared with animals on a wood-only diet (Fig. 3). The presence of degraded microcapsule matter in the Naked Clam faeces, shown by the SEM images and EDS analysis, are further proof of breakdown and absorption of the microcapsules. There is still scope for further work to confirm this analysis, for example a nutritional profile of Naked Clam faeces may allow the quantitative assessment of what proportion of the feed ingested by Naked Clams is fully broken down, and allow us to take further steps in the formulation of Naked Clam feeds to optimise this.

Nutritional analyses revealed that Naked Clams are naturally rich in B_{12}, alongside the monounsaturated fats oleic acid (C18:1)

and palmitoleic acid (C16:1). B_{12} levels in Naked Clams were nearly twice that of B_{12} levels in blue mussels, at a concentration of 140 µg per 100 g dry weight. The abundance of B_{12} is a key nutritional selling point of Naked Clams - B_{12} is made only by certain bacteria[44,45], and plants cannot make this vitamin. As such increasing dietary trends towards plant-based diets is resulting in increased occurrence of B_{12} deficiency or insufficiency[44]. A serving of just 10 g (dry weight) of Naked Clams per week would meet an individual's entire B_{12} requirements. We note that the B_{12} levels of blue mussels analysed in our study fall in line with those published in the literature[46]. Of further importance, levels of oleic acid in Naked Clams were over 3 times that of the levels in blue mussels. Oleic acid, a monounsaturated fat also found in olive oil, has been repeatedly shown to offer various health benefits, including improvements to cholesterol levels, blood pressure and inflammation, along with decreased heart disease risk and the potential to improve mood and cognition[47]. The nutritional analyses also revealed that Naked Clams had a higher ash content than blue mussels. This ash, or inorganic mineral content left after analysis, is likely explained by the inclusion of calcareous structures (shells and pallets) and the presence of wood in the guts of Naked Clams. The nutritional results from our study provide a strong foundation to support Naked Clams as a food for mass-market consumption.

The nutritional analyses also emphasised the powerful potential of supplemental feeds, such as microcapsules, to further optimise the biochemical profile of Naked Clams. The microcapsules we used were highly effective in boosting PUFA content; total polyunsaturated fatty acid content of Naked Clams supplemented with microencapsulated feed was increased by 76% compared to wood only feed, and brought EPA levels in line with those of conventional blue mussels. This is explained by the high PUFA content of the microcapsules themselves, which shared a similar formulation to those used in Willer et al. 2020[19]. It is well established that consumption of PUFAs including EPA can help to reduce inflammation, triglyceride levels, and cardiovascular disease risk factors in humans[48]. Fish currently stands as the primary means of obtaining these nutrients via food, with the UK government recommendation being an intake of 280 g a week[49], and 2020 consumption currently standing at around 160 g per week[50]. Increasing consumption to recommended values with our current production systems would be environmentally unsustainable if adopted by the UK and other nations[51], and Naked Clam meat could offer a means by which to sustainably meet this intake. The waxy encapsulant of the microcapsules may also contribute to the higher lipid content in the Naked Clams. We do note that DHA levels in Naked Clams supplemented with microencapsulated feed were still slightly lower than those in blue mussels, and that we also did not run a nutritional profile on Naked Clams fed on suspended algal feed, and hence don't know the performance of algal feed versus microcapsules. This highlights the outstanding need for further optimisation of supplemental feeds for Naked Clams, to identify which formulations and delivery approaches represent the best way to optimise their nutritional profiles. The microcapsule itself offers a powerful delivery vehicle, and as demonstrated in other studies[18,19,52,53] may offer a means by which to fortify Naked Clams with specific nutrients lacking in a specific population or socio-demographic sector[53].

Beyond the steps suggested above and the continued development of the Naked Clam aquaculture system, there is still a requirement for engagement across the value chain in order to realise the potential benefits of Naked Clam consumption to human health and environmental sustainability. Attracting investment from aquaculture corporations or startups to engage with and adopt the Naked Clam aquaculture system will be key in this regard. Sustainable and reliable supplies of wood feedstock also need to be carefully selected, and cold-chain solutions for the effective harvest, distribution, and processing of Naked Clam meat. Engagement with food standards authorities will be required; while Naked Clams are sold as food in Asia they are not yet in Western economies. We also suggest that at this point in time, development focuses on indoor modular aquaculture systems as piloted in our study, as opposed to open water aquaculture systems, where additional care is required given the economic damage teredinids cause to submerged wooden coastal structures[54]. At the food manufacturer and consumer end, there is a critical requirement to identify the most effective means to turn Naked Clam meat into a mass market product. For example, will Naked Clams be best sold as a fresh meat item like in southeast Asia, or in simply processed formats (e.g. minced, purees), more complex formats (e.g. supplemental dry powders), highly advanced formats (e.g. textured flavoured extruded proteins), or a combination of the previous? Effective consumer research and marketing will be pivotal to the success of attempts in this field.

Overall, this study has provided the experimental foundation for a new form of sustainable food production that could turn wood into a protein and nutrient source for mass market human consumption. Naked Clams are hardy, grow exceptionally fast, and can be produced in static saltwater systems. Here we have demonstrated a viable Naked Clam aquaculture system, assessed feeding efficacy, revealed a naturally rich nutritional profile, and outlined an opportunity for further fortification with supplemental feeds. There is an opportunity here to build a completely new aquaculture sector and open up a wealth of avenues for sustainable food production and consumption.

METHODS

Sample collection

Teredo navalis specimens were sourced from north-eastern US coastal waters. To obtain samples for the experiments, two Eastern pine (*Pinus strobus*) panels of 200 × 120 × 20 mm were placed in Gloucester Harbour, MA, USA on 4/5/2021, to allow settlement of *Teredo navalis* larvae. These panels were retrieved on 13/3/22. Larval settlement will have taken place during the warmer summer months of July, August and September in 2021, and so the *T. navalis* were approximately 9-month-old adults at the point of collection. Blue mussels (*Mytilus edulis*) for the nutritional analysis were commercially farmed and were sourced from Shetland, Scotland. These mussels were rope-grown, fed on wild marine phytoplankton, and of two years age and market size at the point of harvest in February 2023.

Microencapsulated feed manufacture and profiling

Lipid-walled microcapsules containing 30% powdered *Schizochytrium* algae by weight were manufactured under patent by BioBullets (BioBullets Ltd, Cambridge, UK). To manufacture the microcapsules a premix slurry containing a waxy encapsulant with antibacterial properties and powdered algae were prepared under conditions of controlled shear. The slurry was pumped into an ultrasonic atomizing nozzle at the top of a cooling chamber. The atomized particles formed near-perfect spheres as they cooled and fell to the chamber base. Further particle cooling was achieved with an air-conveying system before discharge via cyclone to a fluid bed processor. The encapsulated feed was then coated with a proprietary non-ionic surfactant to aid dispersion in water. Further cooling in the fluid bed removed all heat of crystallization from the microcapsules before packaging. All components of the formulation were food grade. The physical characteristics of the microcapsules were quantified using a Malvern Mastersizer particle size analyser. The microcapsules had a mean diameter of 46.6 µm, with a DV(10) of 17.7 µm and DV(90) of 104 µm. The microcapsules had spherical shape, near neutral buoyancy, and were tailored for bivalve consumption and growth[9,18,19,52,53].

Laboratory conditions

Laboratory experiments took place in the Davy Building aquarium, University of Plymouth, England, in aerated tanks in temperature-controlled rooms maintained at 15 °C.

For the feed assimilation efficacy experiments, three wooden panels containing *T. navalis* specimens were placed in three separate 1.6 litre tanks (MW, SDW, and W) from 21/11/2022 till 09/12/2022 (Fig. 1). The panels in tanks MW and SDW had 7 pairs of siphons each, and the panel in tank W 5 pairs of siphons, indicating the presence of 7, 7 and 5 individuals respectively. The panels were exposed to three different dietary regimes – microcapsules + wood (MW), Shellfish Diet 1800 + wood (SDW), and wood only (W). Shellfish Diet 1800 is an algal concentrate blend (Shellfish Diet 1800, Reed Mariculture, California, USA). To ensure valid observations, feeding rates were optimised to minimise pseudofaeces expulsion, given faecal expulsion was the measure of feeding rate in this study. Bivalves are known to expel indigestible particulates in the form of pseudofaeces in high concentrations of particulate matter, and studies on pseudofaeces production have found that particulate concentrations around 2 mg/L show minimal production of pseudofaeces within oysters[55,56]. This correlated with using a recommended feeding rate of 3% dw (dry weight) feed per dw bivalve per day[57]. Feeding took place at 09:00 every Monday through Friday, and at 15:00 every Monday through Thursday. Feeding did not occur at 15:00 on Friday as that was when faeces were both counted and collected for weighing. Two half feeds were used in these experiments to avoid the production of pseudofaeces, which could have risen from oversaturation.

For the nutritional profiling experiments, the two wooden panels containing *T. navalis* juveniles were placed into two separate 10 litre tanks (MW and W) on 09/05/2022 (Fig. 1). The panel in tank MW had 40 pairs of siphons and the panel in tank W 28 pairs of siphons, indicating the presence of 40 and 28 juveniles respectively. The panels were exposed to two different dietary regimes – microcapsules + wood (MW), and wood only (W). Initial juvenile dry weight was measured as 0.069 g, and used to calculate feeding ration for microcapsules at a rate of 3% dry weight (dw) capsule per approx dw bivalve per day[57]. Microcapsules were fed at this rate via a three times weekly feed, with care taken to fully disperse the microcapsules. Juveniles from the MW tank were harvested on 30/06/2022, and juveniles from the W tank were harvested on 02/02/2023.

Feed assimilation efficacy

Faecal rate was observed through two methods, daily digital recording and weekly visual counting. Recording was performed after the 3PM feeding every Monday through Friday using GoPro HERO 11 cameras. For each sample, 10 mins of recording on the siphons was performed for each visible individual in each tank. Recordings were viewed later, and a daily rate was calculated based on the number of faecal pellets seen expelled from the syphons within the timeframe.

The weekly faecal count was observed every Friday at 15:00. High quality top-down pictures of the containers were taken using the GoPros, capturing all the faecal pellets within the container. If one picture of the entire container was not sufficient, smaller pictures were taken instead of each quarter of the tanks. Faecal pellets were counted using visual identification assisted with Microsoft Paint (2023 Version, Microsoft, California, USA), which was used to section off parts of the image and mark counted pellets in an obvious colour, noting the number of pellets counted in each segment. Once these segments were accurately counted and added up, the average rate of each individual was calculated, and the total number would be used for calculating average pellet weight.

Faecal weight was also gathered at 15:00 every Friday. Once pictures of faecal pellets were taken, a syringe was used to collect all the faecal pellets from each sample. These pellets were subsequently filtered from the water using a stand and filter paper, and then washed down with pure water to remove excess salt. The weight of the filter paper was recorded prior to filtering. Following this, the pellets and filter paper were placed in an oven and left over the weekend. After the 09:00 feed on Monday, the dry weight of the pellets was recorded, and by extension the average weight of each pellet from each diet.

Faecal pellets were also collected and pooled from animals under different dietary regimes (wood only, and wood plus microcapsules), and dried in a drying over at 36 °C for 48 h prior to processing for electron microscopy.

Scanning electron microscopy (SEM) and energy dispersive X-ray spectroscopy (EDS)

For SEM imaging, faecal pellets were applied to a carbon infiltrated tab prior to being sputter coated with approximately 10 nm of gold (Emitech K550, Quorum Technologies, England). Samples were imaged using a JEOL IT800HL Scanning electron microscope (JEOL, Japan) operating in hybrid lens mode. Images were obtained using the secondary electron detector with an accelerating voltage of 2 kV and standard probe current 25. Electron dispersive spectroscopy was carried out using the same instrument utilising an Oxford Instruments Ultim Extreme EDS detector and Oxford Instruments AZtec software (v6.1) (Oxford instruments, England). Samples for EDS were ground using an agate pestle and mortar, before being pressed on to a carbon infiltrated tab and coated with approximately 10 nm of carbon (Q150T, Quorum Technologies, England). EDS maps were collected for 40 min per site at 1024 resolution and 30µs dwell time, using the following working conditions: 6 kV accelerating voltage, analysis probe current 50 (5.7 nA) and 7 mm working distance. Data is normalised by all elements to a 100% total.

Nutritional profiling

For the nutritional profiling, the whole animal tissue from the 40 Naked Clam individuals in the MW tank and 28 in the W tank were homogenised and pooled into 12 samples for each tank type. The following steps of nutritional analyses were then performed on each sample individually.

Biochemical composition

Frozen bivalve tissues, ~2 g from each sample type (Naked Clams fed with wood only, Naked Clams fed with wood + microcapsules, and commercially farmed blue mussels) were freeze-dried, reduced to a fine powder with bead milling and stored at −80 °C before the further analysis. Shells were removed from the blue mussels, we did not remove the tiny pallets from the Naked Clams. The ratios of different biochemical compounds (proteins, carbohydrates, lipids) were determined using Fourier-transform infrared (FTIR)-attenuated total reflectance (Spectrum Two, PerkinElmer, Germany). Approximately 3–5 mg of finely powdered freeze-dried tissue was pressed on the crystal surface (iATR reflectance cell with a DTGS detector), and scans (wavenumber range of 4000–450 cm^{-1} at a resolution of 4 cm^{-1}) were recorded and baseline-corrected using Spectrum (version 10, PerkinElmer, Germany). The amide I peak (1624 cm^{-1}), the methyl/methylene peak (2800–3000 cm^{-1}), and the pronounced peak at 1050 cm^{-1} were used for protein, lipid, and carbohydrate quantification, respectively[58,59]. BSA, C-16, and glucose mixed with potassium bromide (KBr) were used as analytical standards. Protein, carbohydrate, and lipid content were then expressed as percentages of dry biomass weight after determining the absolute protein content by a colorimetric method. Powdered biomass (5 mg) was suspended in 5% (v/v) SDS extraction buffer, incubated at 100 °C for 20 min and centrifuged (5000 × g for 5 min). After 1:5 dilution with water, aliquots of the supernatant extracts

underwent a 96-well microplate Lowry assay using the Pierce™ Modified Lowry Protein Assay Kit. After the reaction, absorbance at 750 nm was measured in a microplate reader (CLARIOstar Plus, BMG, Germany), and protein content was quantified using a standard BSA curve fitted into a quadratic model as recommended by the manufacturer.

B_{12} content

Freeze-dried, powdered bivalve tissues from each of the sample types (~2 mg) were suspended in 1 mL of water and boiled for 20 min. The samples were centrifuged, and the supernatant was used for B_{12} content measurement. The B_{12} content was determined by a microbiological bioassay method using a recently evolved B_{12}-dependent strain of *Chlamydomonas reinhardtii* (metE7[60]). This strain was incubated for 4 days in a TAP-based medium at ~90 µE m^{-2} s^{-1} continuous light, 120 rpm, plus the B_{12}-containing samples, diluted in 24-well plates at a total volume of 2 ml per well. Growth was quantified by measuring optical density at 730 nm. B_{12} concentration in the samples was estimated by comparing the optical densities obtained to a standard curve of known B_{12} concentrations (between 8–200 pM B_{12}) fitted with a 4-parameter logistic model (as described in Harrison et al., 2023 under review).

Lipid analysis

Freeze dried tissues from each sample type were dispersed in an aqueous solution of guanidine and thiourea (6 M/1.5 M); (20% w/v) and diluted with methanol (30%) and TBME (10%)[19]. Then lipids were extracted as outlined by Davey et al (2014)[61]. Briefly, 200 µL of the dispersions were suspended in 10 mL of (2:1) chloroform and methanol mix, spiked with 200 mL of pentadecanoic acid (C15) (1 mg·mL^{-1}) and sonicated for 30 min on ice. A total lipid extraction was performed as outlined by Davey et al., (2014). Briefly, samples of ~2 mg of freeze-dried biomass were suspended in 10 mL of (2:1) chloroform and methanol mix, spiked with 200 mL of pentadecanoic acid (C15) (1 mg mL^{-1}) and sonicated for 30 min on ice. Then, after addition of 5 mL of water, the tubes were centrifuged at 1000 × g for 3 min at 4 °C to achieve phase separation. The aqueous phase was discarded, the solvent was evaporated from the lower phase with N2 gas (45 °C; GeneVac EZ-2; SP Scientific, Ipswich, United Kingdom), and the extract was then resuspended with 200 mL of n-heptane.

Three 100 mL aliquots of the extract were transferred to a glass tube and trans-esterified with 3 mL of a 2.5% v/v H2SO4/methanol mix, vortexed and placed in a 60 °C water bath for 4 h and then allowed to cool. Following this step, after addition of 3 mL of water and 3 mL of hexane, the tubes were centrifuged at 2000 × g for 3 min to achieve phase separation. The upper hexane phase was then separated, re-extracted and evaporated under the previously defined conditions (Davey et al., 2014). The fatty acid methyl ester (FAME) extracts were resuspended with 120 mL of hexane, separated, and identified using GC (Thermo Scientific Trace GC Ultra) with a Zebron ZB-Wax Capillary GC column (30 m × 0.25 mm, 0.25 µm film thickness, Phenomenex, UK). The injection volume was 1 µL with a 35:1 split ratio with an injector temperature set to 230 °C, using helium as a carrier gas at a constant flow of 1.2 mL·min-1. For the run, the following gradient was used: initial oven temperature 60 °C, 2 min; 150 °C at 15 °C min^{-1}; 230 °C at 3.4 °C min^{-1}. The detector temperature was 250 °C. FAMEs are identified by co-elution with a FAME standard mix (Supelco, 37 Component FAME Mix). The peaks were identified based on the standard mix peak RT and through library search (NIST). The areas were compared as a percentage of the total identified FAMEs.

Statistical analyses

Feed assimilation efficacy. Data and statistical analysis were processed using RStudio (RStudio Team, 2020) accompanied with the car package (Fox and Weisberg, 2019). For all variables to be analysed, those being faecal pellet weight, faecal rate, and faecal output, three respective one-way ANOVA (Analysis of Variance) tests were performed to compare changes of these variables under the three diets. Prior to this, homogeneity of variance was verified using Levene's test. Afterwards, a Tukey's HSD post-hoc test was made to observe the differences between groups.

Nutritional profiling. For all parameters analysed (proteins, carbohydrates, lipids, vitamin B_{12}, and FAME profile), changes between the three sample groups (naked clams fed with wood only, naked clams fed with wood and microcapsules, and commercial blue mussels) were compared with one-way analysis of variance (ANOVA) tests. Then, a Tukey–Kramer post-hoc test was performed to observe the differences between groups. The criterion for statistical significance was set at $p < 0.05$. All analyses were performed using Microsoft Excel 2021.

DATA AVAILABILITY

All data is available in the manuscript or Supplementary Materials.

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AUTHOR CONTRIBUTIONS

D.F.W., D.C.A., P.M., K.P.P., L.A., A.G.S., M.L., A.S., and J.R.S. all participated in study design and data analysis. D.F.W and J.R.S. wrote the final manuscript. All authors reviewed and approved the manuscript before submission.

COMPETING INTERESTS

D.C.A. is a Director of BioBullets Ltd, who manufacture microencapsulated feeds for bivalves. Naked Clam is a Trade Mark (UK00003939007).

ADDITIONAL INFORMATION

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