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Feasting in mussel farms fattens up snapper (*Chrysophrys auratus*) compared to snapper in adjacent natural habitats

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Abstract

The presence of wild fish in and around aquaculture habitats is often assumed a response to food resources within these habitats, either from input feed, the presence of cultured species, and/or the assemblage of biofouling that naturally colonises aquaculture structures. The nutritional quality of the food resources consumed by wild fish in aquaculture habitats is also important in determining their nutritional condition and subsequent productivity. Few studies have investigated the nutritional quality of prey in aquaculture habitats, and these have mostly focused on fed aquaculture by tracking manufactured fish pellets into the diets of wild fish. However, in non-fed aquaculture, the assemblage of cultured and biofouling species may also provide a nutritional benefit to fish feeding in these habitats. The Australasian snapper, *Chrysophrys auratus*, are commonly present as adults within coastal mussel farms in New Zealand and tend to become a resident species. This study investigated the nutritional quality of the gut contents of snapper in soft-sediment habitats within and outside of New Zealand green-lipped mussel farms. Total lipid, protein, carbohydrate and total calorific content were measured from the gut contents of snapper sampled from mussel farm and natural (i.e. control) habitats. Snapper in mussel farms had double the dietary intake of lipid (16% vs. 8%) from consuming lipid-rich bivalves and barnacles which are in abundance in mussel farms. Higher lipid intake can contribute to improved nutritional condition, reproduction and growth in snapper. However, the higher dietary lipid intake of snapper in mussel farms did not increase their overall body condition (i.e. Fulton condition index). This may be due to the coarse nature of this measure, or the use of the additional lipid in more rapid somatic growth or reproductive outputs, possibilities that warrant examination through further research. Overall, this study shows for the first time the potential ecosystem benefits of shellfish aquaculture in provisioning nutritionally valuable prey for coastal fish populations.

KEYWORDS
aquaculture, ecosystem services, lipid, nutrition, snapper

1 | INTRODUCTION

The establishment and operation of aquaculture in coastal environments creates unique habitats within which there are typically marked changes in the diversity and abundance of fish species compared to reference sites (Barrett et al., 2022). An increased abundance of some fish species within the aquaculture habitat is commonly observed and is thought to be due to improved feeding opportunities provided by the aquaculture habitat. This includes the massive presence of the monocultured species, as well as the biofouling and epifauna which colonises the aquaculture structures, as well as external feed input in the case of fed fish aquaculture (Barrett et al., 2022; Callier et al., 2018; Sanchez-Jerez et al., 2011; Theuerkauf et al., 2022). To determine how feeding opportunities may influence the abundance of some fish species within aquaculture habitats, it is important to understand the quantity and quality of food consumed by fish living in these habitats in comparison to similar natural habitats that do not include the presence of an aquaculture operation. The identification, quantification and comparison of food items in the gut contents of fish living in these two habitats can provide information that can be used to infer differences in the diet between habitats, whereas nutritional analyses of these food items can be used to help define the differences in their nutritional contribution to the fish. Relatively few studies have investigated the nutrition of fish living in aquaculture habitats, with most of these studies focused on fish aquaculture where the supplied feed intended for the cultured fish is consumed by wild fish living in and around the aquaculture habitat (Barrett et al., 2019; Dempster et al., 2002; Fernandez-Jover et al., 2007; Skog et al., 2003). Typically, these studies confirm that the generally high quality of the supplied aquaculture feed and its availability for consumption by wild fish in the vicinity of the aquaculture structure provides a significant nutritional incentive for wild fish to reside and feed in fish aquaculture habitats. For example, artificial feed supplied to seabream sea cage aquaculture habitats in the Mediterranean Sea has been identified as the source of higher lipid resources in wild seabream species (*Oblada melanura* and *Boops boops*) and silver mullet (*Liza aurata*) that live around the farms compared to wild fish of the same species caught from nearby natural habitats (Arechavala-Lopez et al., 2011; Barrett et al., 2019; Fernandez-Jover et al., 2009; Skog et al., 2003). These changes to fish nutrition, particularly the increase in lipid, have resulted in wild fish becoming larger and heavier and often in better nutritional condition, indicating that the changes to the nutritional quality of diet can have a direct and significant effect on the physiology and performance of fish utilising aquaculture habitat (Barrett et al., 2019; Dempster et al., 2002; Fernandez-Jover et al., 2007). Although there is good evidence that wild fish benefit from the feeding opportunities provided by fed fish aquaculture operations, there is a lack of equivalent research for extractive or non-fed aquaculture species (e.g. shellfish and seaweed) where there are no external feed inputs (Barrett et al., 2019). Specifically, there is no published research into differences in the nutritional quality of the diet of fish species feeding within extractive aquaculture habitats (i.e. non-fed aquaculture species) versus equivalent natural habitats without aquaculture.

Comparative analyses of fish diets including the biochemical composition of diets can assist with understanding the dietary preferences of fish species and identify any differences in the availability and nutritional quality of food provided by different habitats (Amundsen & Sánchez-Hernández, 2019; Braga et al., 2012; Dixon et al., 2017). Such differences in the diet of fish can have significant effects on their physiology and autoecology. For example, the dietary availability of lipid can greatly affect the regulation of a variety of functions in fish (e.g. cellular metabolism, detoxification, reproduction and behaviour), including acting as the principal energy reserve in many teleost species and commonly playing a major role in determining spawning success and egg quality (Adams, 1999; Lloret & Planes, 2003). In contrast, most fish species have a high dietary requirement for protein to support the maintenance, replenishment and growth of tissues (Cowey & Sargent, 1972). Differences in the nutritional composition of food items are important in determining the selection of food items and in turn the composition of diet. This can lead to fish actively consuming the more nutritionally valuable prey species within a habitat, before moving to less nutritious food resources once the abundance of the food species is reduced to the point that subsequent competition or time spent accessing the food species is increased (Dixon et al., 2017; Taylor, 1991).

Proximate analyses of dietary material involve assaying the protein, lipid and carbohydrate composition of dietary material to determine the overall nutritional quality (Wang et al., 2014). Proximate analyses can also be used to estimate dietary energy intake and when combined with measures of ash-free dry weight (AFDW) of diets can be used to determine the energy density of diets (Wang et al., 2014). Therefore, proximate and AFDW determinations of the dietary material from fish sampled from different habitats can be used to help identify differences in the nutritional quality of the diets associated with those habitats, for example between aquaculture habitat and adjacent natural habitat without aquaculture structures.

The Australasian snapper (*Chrysophrys auratus*) is a common demersal species of sparid that inhabits a wide variety of coastal habitats in New Zealand, including Greenshell mussel longline farms, within which the abundance of adult fish appears to be elevated (Gibbs, 2004; Stenton-Dozey & Broekhuizen, 2019). Adult snapper also tend to become resident within coastal habitats, such as within mussel farms, in New Zealand (Usmar, 2012). Snapper are targeted by recreational fishers at mussel farms, suggesting that they aggregate within mussel farm habitat. The habitat plasticity of snapper is supported by their omnifarious diet, with gut content analyses finding over 100 different species of invertebrates and small fishes, especially crustaceans, worms, molluscs and echinoderms (Ayling & Cox, 1987). Consequently, food availability within different habitats is a major determinant of the composition of the diet of snapper (Usmar, 2012). These ecological characteristics of snapper make them an ideal species for researching potential differences in diet of fish living in extractive aquaculture habitats versus adjacent natural habitats.

The overall aim of this current research was to use proximate and AFDW assays of the gut content of snapper to determine whether
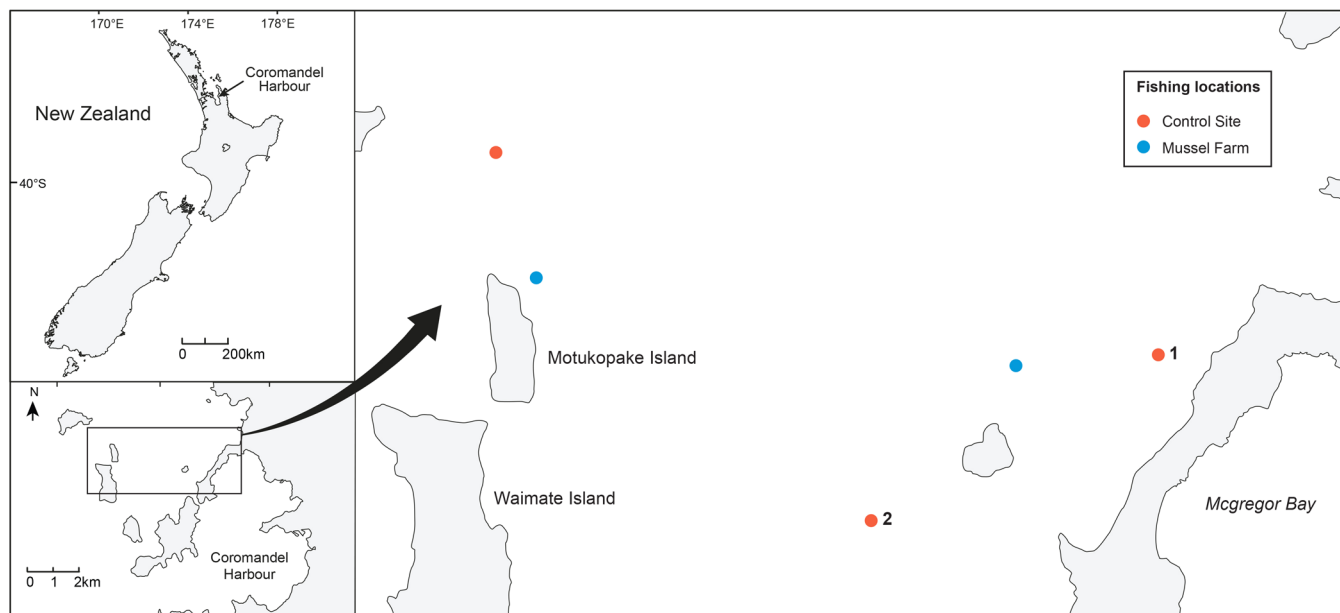
FIGURE 1 The four sampling sites within the Firth of Thames, New Zealand, where snapper were sampled from two mussel farm sites, and two control sites that are all located on benthic soft sediment in 8–13 m of water depth. The control site at Rat Island consisted of two sampling locations (Labelled 1 and 2) over similar natural soft-sediment unstructured benthic habitat, with the samples being pooled.

there were differences in the nutritional quality of the diet of snapper feeding in coastal Greenshell™ mussel farms versus adjacent natural habitats without a mussel farm. The research aimed to test the hypothesis that the presence of mussel farm infrastructure over soft sediment benthic habitat improves the nutritional quality of the diet of snapper living within the habitat that may help to explain the increased abundance of snapper associated with these mussel farms.

2 | METHODS

2.1 | Site locations

Snapper were sampled from four sites in the Firth of Thames, a large and relatively shallow coastal embayment in northern New Zealand (Figure 1). Two sites were long established longline mussel farms, and two sites were natural habitat in adjacent waters but without mussel farms, that is control sites. Mussel farm sites were Motukopake Island (36° 45′ 2.87″S, 175° 25′ 22.8″E) and Rat Island (36° 45′ 25.9194″S, 175° 26′ 59.99″E). Control sites were located at least 500 m away from mussel farms, Motukopake Island control site (36° 57′ 32.03″S, 175° 28′ 51.59″E) and Rat Island control site (36° 45′ 23.03″S, 175° 27′ 39.6″E; 36° 45′46.07″S, 175° 26′ 49.2″E). Two locations were used for the Rat Island control site due to the lack of fish caught at the first control site. Sampling undertaken at both locations targeted the same habitat (soft-sediment unstructured benthic habitat) with the samples pooled for the analyses. The longline green-lipped mussel farm operations at the aquaculture sites consisted of a series of paired parallel backbone lines held near the surface by large plastic floats that sup-

port suspended loops of dropper ropes covered with attached mussels (Jeffs et al., 1999). The loops of dropper rope that are used to culture attached mussels extend to approximately 6–8 m below the surface floats and are suspended above the soft-sediment seafloor. Depth was standardised for both aquaculture and control sites and ranged from 8 to 13 m.

2.2 | Sample collection and processing

Adult snapper only within a size range of 26–42 cm total length were sampled in May and June 2022. Hook and line fishing methods were used, with plastic soft-bait and lures utilised as much as possible to avoid possible contamination of gut contents. Where natural bait was used, a minimal amount of bait was deployed of a readily recognisable species (i.e. pilchard, squid or mullet), and any remnant bait was identified and removed from the first section of the alimentary tract of snapper after capture. Crepuscular periods of snapper feeding activity were primarily targeted for the sampling to increase the probability of capturing snapper with gut contents. Sixteen fish were obtained from each of three sampling sites; Motukopake Island mussel farm, Motukopake Island control site and Rat Island mussel farm, whereas thirteen snapper were sampled from Rat Island control site. Immediately upon capture, all fish were humanely euthanised according to animal ethics approval (NZ Animal Welfare Act 1999, UoA-AEC Approval 21619), labelled and put into salted ice slurry. Each snapper was measured (fork length) and weighed back on land (approximately 2–6 h after capture) before being frozen for subsequent gut analyses. Previous studies have indicated that freezing snapper gut contents was an appropriate method of preservation that facilitates both visual,

molecular genetics and biochemical analysis of gut contents to be undertaken, for example (Supono et al., 2021; Third, 2022).

2.3 | Snapper gut processing

Frozen snapper samples were thawed at room temperature and then dissected. The alimentary tract was removed via incisions at the oesophageal opening and at the anus. The foregut and hindgut were separated and each opened. Any bait identified in the foregut was removed and weighed and not considered further in this study. The remaining material in the foregut was weighed, followed by the foregut lining after the gut contents had been emptied. The process was repeated for the hindgut. Snapper jaw gape was measured by using callipers to push the mouth open and measure the vertical distance between anterior incisors at maximum jaw extension.

Gut contents for the foregut and hindgut were combined and then spread onto a sterile tissue culture dish (2×2 cm^2 grid) and sorted into 35 groups of similar prey items, for each sample (see Table 1 for prey groups). Distilled water was used to separate and clean prey items. Each prey group was classified to the lowest practical taxonomic level. An adapted version of the relative-fullness method was used to quantify the proportions of each prey grouping in each individual snapper gut (Amundsen & Sánchez-Hernández, 2019; Baker et al., 2014; Binning & Chapman, 2010). The relative-fullness method then uses proportions of each prey group and standardises by the fullness of the gut to calculate 'points' for each individual prey group within the snapper gut contents. This was undertaken by first estimating the two-dimensional coverage of each prey group in the culture dish (e.g. Bivalvia covering 2 squares). All prey groups were then summed together to estimate the total coverage within each snapper gut, including the unidentifiable digested material which had its own category. This estimate was then used to calculate the relative proportion of each prey group within the gut of the sampled snapper. Proportions were multiplied by the average fullness estimate (foregut and hindgut calculated independently but averaged to produce one fullness score) to calculate the points of each prey group within each individual snapper, thereby standardising the relative proportion of each prey group to facilitate comparisons among samples. For example, if the relative proportion of the gut content of a snapper was 0.8 (i.e. 80% coverage of the gut contents in the culture dish) for green-lipped mussel (*Perna canaliculus*) and the average fullness estimate was 3, this would be calculated as 0.8×3 which equals 2.4 points. In addition, the presence/absence of a prey group in each snapper was used to calculate a frequency of occurrence for each prey group for each of the four sampling sites.

Once gut contents had been used for visual gut analysis and subsamples taken for later DNA metabarcoding, they were separated from any pieces of mollusc shell material (e.g. green-lipped mussel shell) so that the tissue components could be homogenised via Ultra-Turrax. The homogenised tissues and shell material were freeze-dried for 48 h until samples were completely moisture free before weighing.

2.4 | Fulton condition index

The Fulton condition index was calculated from fish length and weight for every fish to provide a gross indicator of overall nutritional condition of each fish (Nash et al., 2006). The index is calculated as

$$K = \left(W / \left(L^3 \right) \right) \times 100$$

where W is the weight (g), and L is the length (cm) (fork length).

2.5 | Biochemical analyses

Triplicate samples of 60 mg dry weight of homogenised tissue from the gut contents of each fish were used for the analysis of AFDW. The samples were ashed in a muffle furnace at 450°C for 4 h, and the remaining mass of ash (i.e. inorganic matter) was used to establish the proportion of AFDW to total dry weight for the tissue material, that is the gut contents once the shell material had all been removed. The process was repeated on the entire shell sample so that the AFDW in the tissue and shell material could be calculated. This resulted in four metrics used in analysis, first dry weight of all tissue material in gut contents (i.e. consisting of total gut contents with shell material extracted), the dry weight of shell material in gut contents which is the dry weight of extracted shell material only and percentage AFDW for only the tissue material in the gut contents.

Lipid content was calculated gravimetrically on triplicate samples of 20 mg freeze-dried gut contents using a modified version of the methanol–chloroform solvent extraction method (Bligh & Dyer, 1959).

To determine the total protein content of gut contents, the lipid-free residues remaining from the lipid analyses were freeze-dried for 16 h to remove residual water and methanol and used in a bicinchoninic acid protein determination (Pierce Micro BCA Protein Assay, Thermo Fisher Scientific) (Smith et al., 1985). An aliquot of 6 mL of 0.1 M NaOH was added to each sample and incubated for 16 h at 50°C. Samples were then centrifuged at 4000 rpm at 4°C for 10 min. The supernatant was extracted and protein measured using a micro BCA protein assay kit with absorbance read at 562 nm on a spectrophotometer (51119700DP, Thermo Fisher Scientific) and compared to a bovine serum albumin standard curve.

To determine the total carbohydrate content of gut contents, the freeze-dried gut contents were ground with liquid nitrogen and homogenised in 1 mL of distilled water via Ultra-Turrax homogeniser. The sample solution was centrifuged at 10,000 rpm at 4°C for 10 min. The supernatant was extracted and carbohydrate measured using the phenol sulphuric acid reagent method, reading absorbance against a D-glucose standard at 490 nm (DuBois et al., 1956; Masuko et al., 2005).

For lipid, protein, carbohydrate and AFDW assays, the mean of the triplicate samples was calculated after the removal of any outliers (i.e. greater than 20% difference) within the triplicate samples to reduce any potential laboratory methodological errors from the data set. Total

TABLE 1 Total amount (derived from relative proportion measure data) of prey groups classified to the lowest taxonomic level consumed by snapper (*Chrysophrys auratus*), and total percentage of individual snapper with a prey group present (derived from presence/absence data), among the sites (Motukopake Island control site n = 16, Motukopake Island mussel farm n = 16, Rat Island control site n = 13, Rat Island mussel farm n = 16).

Prey groups at the lowest taxonomic level in snapper gut contents			Motukopake Island control site (%)	Motukopake Island mussel farm (%)	Rat Island control site (%)	Rat Island mussel farm (%)
Digested material			18.94 and 100	15.34 and 100	14.48 and 100	13.25 and 93
Mollusca	Bivalvia	Unidentified Bivalvia	0.48 and 6	0.00	0.00	0.04 and 6
		Anomia trigonopsis	1.28 and 25	0.03 and 6	0.00	0.00
		Atrina zelandica	2.11 and 37	0.00	0.00	1.07 and 6
		Austrovenus stutchburyi	0.34 and 6	0.00	0.00	0.00
		Dosina spp.	0.59 and 19	0.00	0.00	0.00
		Mytilus galloprovincialis planulatus	0.00	0.60 and 13	0.00	4.04 and 31
		Ostreidae spp.	0.00	0.00	0.075 and 8	0.00
		Paphies australis	0.08 and 6	0.00	0.00	0.00
		Perna canaliculus	0.00	**5.90** and 56	0.00	**6.85 and 56**
	Gastropoda	Trochidae spp.	0.52 and 13	0.00	0.00	0.00
		Cellana ornata	0.00	0.00	0.00	0.16 and 6
	Chitonida	Unidentified chiton	0.11 and 6	0.00	0.00	0.043 and 6
Arthropoda	Brachyura	Unidentified Brachyura	0.1 and 6	0.61 and 19	0.38 and 8	0.17 and 6
		Halicarcinus innominatus	0.00	1.49 and 6	0.00	0.00
		Halicarcinus spp.	0.00	0.18 and 6	0.00	0.00
		Liocarcinus corrugatus	**3.70** and 13	0.00	0.00	0.00
		Nepinnotheres novaezelandiae	0.00	0.20 and 6	0.00	0.25 and 6
		Notomithrax spp.	0.04 and 13	0.86 and 13	0.00	0.72 and 6
		Pilumnus novaezelandiae	0.00	0.77 and 13	0.00	0.00
		Portunidae	0.00	0.057 and 6	0.00	0.00
	Paguroidea	Paguridae spp.	2.86 **and 38**	0.00	0.83 and 23	0.02 and 6
		Lophopagurus spp.	0.50 and 19	0.00	0.00	0.00
	Decapoda	Unidentified decapod	0.53 and 13	0.94 and 6	**5.99 and 62**	–
	Crustacea	*Balanus trigonus*	0.00	3.33 **and 68**	0.42 and 15	5.76 and 44
		Epopella plicata	0.00	0.00	0.00	0.32 and 6
		Meiura	0.35 and 6	0.00	0.00	0.00
	Caridea	Unidentified Caridea	0.02 and 6	0.00	0.33 and 15	0.11 and 6
		Alpheus richardsoni	0.00	0.00	0.07 and 8	0.00
		Biffarius filholi	0.48 and 6	0.00	0.00	0.00
Annelida	Polychaeta	Unidentified polychaete	0.04 and 6	0.00	0.00	0.05 and 6
		Eulalia microphylla	0.00	0.45 and 6	0.00	0.00
		Serpulidae spp.	0.00	0.43 and 38	0.00	0.47 and 13
Chordata	Teleostei	*Fosterygion* spp.	0.00	0.00	2.42 and 8	0.00
	Ascidiacea	*Styela clava*	0.00	0.32 and 6	0.00	0.00
Shell debris		Misc shell debris	0.1 and 6	0.00	0.00	0.16 and 6

Note: The relative proportion measure identifies the relative contribution of each prey group combined with a measure of gut fullness. The percentages represent the proportion of snapper samples that had the prey item present, over the total number of individual snapper sampled within each site. Bold values represent the highest value, excluding unidentifiable digested material.

calorific content of gut contents was estimated using standard calorific conversions for the assayed protein, lipid and carbohydrate for the mean of the sampled snapper within each site (Lloret & Planes, 2003).

2.6 | Statistical analyses

To compare differences in Fulton condition index, snapper size (fork length – cm) and snapper jaw gape (mm), a two-way ANOVA was used with the main factors of Location (Motukopake Island and Rat Island) and Treatment (mussel farm or control). Data were plotted and visually assessed to confirm that parametric assumptions were met. Tukey's honest significant difference post hoc tests were conducted if an overall significant difference was identified.

Linear regressions were used to compare snapper size (fork length – cm) to four variables; snapper jaw gape (mm), dry weight of tissue material in gut contents and dry weight of shell material in gut contents of snapper gut contents. To compare differences in dry-weight of snapper gut contents for tissue and shell material (g), AFDW, total lipid (mg g dry tissue^{-1}) and total protein (mg g^{-1} dry tissue), total carbohydrate (mg g^{-1} dry tissue) and total calorific content (kJ g dry tissue^{-1}), two-way ANCOVAs with the main factors of Location (i.e. Motukopake Island and Rat Island) and Treatment (mussel farm or control) and the co-variate of snapper size were used to partition any effect of size of snapper on the gut contents regardless of the main factors in the analysis. Data were visually assessed to confirm parametric assumptions were met. A log(x + c) transformation was used for the shell material data, and an arcsine transformation was used for percentage data to normalise the data prior to analyses. Where the overall model results were significant, 'emmeans' post hoc analyses were used to compare each of the combinations among the two interacting factors (location and treatment).

All statistical analyses and plots were produced using R v4.0.4 (R Core Team, 2021). All analyses used a significance α = 0.05. All means are presented as mean ± standard error. Plots made with ggplot RStudio package.

3 | RESULTS

3.1 | Snapper size

Snapper size ranged from 27.4 to 41.2 cm at Rat Island mussel farm, 27 to 41.6 cm at Motukopake Island mussel farm, 25.8 to 30.2 cm at Rat Island control site and 26.8 to 37.4 cm at Motukopake Island control site (Figure 2). From the snapper captured at each site, there were differences in mean snapper length for Treatment ($F_{(1,57)}$ = 5.41, p = 0.024) and Treatment × Location ($F_{(1,57)}$ = 9.51, p = 0.0032), but not for Location, that is Motukopake Island versus Rat Island ($F_{(1,57)}$ = 1.04, p = 0.31) (Figure 2). Post hoc analysis identified that snapper sampled at the Motukopake Island control site were larger on average than at the Rat Island control site (p = 0.024, 31.6 ± 1.0 and 27.8 ± 0.3 cm, respectively), whereas snapper from Rat Island mussel farm were

larger than those sampled from the Rat Island control site (p = 0.002, 32.8 ± 1 and 27.8 ± 0.3 cm, respectively).

3.2 | Snapper jaw gape

Mean snapper jaw gape (mm) caught at each site ranged from 29.9 to 34.2 mm for mussel farm and 29.1 to 32.4 mm for control sites. There was a significant difference for Treatment × Location ($F_{(1,57)}$ = 9.53, p = 0.003) but not for gape between either Treatment or Location. Post hoc analyses identified that snapper jaw gape at Rat Island mussel farm was significantly larger than Rat Island control site (p = 0.03, i.e. 34.2 ± 1.36 vs. 29.05 ± 0.77 mm). There was a significant and relatively strong linear relationship between snapper size and snapper jaw gape (mm) (r^2 = 0.49) with a moderate slope (0.939×).

3.3 | Snapper condition

The mean Fulton condition index ranged from 2.0 to 2.1 for mussel farm and control sites. There were no differences for the Fulton condition index between Treatment ($F_{(1,57)}$ = 0.81, p = 0.37), Location ($F_{(1,57)}$ = 1.26, p = 0.27) or for Treatment × Location ($F_{(1,57)}$ = 0.4, p = 0.53).

3.4 | Snapper gut content composition

The prey items identified to the lowest taxonomic level from the gut contents of snapper produced two sets of data. First, points data derived from the relative proportions of each prey group combined with the relative fullness of the gut identified the relative amount of each prey group present in the gut contents of all sampled snapper (Table 1). Second, presence/absence data were used to calculate the percentage of individual snapper within a site that had each prey group present (Table 1). The highest relative amounts of prey consumed by snapper sampled from the Motukopake Island mussel farm were green-lipped mussels (*P. canaliculus*); however, the prey item most frequently present in gut contents of snapper was the triangle barnacle (*Balanus trigonus*) (Table 1). At Rat Island mussel farm, the prey item with the highest quantity and most frequently present was green-lipped mussels (Table 1). The highest amount of prey consumed by snapper at the Motukopake Island control site was wrinkled swimming crab (*Liocarcinus corrugatus*), and the most frequently present prey species was hermit crabs in the Paguridae (Table 1). At the Rat Island control site, the highest amount and most frequently present prey in snapper gut contents was Decapoda (Table 1).

3.5 | Dry weight and organic content

The dry weight of tissue material within snapper gut contents ranged from 0.28 to 2.78 g for Rat Island mussel farm, 0.52 to 3.36 g for
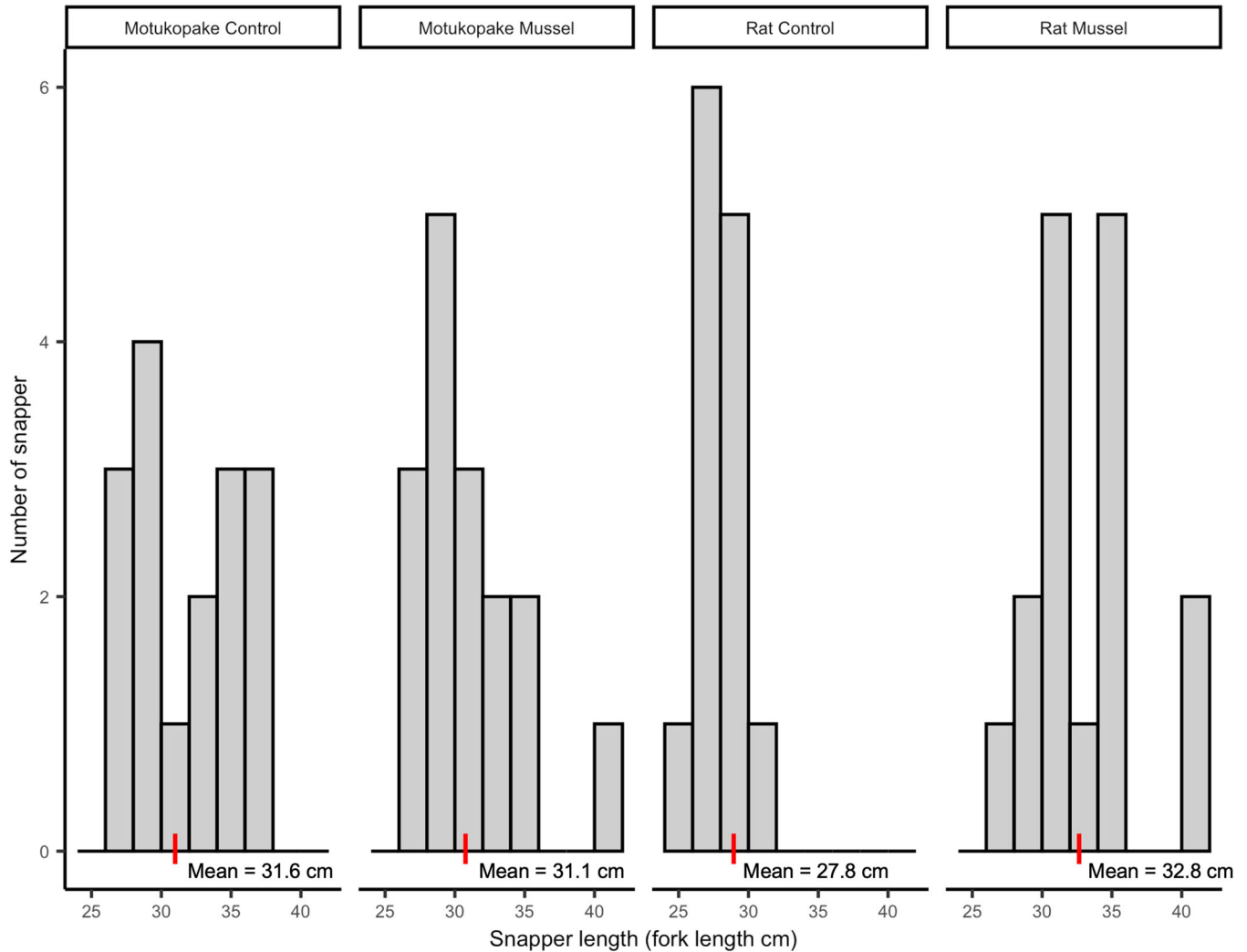
FIGURE 2 Size frequency of snapper (*Chrysophrys auratus*) length (as fork length cm) (bin width = 2 cm) sampled at four sites in the Firth of Thames (Motukopake Island control site $n = 16$, Motukopake Island mussel farm $n = 16$, Rat Island control site $n = 13$, Rat Island mussel farm $n = 16$). Red lines indicate mean snapper length for each site.

Motukopake Island mussel farm, 0.31 to 3.29 g for the Rat Island control site and 0.38 to 2.64 g for Motukopake Island control site. Dry weight of shell material within gut contents ranged from 0 to 7.7 g for Rat Island mussel farm, 0 to 2.5 g for Motukopake Island mussel farm, 0 to 0.3 g for Rat Island control site and 0 to 1.6 g for Motukopake Island control site. Overall, there were differences in the total dry weight of snapper gut contents among the four sites; however, this was mostly due to differences in shell material (e.g. mean of 2.7 g of shell in Rat Island mussel farm snapper vs. mean of 0.6 g of shell at the Rat Island control site) (Figures 3 and 4).

There was a difference in the dry weight of tissue material in gut contents (g) relative to snapper size ($F_{(1,56)} = 12.68, p < 0.0001$), but no significant differences among Treatment ($F_{(1,56)} = 0.86, p = 0.36$), Location ($F_{(1,56)} = 0.27, p = 0.61$) or Treatment × Location ($F_{(1,56)} = 1.6, p = 0.22$) (Figure 3). There was a significant but weak linear relationship between snapper size and dry weight of tissue material in their gut ($r^2 = 0.1$) with a low slope ($0.077\times$) (Figure 3). There was also a

difference in dry weight of shell material in gut contents compared to snapper size ($F_{(1,56)} = 4.37, p = 0.04$), Treatment ($F_{(1,56)} = 7.07, p = 0.01$) and Location ($F_{(1,56)} = 5.81, p = 0.02$) but not Treatment × Location ($F_{(1,56)} = 3.2, p = 0.08$) (Figure 4). Post hoc analyses indicated that Motukopake Island control site and Rat Island control site had less shell material in snapper gut contents than at Rat Island mussel farm ($p = 0.004$ and $p = 0.003$, respectively). As snapper size increased, there was also an increase in dry weight of shell material (slope = $0.17\times$); however, this was a weak linear relationship ($r^2 = 0.14$) (Figure 4).

Mean percentage AFDW of the tissue material in gut contents of snapper sampled in mussel farms ranged from 67.6% to 72.4% and 63.9% to 69.8% for control sites. There was no significant difference in percentage AFDW of tissue material in gut contents versus snapper size ($F_{(1,56)} = 0.27, p = 0.0.6$), or among Treatment ($F_{(1,56)} = 0.18, p = 0.7$), Location ($F_{(1,57)} = 0.012, p = 0.91$) and Treatment × Location ($F_{(1,56)} = 0.89, p = 0.35$).
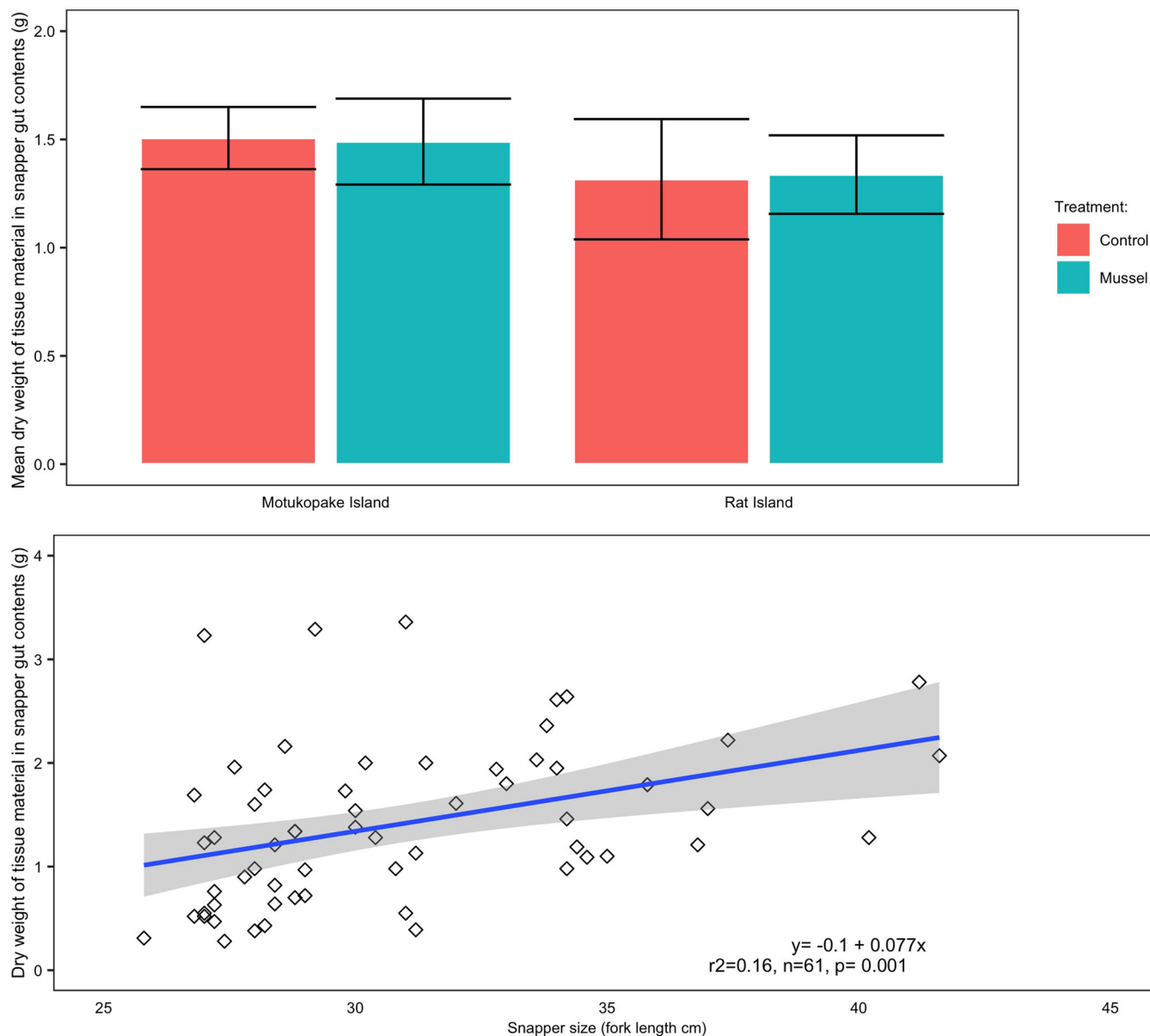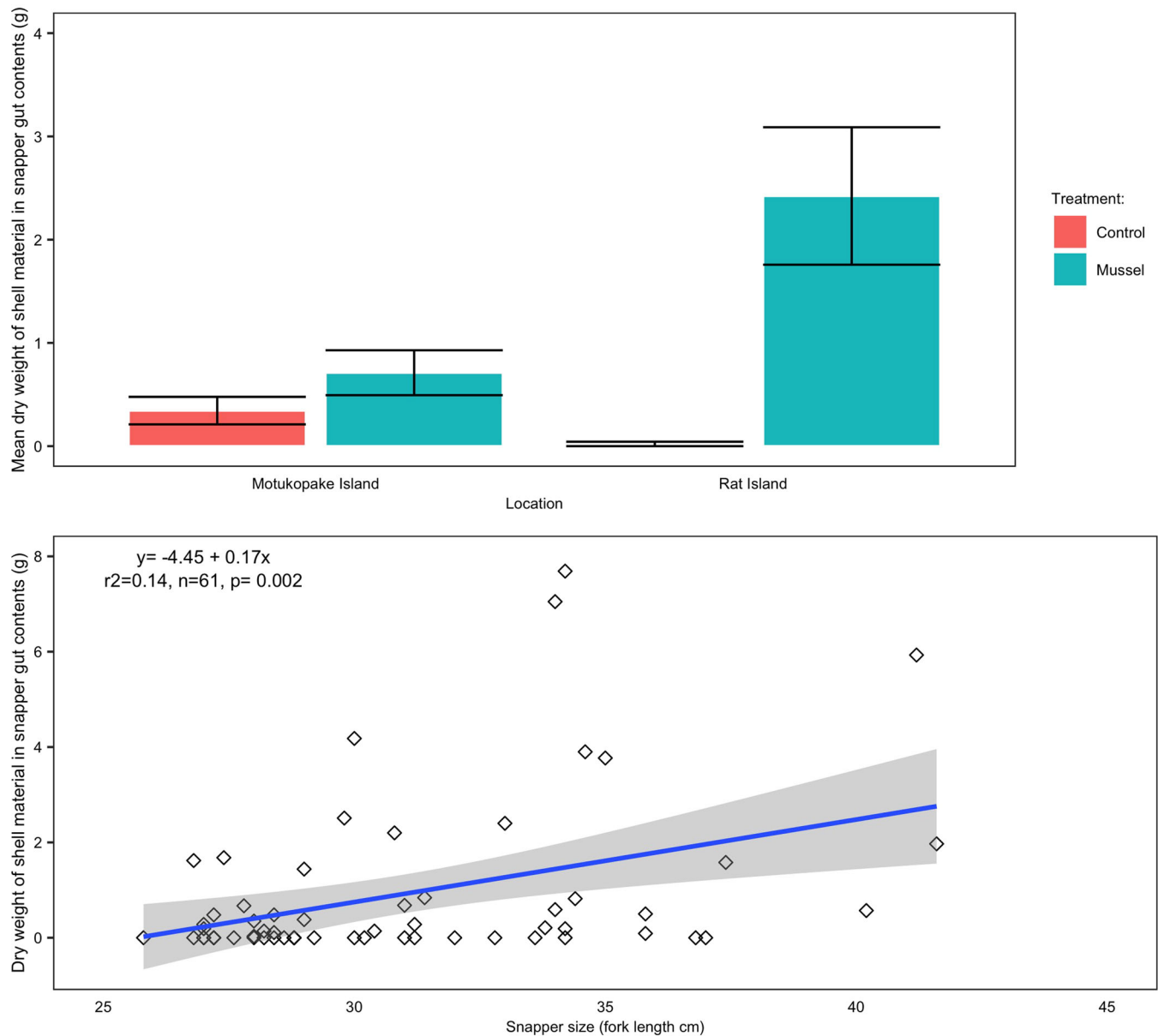
FIGURE 3 Top figure mean dry weight of tissue material in gut contents (g) of snapper caught at each of four sampling sites in the Firth of Thames; Motukopake Island control site, $n = 16$, Motukopake Island mussel farm, $n = 16$, Rat Island control site, $n = 13$, Rat Island mussel farm, $n = 16$ (error bars represent standard error). Bottom figure linear regression of snapper size (fork length cm) compared to the dry weight of tissue material in snapper gut contents (g) regardless of sampling site for snapper in the Firth of Thames. Solid line represents linear regression line, and grey shading represents 95% confidence limits.

3.6 | Lipid content

Mean lipid content of tissue material from the gut contents from individual snapper ranged from 168.4 to 150.9 mg g^{-1} dry tissue in mussel farm sites and 85.1 to 78.4 mg g^{-1} dry tissue at control sites (Figure 5). There was no difference in lipid content of gut contents in relation to snapper size ($F_{(1,56)} = 0.09$, $p = 0.08$); however, there were differences in total lipid for the main factor of Treatment ($F_{(1,56)} = 17.69$, $p < 0.0001$), but not for Location ($F_{(1,56)} = 0.18$, $p = 0.07$) or Treatment × Location ($F_{(1,56)} = 0.29$, $p = 0.06$) (Figure 5). Post hoc analyses

indicated that the tissue material in the gut contents of snapper sampled at Motukopake Island mussel farm had 77.3% greater lipid than the Motukopake Island control site ($p = 0.03$, i.e. 150.9 ± 22.1 vs. 85.1 ± 6.7 mg g^{-1} dry tissue) and 92.5% greater than the Rat Island control site ($p = 0.04$, i.e. 150.9 ± 22.1 vs. 78.4 ± 8.7 mg g^{-1} dry tissue). The tissue material in the gut contents of snapper sampled from Rat Island mussel farm also had greater lipid content compared to Motukopake Island control site ($p = 0.005$, i.e. 168.4 ± 21.1 vs. 85.1 ± 6.7 mg g^{-1} dry tissue) and Rat Island control site ($p = 0.02$, i.e. 168.4 ± 21.1 vs. 78.4 ± 8.7 mg g^{-1} dry tissue).
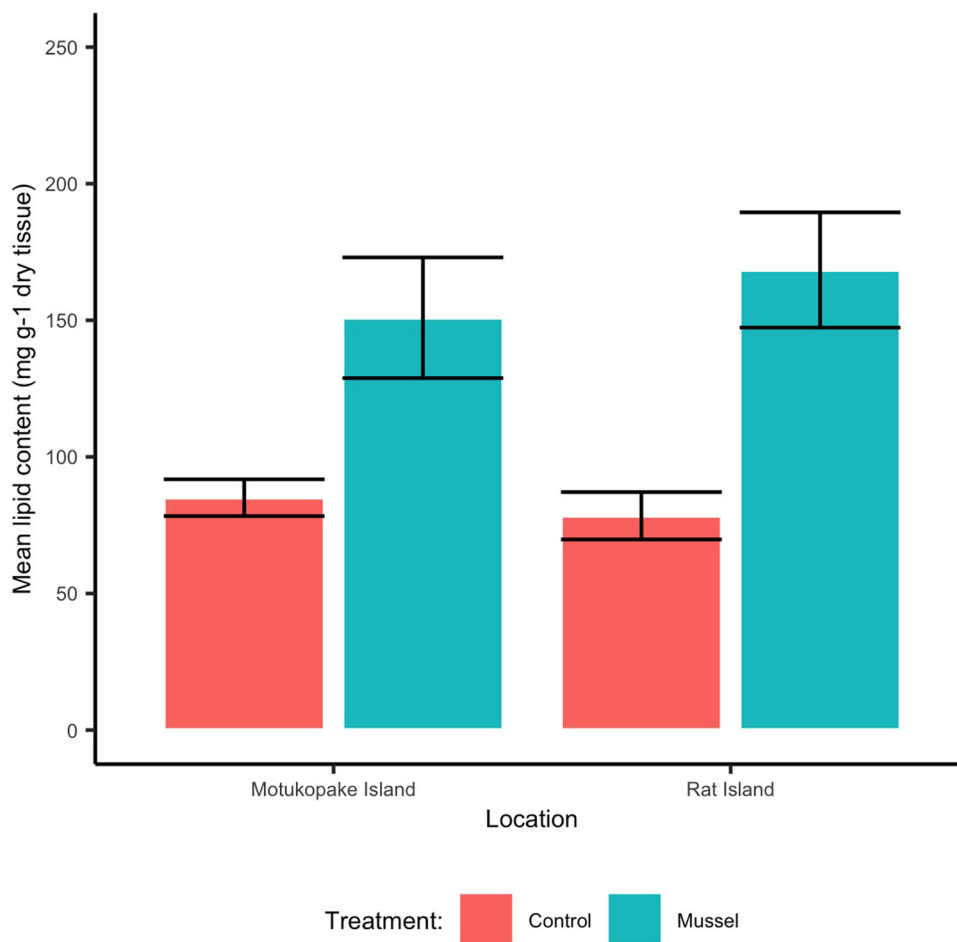
FIGURE 4 Top figure mean dry weight of shell material in gut contents (g) of snapper caught at each of four sites in the Firth of Thames; Motukopake Island control site, $n = 16$, Motukopake Island mussel farm, $n = 16$, Rat Island control site, $n = 13$, Rat Island mussel farm, $n = 16$ (error bars represent standard error). Bottom figure linear regression of snapper size (fork length cm) compared with dry weight of shell material in snapper gut contents (g) for snapper sampled from four sites in the Firth of Thames. Solid line represents linear regression line, and grey shading represents 95% confidence limits.

3.7 | Protein content

Mean protein content of dry tissue material in the gut contents of individual snapper ranged from 180.8 to 166.3 mg g^{-1} for mussel farm sites and 162 to 161.8 mg g^{-1} dry tissue for control sites. Protein content of snapper gut contents was not related to snapper size ($F_{(1,56)} = 0.1$, $p = 0.7$), or due to the main factors of Treatment ($F_{(1,56)} = 0.14$, $p = 0.7$), Location ($F_{(1,56)} = 0.16$, $p = 0.7$) or Treatment × Location ($F_{(1,56)} = 0.04$, $p = 0.9$).

3.8 | Carbohydrate content

Mean carbohydrate content of tissue material in the gut contents of individual snapper ranged from 9.0 to 12.2 mg g^{-1} dry tissue for mussel farm sites and 9.5 to 11.0 mg g^{-1} dry tissue for control sites (Figure 6). There was no difference in mean carbohydrate content in relation to snapper size ($F_{(1,56)} = 0.003$, $p = 1.0$), or due to the main factor Treatment ($F_{(1,56)} = 0.05$, $p = 0.8$) or Treatment × Location ($F_{(1,56)} = 1.1$, $p = 0.3$). However, there was a difference related to Loca-

FIGURE 5 Mean lipid content of dry tissue mass (mg g^{-1} dry tissue) for gut contents of snapper caught at each of four sampling sites in the Firth of Thames; Motukopake Island control site – $n = 16$, Motukopake Island mussel farm – $n = 16$, Rat Island control site – $n = 13$, Rat Island mussel farm – $n = 16$) (error bars represent standard error).

tion ($F_{(1,56)} = 6.8$, $p = 0.01$) (Figure 6). Post hoc analyses indicated that the tissue material in the gut contents of snapper from sites at Rat Island had a 25.8% higher carbohydrate content than those from the sampling sites at Motukopake Island, regardless of whether were inside mussel farms or at control sites outside mussel farms ($p = 0.02$, i.e. 11.7 ± 0.6 vs. 9.3 ± 0.7 mg g^{-1} dry tissue).

3.9 | Total calorific content

Mean total calorific content of tissue material in the gut contents of individual snapper ranged from 10.1 to 11.2 kJ g^{-1} dry tissue in mussel farm sites and 7.2 to 7.4 kJ g^{-1} dry tissue at control sites (Figure 7). The calorific content of the tissue material in the gut contents of snapper was different between Treatment ($F_{(1,56)} = 8.50$, $p = 0.005$), but not different in relation to snapper size ($F_{(1,56)} = 0.1$, $p = 0.7$), or Location ($F_{(1,56)} = 0.26$, $p = 0.6$) or Treatment × Location ($F_{(1,56)} = 0.21$, $p = 0.65$) (Figure 7). Post hoc analyses indicated that mussel farm snapper had a 46.6% higher calorific content than control site snapper ($p = 0.005$, i.e. 10.7 ± 0.8 vs. 7.3 ± 0.6 mg g^{-1} dry tissue).

4 | DISCUSSION

This study compared the differences in the quantity and quality of snapper diet between mussel farm habitat and nearby soft-sediment control habitat without mussel farm infrastructure. Fish sampled from the mussel farm habitat had consumed a greater overall amount of food material; however, the digestible portion of the diet measured as the dry weight of tissue material was similar. Snapper feeding within mussel farm sites also had on average of an additional 7.8% lipid per gram of dry mass of tissue material in their gut contents than fish sampled in control sites. However, the protein and carbohydrate content in the tissue material in their gut contents were not substantively different between mussel farm habitat and adjacent natural habitat. The higher lipid content of the gut contents of mussel farm snapper compared to control site snapper resulted in a more energy-rich diet with a 46.6% higher calorific value. The size of snapper also appeared to have some effect on the amount of prey consumed, with small increases in dry weight of tissue material present in the gut contents of snapper with increasing size of adult snapper even within the relatively narrow size range of fish that was sampled, that is 26–42 cm. Overall, these
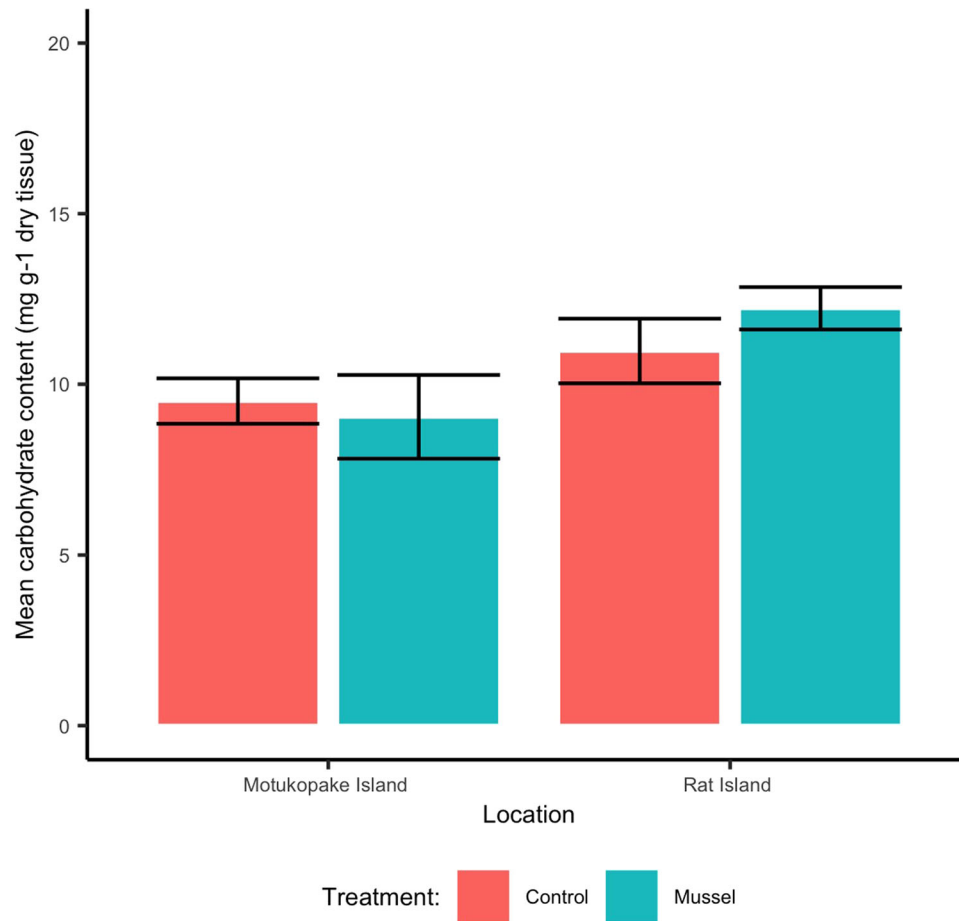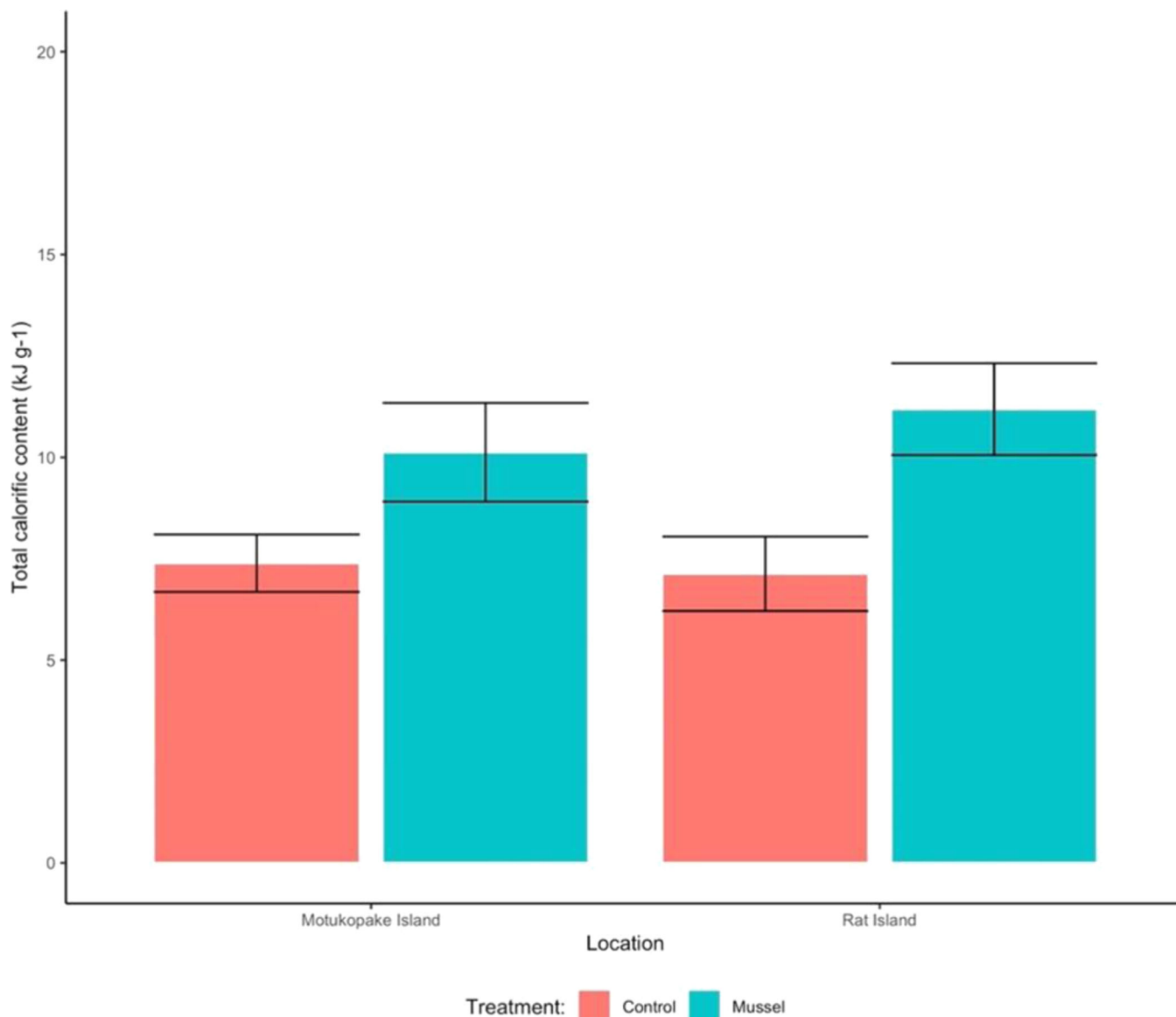
FIGURE 6   Mean carbohydrate content of dry mass of tissue material (mg g^{-1} dry tissue) from gut contents of snapper sampled at each of four sites in the Firth of Thames; Motukopake Island control site – $n = 16$, Motukopake Island mussel farm – $n = 16$, Rat Island control site – $n = 13$, Rat Island mussel farm – $n = 16$ (error bars represent standard error).

results indicate that although the overall quantity of digestible food that is consumed is similar for snapper feeding inside and outside mussel farms, the quality of the food consumed inside the mussel farm is higher, due to a greater quantity of lipid translating to a higher energy diet. Therefore, the quality of food within mussel farm habitats may partially explain why there are higher abundances of snapper within mussel farms compared to adjacent natural soft-sediment habitats without mussel farms (Underwood, 2023).

4.1 | Composition of diet

The similarities in the quantity of digestible gut contents, including the similarities in the organic content of diet, suggest that the overall availability of food for intake by snapper is not different from nearby natural habitats. Although snapper are consuming a greater total mass of food in mussel farms, the indigestible component of the diet is higher, because of the inclusion of a greater quantity of shell material (i.e. mean of 1.79 g vs. 0.48 g of dry shell material in gut contents) which is mostly derived from bivalves and crustaceans, especially blue mussels (*Mytilus aoteanus* and *Mytilus galloprovincialis*), green-lipped mussels (*P.*

canaliculus) and triangle barnacles (*B. trigonus*). This suggests that snapper feeding within mussel farms are selecting prey items that are more nutritionally valuable with the potential aim of reducing the effort and energetic costs of foraging, consistent with optimal foraging theory (Wootton, 2012). Mussels and barnacles can be present on the dropper lines and the seafloor underneath mussel farm habitats; however, they are much more abundant on the hard substrate of dropper lines (Woods et al., 2012; Zazzaro et al., 2018). Previous investigations have also linked prey consumed by snapper to the mussel farms (Underwood et al., 2023). Additionally, investigations of the abundance of snapper within mussel farms in the Firth of Thames using remote underwater video recordings (Underwood, 2023) showed that snapper were frequently near the surface (2 m depth) with 34% of the total abundance of all snapper observed at the surface and 66% of the total abundance observed at the seafloor based on a total of 89.6 h of remote video observations taken at these two depths. This confirms that snapper were present among the dropper lines, with a relatively small number of feeding events ($n = 6$) observed within the dropper lines. Therefore, it appears that snapper are utilising two food resources made available by the mussel farm habitat, food on mussel farm dropper lines and the benthos beneath the farm, which is altered because of organic enrich-

FIGURE 7 Mean calorific content of dry mass of tissue material (kJ g^{-1} dry tissue) from gut contents of snapper sampled at each of four sites in the Firth of Thames; Motukopake Island control site – $n = 16$, Motukopake Island mussel farm – $n = 16$, Rat Island control site – $n = 13$, Rat Island mussel farm – $n = 16$ (error bars represent standard error).

ment and mussel drop-off from the mussel farm above (De Jong, 1994; Wilding & Nickell, 2013; Wong & O'Shea, 2011).

Snapper size and corresponding jaw gape were the only variable that appeared to influence the various measures of food consumption, with increasing fish size associated with an increase in tissue material of gut contents. This is consistent with general allometric theory that indicates as fish size increases so does the size of food items, so that larger fish can consume larger and heavier prey items to maximise the energy gained from foraging effort (French et al., 2012; Usmar, 2012; Wootton, 2012; Xue et al., 2005). The mean size of snapper was greater in mussel farms, even though a small size range of adult fish was targeted for the sampling (26–42 cm). Furthermore, in mussel farms, the proportion of sampled snapper above 30 cm in length was 59%, whereas, in control sites, it was 34%. Previous research in mus-

sel farms in the Firth of Thames has found that snapper observed in mussel farms were larger than those in nearby soft sediment habitats (Underwood, 2023), that is mean fork length = 37.2 versus 22.9 cm. There are several possible explanations for the presence of larger snapper in mussel farms. Either snapper in mussel farms are growing faster because of better food supplies that support faster growth, or snapper are moving into mussel farm habitats at larger sizes or there are differences in survival or long-term fidelity of fish living in the two different habitats. Analyses of otolith growth increments could isolate these competing possibilities. Understanding why there is a difference in size structure of snapper within mussel farms is important because if these fish are growing faster within mussel farm habitats, this has implications for fish productivity, as larger snapper have exponentially greater reproductive output, producing larger gamete batch

sizes and therefore greater production during spawning (Parsons et al., 2014).

4.2 | Differences in nutritional composition

The total lipid content within the tissue material of the snapper gut contents from within mussel farm snapper was double (i.e. on average 15.9% vs. 8.15% of dry mass of tissue) that of control site snapper. Studies of optimal diets for seabream species (*Sparidae* spp.) in aquaculture production have identified that a lipid content of at least 9% is required for successful rearing, with commercial artificial feeds typically including over 12% lipid (Glencross et al., 2003; Kalogeropoulos et al., 1992; Kokou et al., 2021; Oliva-teles, 2000; Santigosa et al., 2021). Optimal growth performance for gilthead seabream was observed at 15%–16% lipid content, whereas lipid content above 21% had no impact on growth (Oliva-teles, 2000). Therefore, lipid content in mussel farm snapper diets is within the range of optimal aquaculture feeds, further highlighting the likely importance of the high lipid diet consumed by snapper in mussel farms. Given that the key differences in the diet between mussel farm and control site snapper was their greater intake of species of mussels, barnacles and brachyurans, it is expected that these species are responsible for the increased lipid content observed in snapper gut contents. All of these species are characterised by relatively high lipid content, that is green-lipped and blue mussels at 12.7% and 12.1% total lipid of dry tissue material, respectively (Barclay et al., 2006), barnacles (*Balanus* spp.) 19% lipid (Barnes & Achituv, 1976), with brachyuran species more variable from 1% to 7% lipid (Küçükgülmez et al., 2006; Premarathna et al., 2015; Skonberg & Perkins, 2002; Sreelakshmi et al., 2016). Lipids are energy dense, that is $39.5 \ kJ \ g^{-1}$ compared to proteins and carbohydrates (23.9 and $17.5 \ kJ \ g^{-1}$, respectively), and are important for a range of biological functions, such as cellular metabolism, detoxification, reproduction and behaviour, including acting as the principal energy reserve in many teleost species and commonly playing a major role in determining spawning success and egg quality (Adams, 1999; Lloret & Planes, 2003). The energy dense lipid content has resulted in a higher total calorific value of the diet of mussel farm snapper, confirming that these snapper are consuming substantially more energy than those in soft-sediment habitats. Therefore, the higher lipid and corresponding calorific value in the gut contents of tissue material within mussel farm snapper can contribute to the total productivity of the snapper population by providing snapper with the nutritional resources for biological function and potentially allowing snapper to make a greater reproductive contribution. These potentially consequential outcomes from the differences in dietary intake of lipid by snapper feeding in mussel aquaculture habitat require further investigation.

For another important nutritional component of the diet of snapper, protein, there was no difference between mussel farms and control sites. Protein content of snapper gut contents ranged from 16.0% to 17.9% of dry mass of tissue in mussel farm snapper gut contents and 15.8% to 16.2% in the control sites. Protein is critical for somatic growth, and so in finfish farming, reared seabream are given high-protein diets to optimise growth (Oliva-teles, 2000; Pulido-Rodriguez et al., 2021; Wang et al., 2019; Zhang et al., 2010). Seabream have a high dietary demand for protein with at least 40% protein content required for optimal aquaculture rearing and limited further increase in growth for dietary protein levels above 55% (Koshio, 2002; Oliva-teles, 2000; Zhang et al., 2010). However, the diets with elevated lipid content can serve to reduce the dietary protein requirement in aquaculture feeds, with the protein content of a formulated diet for the seabream species (*Acanthopagrus schlegelii*) being reduced to only 37% by increasing the lipid in the diet (Wang et al., 2019). Overall, these results indicate that the protein contents in the natural diets of snapper from both mussel farm and control habitats are likely to be well below what is considered optimum in aquaculture. Aquaculture feed is made up of high-quality and highly digestible protein ingredients, most commonly processed fish meal and terrestrially sourced proteins such as soy and poultry by-product that are typically pre-processed to improve their digestibility (Pulido-Rodriguez et al., 2021). Even though there were differences in the diet of snapper between control and mussel farm sites, this did not translate to a difference in protein intake. This was likely due to the common presence of species of Decapoda, Paguroidea and Brachyura in the diet of snapper from the control sites, species of which have relatively high-protein content. For example, brachyuran species typically contain 62%–86% protein by dry tissue mass (Küçükgülmez et al., 2006; Premarathna et al., 2015; Skonberg & Perkins, 2002; Sreelakshmi et al., 2016). In contrast, the protein in the diet of snapper sampled from mussel farms was most likely contributed by mussels and barnacles. For example, the protein content of green-lipped and blue mussels is 68% and 65.4%, respectively (Barclay et al., 2006), whereas barnacles (*Balanus* spp.) have 43% protein by dry tissue mass (Barnes & Achituv, 1976).

There were no significant differences in the carbohydrate component of the gut content of snapper between mussel farms and control sites. Carbohydrate content ranged from 13.9% to 17.5% of dry mass of tissue in mussel farm snapper gut contents and 14.2% to 17.1% for control sites. Carbohydrates can be a key source of energy in some fish, but not consistently due to the varied quality of natural carbohydrate sources available in marine ecosystems (Cowey & Sargent, 1972). In this instance, lipids were the key source of energy in the snapper sampled, with the higher lipid content driving the higher total energy of snapper diet in mussel farms.

4.3 | Linking diet to snapper morphology and feeding mechanisms

Jaw gape can be an important determinant of prey choice for some fish species; however, this has not been determined as being important for diet selection within snapper sub-populations (Parsons et al., 2016; Third, 2022). This is likely due to the dominance of small–moderate-sized crustaceans in their diet, which can be consumed by those snapper with a wider gape range (Parsons et al., 2016; Third, 2022; Usmar, 2012). The crushing strength of the jaw has therefore been considered a more important variable in determining prey selec-

tion, with larger snapper showing some jaw specialisation with wider and more robust jaws (Third, 2022; Usmar, 2012). In this current study, there were some differences in the jaw gape of snapper (Rat Island mussel farm > Rat Island control site), and jaw gape increased with snapper size. It is possible that the differences in jaw morphology have allowed larger snapper to more readily consume hard-shelled organisms, such as bivalves, in the mussel farm habitats. Snapper of 20–23 cm (large juveniles) in size are able to consume hard-shelled benthic invertebrates, including brachyuran crabs and bivalves, and once snapper reach over 30 cm, they tend to consume more hard-shelled molluscs, especially bivalves (Usmar, 2012). Therefore, even though all snapper had the opportunity to consume hard-shelled organisms, the reliance on the food resources present within mussel farm habitats may shift towards hard-shelled prey (e.g. mussels and barnacles) with greater snapper size. This could provide a possible explanation for the larger size of snapper found within mussel farm sites.

Even though the total lipids in gut contents were higher in mussel farm snapper, this did not have an impact to the overall nutritional condition of snapper as measured by the Fulton index compared to those from the control sites. New Zealand snapper experience peak condition in spring just before spawning, with an associated decline in nutritional condition after spawning (November–December) (Cassie, 1957). It is thought that post-spawning snapper then increase energy reserves through summer so that, by autumn, they have high nutritional condition in preparation for reproduction, before their metabolism slows in winter (Darren Parsons pers. comm.). This is consistent with other temperate marine fish such as the Atlantic cod (*Gadus morhua*) that reaches higher nutritional condition in autumn, after the spawning season in spring (Mello & Rose, 2005). In the current study, snapper were caught in late autumn – early winter; therefore, condition indices are expected to be moderate as condition begins to decline into winter. The similarity in the nutritional condition of snapper between the two sampled habitats, despite the marked difference in the diet between them, maybe due to dietary protein sparing, where they are utilising protein for increasing growth whilst burning available lipid for energy, a common phenomenon among teleost fishes (Vergara et al., 1996).

The Fulton condition index is a relatively coarse metric used to investigate physiological differences in fish related to their habitat that is more related to the overall health and fitness of the fish rather than their growth (Arismendi et al., 2011; Nash et al., 2006; Vasconcelos et al., 2009). Therefore, even if the condition index does not differ between snapper from mussel farm versus control habitat, it is possible that the snapper growth rate may differ in response to the marked differences in the nutritional quality of their respective diets. Previous research of fish productivity in shellfish aquaculture provided no evidence to suggest that productivity (measured as instantaneous growth rate) increased for a benthic-dwelling fish species (winter flounder) (Clynick et al., 2008). Additionally, previous research on scup (Sparidae species) in oyster-grow out structures showed increased abundances and increased site fidelity compared to rocky reef habitat, however, the growth of scup was higher (by 40%) within natural rocky reef sites (Tallman & Forrester, 2007). Both studies failed to link diet with growth, to determine whether the fish species was benefitting from increased

nutrition within either the aquaculture or natural habitats. In this current study, there was a marked nutritional benefit from consuming prey within the mussel farm habitat compared to adjacent natural habitat without a mussel farm structure, therefore future work should examine whether the growth and reproductive output of snapper feeding in mussel farm habitat is higher due to their dietary differences. The current study only examined one feeding event for each individual snapper, therefore there are some potential limitations with extrapolating these data to understand long-term physiological changes and productivity. These findings should be supplemented with biochemical analyses of snapper, and population studies of snapper in the area to understand possible migration between nearby habitats, food availability and fish size distribution. Overall, this study shows for the first time the potential ecosystem benefits of shellfish aquaculture in provisioning nutritionally valuable prey for coastal fish populations.

5 | CONCLUSIONS

The results from this study indicate that there was a marked nutritional benefit for snapper feeding within mussel farm habitat, in the form of higher dietary lipid intake, most likely from consuming lipid-rich bivalves and barnacles associated with the mussel farms. The higher lipid content of the diet of snapper within mussel farms did not translate to an increase in the overall nutritional condition of these fish, which may be due to faster growth and/or reproductive output in these fish. Larger snapper were more common within mussel farms, which could be a result of faster growth due to the energy-rich food resources available, or the movement of larger snapper into mussel farm habitat to take advantage of the feeding opportunities presented in the mussel farm habitats. The greater nutritional benefit for snapper from feeding in mussel farms is likely to explain why snapper are observed at higher abundances within mussel farm habitats in parts of northern New Zealand compared to adjacent soft-sediment habitats. Overall, the results demonstrate the ecological significance of mussel farm habitat to snapper, providing important evidence of potential additional ecosystem benefits of extractive aquaculture activities on populations of some coastal fish species.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The underlying data for statistical analyses will be shared on reasonable request to the corresponding author.

ETHICS STATEMENT

This research was conducted in accordance with animal ethics approval under New Zealand's Animal Welfare Act 1999 (UoA-AEC Approval 21619), which ensures the humane treatment of animals for research.

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PEER REVIEW

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