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Effect of Feed Texture and Dimensions, on Feed Waste Type and Feeding Efficiency in Juvenile *Sagmariasus verreauxi*

Katarzyna Kropielnicka-Kruk †, Quinn P. Fitzgibbon, Mohamed B. Codabaccus *, Andrew J. Trotter, Chris G. Carter and Gregory G. Smith

Institute for Marine & Antarctic Studies (IMAS), University of Tasmania, Private Bag 49, Hobart, TAS 7001, Australia; k.kruk@utas.edu.au (K.K.-K.); quinn.fitzgibbon@utas.edu.au (Q.P.F.); andrew.trotter@utas.edu.au (A.J.T.); chris.carter@utas.edu.au (C.G.C.); gregory.smith@utas.edu.au (G.G.S.)

* Correspondence: mohamedc@utas.edu.au; Tel.: +61-474733441

† This manuscript is part of a Ph.D. thesis by the first author Katarzyna Kropielnicka-Kruk. Ph.D. Program in the University of Tasmania.

Abstract: The "messy" feeding behaviour of spiny lobsters remains an obstacle for formulated feed development. This study examined the relationship between feeding efficiency and feed waste by juvenile spiny lobster, *Sagmariasus verreauxi*, fed different formulated pellet diameters or lengths across two separate experiments. Feed texture (hard and dry pellet, HDP; soft and moist pellet, SMP) was also examined. Juvenile lobsters were fed experimental feeds at 0.5% BW daily over a 6 h duration. The resulting feed waste was categorised as either feeding-related waste (FRW) or non-feeding-related waste (NFRW). For all feed types, the FRW increased with increasing pellet diameter and pellet length. The increase in FRW corresponded with a decrease in NFRW, particularly for HDP, resulting in no difference in total feed waste in any treatment investigated. Thus, even with improved feeding efficiency with small feed dimensions, feed intake was not improved. Feed leaching rate decreased with increasing pellet size, suggesting a more rapid decline in feed attractiveness for smaller pellets. This finding indicates that currently a counteractive interaction exists between pellet size and feed attractiveness and suggests improving attractiveness would further enhance feeding. Future research should aim at optimising feed dimensions simultaneously to support efficient feeding whilst enhancing attraction/gustatory stimulations.

Keywords: spiny lobster; feed dimensions; feed waste; feed intake; feeding efficiency

Key Contribution: This study is the first examining in detail the type of feed waste produced when spiny lobster is fed formulated feeds varying in texture and dimensions. Improvement of feeding efficiencies, i.e., less waste feed, exists when optimizing feed size. However, feed intake is not improved with optimized feeding efficiencies, most probably due to reduced feed attraction.

Citation: Kropielnicka-Kruk, K.; Fitzgibbon, Q.P.; Codabaccus, M.B.; Trotter, A.J.; Carter, C.G.; Smith, G.G. Effect of Feed Texture and Dimensions, on Feed Waste Type and Feeding Efficiency in Juvenile *Sagmariasus verreauxi*. *Fishes* **2023**, *8*, 553. https://doi.org/10.3390/fishes8110553

Academic Editor: Fernando Vega-Villasante

Received: 4 October 2023
Revised: 3 November 2023
Accepted: 9 November 2023
Published: 16 November 2023

1. Introduction

The feeding behaviour of spiny lobsters remains an obstacle for formulated feed development, partly due to the inefficient format and consumption of feeds resulting from high feeding wastage [1]. Spiny lobster feeding behaviour is often described as "messy" due to external fragmentation of feed caused by handling with multiple appendages and maceration of the formulated feeds prior to ingestion [1,2]. Several studies on the feed intake mechanisms of spiny lobsters have enabled an improved understanding of their feeding behaviour [3–6] and set directions for research into minimising feed wastage, and indirectly maximising feed intake and feeding efficiency. Understanding the optimum feed dimensions relative to lobster size, particularly in relation to the size of the mouthparts, is one approach to reduce feed wastage. Such an approach has been investigated with *Panulirus argus* [4], *Jasus edwardsii* [1] and *Panulirus ornatus* [7].

Feed dimensions relative to lobster size is an important factor when investigating feeding related waste; however, other factors such as feed texture and species are additional considerations. For *P. ornatus*, it was found that soft, semi-moist pellets (1 mm diameter) are less efficiently consumed (more waste produced) by small size lobsters (~2 g) in comparison to hard, dry pellets (1 mm diameter); however, there was a preference for small lobsters to consume soft, semi-moist pellets [7]. For larger *P. ornatus* ($\geq$50 g), feed diameter and length appeared to be more critical to feed consumption efficiency than feed texture. In *P. argus*, first instar juveniles feed most efficiently on soft and pulpy feeds and change their preferences to firmer feeds with growth [4]. This shift of texture selectivity may be aligned with the decreasing risk of appendages damage during development [8]. Hence, feeding appendages morphology and animal size is also an important factor to consider when investigating optimal feed pellet dimension and texture. While feed texture and feed dimensions influence the feeding of spiny lobster, Cox et al. (2008) [4] highlighted that feeding behaviour differences exist between spiny lobster species, indicating that formulated feed development for spiny lobsters may be species specific.

The spiny lobster, *Sagmariasus verreauxi* is an emerging aquaculture species which has several favourable characteristics for culture including a gregarious nature, rapid growth rate and high market value [9]. However, the absence of a commercial formulated feed for this species is a major barrier for its culture in captivity. Wild fisheries remain the major source of spiny lobsters for consumption, including *S. verreauxi* which is distributed in south-eastern Australia and New Zealand [1,2,10,11]. The value of *S. verreauxi* fisheries was approximately $11.23 million in the season 2021/2022 (Dept. of Primary Industries, NSW, Australia, 2023) [12] Examination of feed waste when spiny lobsters eat is critical to understanding the feeding behaviour of spiny lobsters in culture [7]; however, to date, the feed waste for *S. verreauxi* has not been studied. Feed waste can either be qualified as uneaten/unmanipulated feed, termed as non-feeding related waste (NFRW), which is unbroken, unfragmented and without any obvious damage, or feeding related waste (FRW) resulting from manipulation and maceration when feeding, which consists of partially eaten, fragmented or macerated pellets and fine feed particles. Distinguishing between the two types of feed waste would be highly beneficial to understand feeding behaviour, such as feed preferences and feeding efficiency. For instance, if the feed waste is composed of a high percentage of NFRW, feed attractiveness and/or gustatory stimulation may be sub-optimal. On the contrary, a high percentage of FRW in feed waste may indicate active feeding but with poor feeding efficiency. The ratios or amounts of the two types of feed waste may vary depending on feed size and/or texture. For example, there may be an optimal feed dimension/texture which maximises feeding efficiency (low FRW) or enhances attraction/gustatory stimulation (low NFRW) or both. In the present study, we aim to investigate the type of feed waste produced by juvenile *S. verreauxi* when fed varied feed dimensions and textures in two separate experiments. In the first experiment, the effect of pellet diameter was investigated with two types of feed textures: hard and dry pellet (HDP) or soft and moist pellet (SMP). Based on the first experiment, D (diameter) expt., an appropriate feed diameter and texture were selected to investigate the effect of pellet length, in the second experiment, L (length) expt.

2. Materials and Methods

2.1. Experimental Animals and Systems

Two feeding experiments, D (diameter) expt. and L (length) expt., were conducted with a total of 24 juvenile *S. verreauxi* lobsters used in each experiment. The experimental juvenile lobsters were hatchery sourced from the laboratories of the Institute for Marine and Antarctic Studies (IMAS) in Tasmania and were reared until they were experimental size by feeding fresh blue mussels. Two weeks prior to the feeding experiment, the lobsters were acclimated to experimental feeds. In D expt., feed waste type was examined when lobsters were fed different diameter HDP or SMP feeds, lobsters were an average wet weight (WW) of 206.5 g $\pm$ 5.7 S.E., and carapace length (CL) of 74.3 mm $\pm$ 0.8 S.E. In L expt., the effect of HDP (diameter of 4.3 mm) length on feed waste type was examined with lobsters 224.6 g ± 6.8 S.E., WW, and CL 76.4 mm ± 0.8 S.E. Prior to experimentation, lobsters were held in a communal tank and co-fed in excess with fresh half shell blue mussels and a commercial shrimp pellet (2 mm diameter). At the start of each experiment, lobsters were randomly allocated to eight rectangular 18-L culture vessels (38 cm length × 24 cm width × 24.8 cm height), with three individuals housed per vessel. Each vessel was covered with a mesh lid above the water's surface to prevent lobsters from escaping (16 mm oyster mesh). Half of the lid was covered with additional mesh (1.6 mm oyster mesh) to provide additional shading. Two oyster mesh rectangles (15 cm long, 20 cm wide) were suspended along the long walls of the vessels to provide climbing substrate. Ozonated and filtered seawater was supplied at an exchange rate of six exchanges h^{-1} $vessel^{-1}$ with aeration provided to each vessel. Water quality was maintained at a temperature of 20.7 °C ± 0.0 S.E., salinity 34.5 ppt ± 0.0 S.E. and dissolved oxygen 9.5 mg L^{-1} ± 0.0 S.E. (106.0% sat. ± 0.2 S.E.). The photoperiod was set at 9:15 L:D and all work during the dark phase was performed with the use of a red-light torch to minimise disturbance on the nocturnal activity of lobsters [13]. The photoperiod at 9:15 L:D was set to accommodate experimental work, including feeding and collection of feed waste during the dark phase and maintenance during light phase. The duration of the photoperiod within the defined range does not negatively affect juvenile spiny lobsters feed intake, growth, or survival [14–16].

2.2. Experimental Feeds

Feed composition for both the D expt. and L expt. were identical except for their physical hardness characteristics and were made exactly according to the krill oil-based formulation, utilised in Shu-Chien, Han [10]. The manufacturing of the feed was performed as described by Landman, Codabaccus [17]. Briefly, after mixing the dry and wet feed components, the resultant feed dough was cold extruded with La Monferrina Dolly II pasta extruder (Imperia & Monferrina S.p.a., Asti, Italy. The feed strands produced after extrusion were designated as SMP and contained 51.6 ± 0.2% moisture. Different dies were used to produce different SMP feed strands which were then further processed to meet the feed characteristics defined in the D expt. and L expt. The pellet characteristics for the D expt. and L expt. were as follows:

(1) D expt.—SMP feed strands of diameters, 1.5, 2.8, 3.7, 5.0, 7.0, 8.7, 10.2 mm were manufactured and cut to a standard length of 20 mm regardless of the diameter to produce SMP. Half of the manufactured SMP feed strands were dried from 6 to 24 h depending on the diameter, in a Steridium DS500 dryer, at 45 °C to a moisture content of 9.9 ± 0.6% to produce HDP. After drying of SMP to HDP, there was a reduction in the aforementioned SMP pellet diameters to 1.3, 2.3, 3.3, 4.3, 5.8, 7.8 and 9.5 mm HDP, respectively. Therefore, in total, 14 different feeds were produced from one batch, 7 SMP and 7 HDP.

(2) L expt.—To test the effect of pellet length, one batch of HDP standard diameter of 4.3 mm were made and cut to lengths 5, 8, 13, 21, 33, 53 and 84 mm. A standard 4.3 mm diameter HDP was selected as it represented the first equal or lower (≤) available point where levels of FRW and NFRW were closest in HDP diameter tested in D expt.

In the D expt., the eight culture vessels containing three lobsters each were randomly allocated a feed treatment each day, such that every individual vessel of lobsters over the 14 days of the study were supplied with each of the fourteen different pellets (see Supplementary Materials—Table S1). There were eight replicates for each pellet diameter and texture tested (HDP, $n = 8$; SMP, $n = 8$). Similarly, in the L expt., eight culture vessels each containing three lobsters were randomly supplied one of the seven different feed lengths (HDP, $n = 8$) each day of the seven days of testing (see Supplementary Materials—Table S2).

2.3. Feeding and Feed Waste Collection

Lobsters were acclimated to the experimental feeds for two days after allocation to the culture vessels. The acclimation to the pellet diameter test (D expt.) included feeding with an equal mix of seven diameters of HDP on one day and an equal mix of seven diameters of SMP on the other, with a random order of feeding with HDP or SMP. The acclimation to the pellet length test (L expt.) included feeding lobsters with an equal mix of pellets of seven lengths for two days after allocation. Each vessel was supplied with a ration at 0.5% lobster WW, on a feed dry matter (DM) basis. The daily feed ration of 0.5% lobster WW was set below the optimal feeding ration of 0.8–1.2% [18] to encourage complete feed consumption. In the D expt., the feeding rations consisted of ~150, ~50, ~26, ~16, ~9, ~5 and 4 pellets from lowest to highest diameter, respectively in either HDP or SMP. In the L expt., the rations consisted of ~44, ~33, ~20, 14, 10, 6 and 4 pellets from lowest to highest length, respectively. The feeding ration was added to vessels 5 min after the beginning of the dark phase. Lobsters were allowed to feed for a period of six hours after which the feed waste was collected by siphoning. The six hours feeding time was set, to provide enough time for lobsters to feed, while maintaining feed stability for further analysis. The siphoned material was captured on a 124 µm mesh screen [17], additionally an identical screen was used on the water outlets continuously, to trap any fine feed particles during the six hours of feed exposure time. The collected samples were gently rinsed with deionised water to remove salts and all NFRW were carefully separated from the total feed waste after careful visual inspection. The feed texture and feed water stability allowed for precise differentiation between FRW and NFRW for both SMP and HDP as the pellets remained intact unless manipulated/macerated. All feed wastes were kept frozen at −20 °C until DM determination. Additionally, feed DM loss due to nutrient leaching was examined in all feeds tested in both the diameter and length experiments at the equivalent feed ration amount of 0.5% of experimental lobsters WW. Briefly, each feed was added to the same culture vessels in triplicate, without lobsters. Each of the triplicate samples were collected after six hours of exposure to the experimental conditions and DM loss was determined. All feeds and feed waste collected were dried at 105 °C for 24 h [19] to determine DM. After correction for leachate loss, NRFW and FRW were expressed as a percentage of the delivered feed ration. The apparent feed intake (AFI) was calculated as = Feed delivered − (NRFW + FRW). The total feed waste (NFFW + FRW) was prior corrected for DM leachate before calculating the AFI as described previously [9]. The feeding efficiency was expressed as 100% − ((100% × FRW)/(AFI + FRW)) and was calculated to investigate how pellet dimensions affected FRW and its correlation with AFI. NFRW was excluded from calculations, to focus solely on the ingestion related aspects.

2.4. Data Analysis

All tanks were exposed to each of pellet diameters and textures in the D expt. (see Supplementary Materials—Table S1) and each pellet length in the L expt. (see Supplementary Materials—Table S2) in randomised order. The used method allowed for collection of 112 (8 per diameter) replications in the D expt. and 56 (8 per length) in L experiment. Linear regression models were used to analyse the relationship between pellet diameter or length and feed waste (NFRW and FRW) expressed as a percentage of feed delivered for HDP and SMP in the D expt. and HDP in the L experiment. The feeding efficiency data were fit to linear and logarithmic regression, for the D expt. and L expt., respectively. Apparent feed intake and feed leaching rate were analysed with linear regressions and ANOVA was used for means comparison. Data were tested for homogeneity of variance with the Shapiro–Wilk W test and arcsine or Log10 transformed when normality was not met. In cases where transformation was not effective, non-parametric Kruskal–Wallis test was used for data comparison and the raw data was fitted to the regressions. An ANCOVA using texture as fixed factor and pellet diameter as covariate was used to compare slopes and intercepts of regression lines of average feeding efficiency and pellet diameters between HDP and SMP.

3. Results

3.1. Diameter Experiment

The NFRW and FRW measured for HDP resulted in significant linear regressions (Figure 1). The amount of NFRW decreased with an increase in pellet diameter, whereas the reverse pattern was observed for FRW. The point of intersection between the two regression lines denoted the pellet diameter at which equal amounts of NFRW and FRW existed. Like HDP, the FRW for SMP increased linearly with larger pellet diameter (Figure 2); however, there was no significant pattern for NFRW with changes in pellet diameter (Table 1). The increase in FRW with larger pellet diameter for both HDP and SMP meant that the feeding efficiencies linearly decreased for both feed textures (Figure 3). There was no significant interaction between texture and diameter (ANCOVA regression lines; d.f. 1,13, F = 0.4, p = 0.545), indicating that there were no differences in the rates at which feeding efficiencies decreased between HDP and SMP. The AFI of lobsters did not differ when fed different pellet diameters (Table 1), indicating that on average the same total amounts of feed waste were produced irrespective of pellet diameters. Likewise, irrespective of pellet diameter and feeding efficiency, the AFI of lobsters fed SMP did not differ, indicating feed waste production did not differ. In general, DM leaching decreased with increasing pellet diameters for both HDP and SMP, and the pairwise comparison showed significant differences, with highest leaching in diameters 4.3 and 1.5 mm, and lowest in 9.5 and 7.0 mm for HDP and SMP, respectively. A significant linear regression was obtained for SMP only (Table 1).

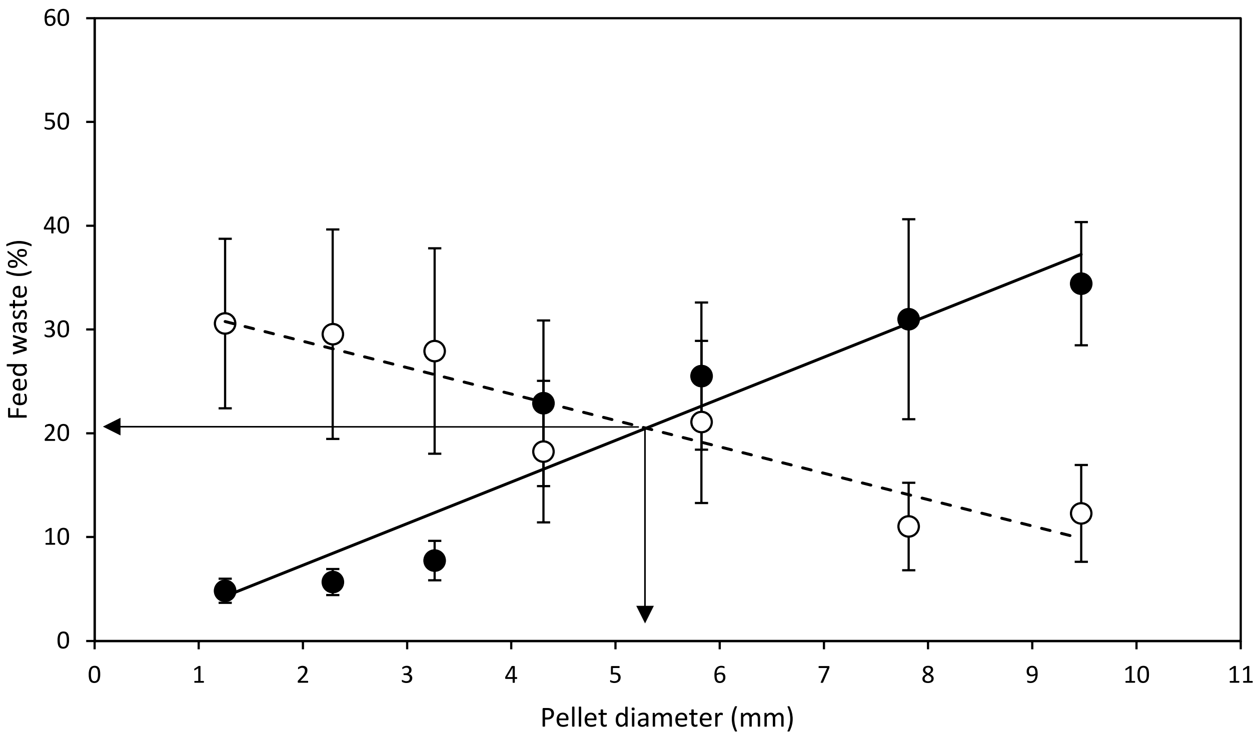

Figure 1. Effect of pellet diameter on hard and dry pellet (HDP); (1) non-feeding related waste (NFRW), white symbols; and (2) feeding related waste (FRW), black symbols. The dashed line shows linear regression for NRFW y = −2.5x + 34.0, R^2 = 0.105, p = 0.015; the solid line shows linear regression for FRW y = 4.0x − 0.7, R^2 = 0.32, p = 0.000. Intercept of regressions, x = 5.3, y = 20.5. Values are average, error bars denote S.E.

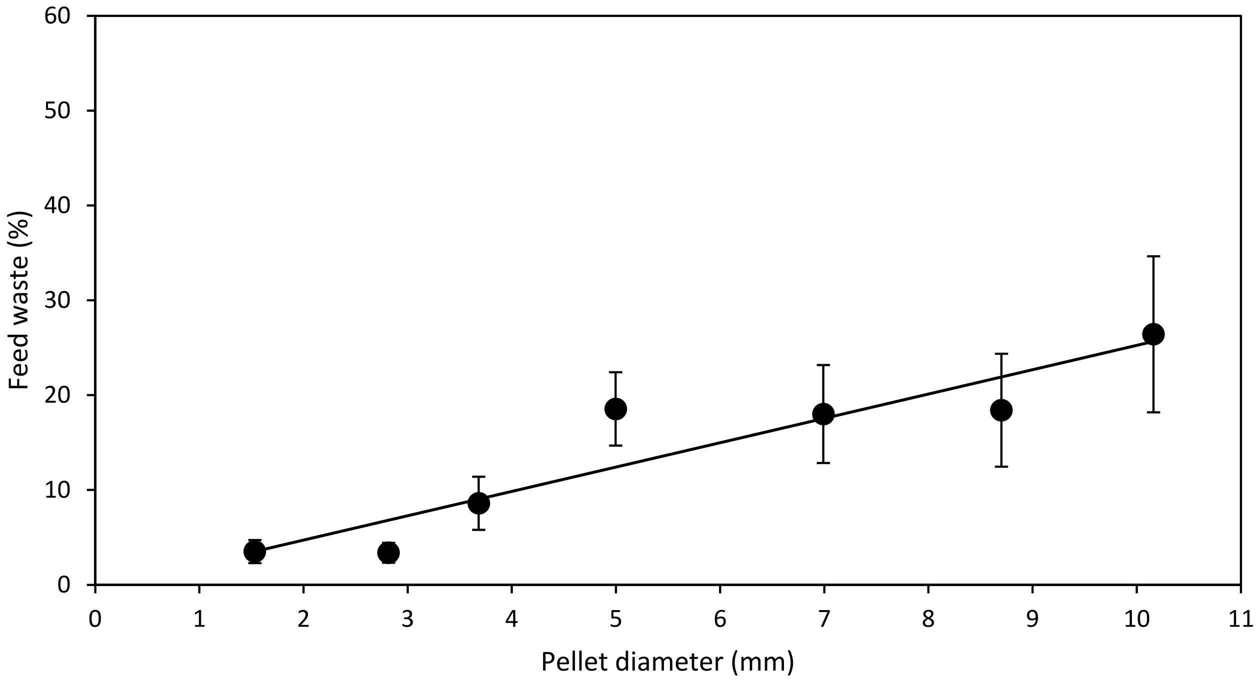

Figure 2. Effect of pellet diameter on soft and moist pellet (SMP) feeding related waste (FRW). The line shows linear regression for FRW y = 0.26x − 0.4, R^2 = 0.26, p = 0.000. Values are average, error bars denote S.E.

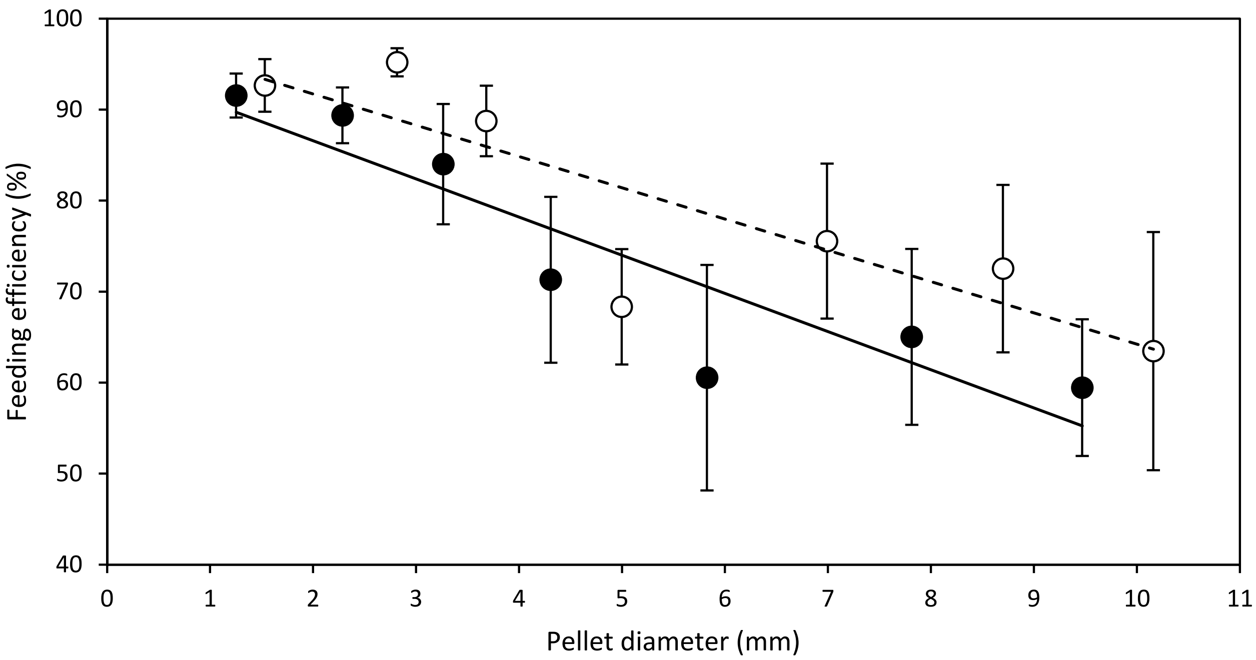

Figure 3. Effect of pellet diameter on feeding efficiency of (1) soft and moist pellet (SMP), white symbols, the dashed line shows linear regression y = −3.4x + 98.6, R^2 = 0.193, p = 0.001 and (2) hard and dry pellet (HDP), black symbols, the solid line shows linear regression y = −4.2x + 95.0, R^2 = 0.222, p = 0.000. Values are average, error bars denote S.E.

Table 1. Apparent feed intake (AFI) and feed leaching rate in juvenile *Sagmariasus verreauxi* when supplied varied feed diameters of HDP (hard dry pellet) and AFI, NFRW (non-feeding related waste) and leaching rate when supplied varied feed diameters of SMP (soft moist pellet). Data represents mean ± S.E. (n = 8 for FI and NFRW; n = 3 for leaching rate), significant differences between means (ANOVA or Kruskal–Wallis (K-W), $p < 0.05$) are marked with superscript and significant linear regressions ($p < 0.05$) are marked with asterisk (*). Survival was at 100%. Bold digits represent feed diameter sizes.

					Diameter (mm)										
Parameter	**Texture**	**1.3**	**2.3**	**3.3**	**4.3**	**5.8**	**7.8**	**9.5**	**Test**	**a**	**b**	**R^2**	**df**	**F/Chi-Sq**	***p***
AFI (% DW)	HDP	64.6 ± 8.8	64.8 ± 10.8	64.3 ± 11.3	58.9 ± 9.9	53.4 ± 12.6	58.0 ± 10	53.3 ± 8.2	ANOVA				6,49	0.290	0.939
									Regression	−1.5	66.8	0.021	1,54	1.179	0.282
Leaching rate (% DW * 6 h^{-1})	HDP	8.0 ± 0.2 ^{a}	6.9 ± 0.8 ^{ab}	8.6 ± 0.9 ^{a}	8.7 ± 0.3 ^{a}	7.3 ± 0.4 ^{ab}	8.6 ± 0.0 ^{a}	5.2 ± 0.1 ^{b}	ANOVA				6,49	6.273	0.002 *
									Regression	−0.2	8.6	0.149	1,19	3.321	0.084
		1.5	**2.8**	**3.7**	**5.0**	**7.0**	**8.7**	**10.2**							
AFI (% DW)	SMP	67.1 ± 11.1	76.3 ± 6.2	73.4 ± 6.6	49.4 ± 10.7	66.5 ± 9.6	59.0 ± 11.0	58.4 ± 13.1	ANOVA				6,49	0.687	0.661
									Regression	−1.5	72.9	0.026	1,54	1.465	0.231
NFRW (% DW)	SMP	29.4 ± 10.5	20.3 ± 5.6	18.0 ± 5.0	32.0 ± 8.6	15.5 ± 5.0	22.6 ± 7.0	15.2 ± 6.3	Regression	−1.0	27.5	0.023	1,54	1.275	0.264
Leaching rate (% DW * 6 h^{-1})	SMP	12.3 ± 0.2 ^{a}	10.0 ± 0.3 ^{ac}	9.1 ± 0.6 ^{abc}	8.2 ± 0.2 ^{abc}	6.1 ± 0.4 ^{b}	7.6 ± 0.3 ^{bc}	6.7 ± 1.6 ^{bc}	K-W				6,20	14.615	0.023 *
									Regression	−0.6	11.7	0.601	1,19	28.611	0.000 *

3.2. Length Experiment

The NFRW and FRW measured for HDP showed significant linear regressions (Figure 4). The NFRW decreased with increase in pellet diameter, whereas the reverse pattern was observed for FRW. The point of intersection between the two regression lines denoted the pellet length at which equal amounts of NFRW and FRW existed.

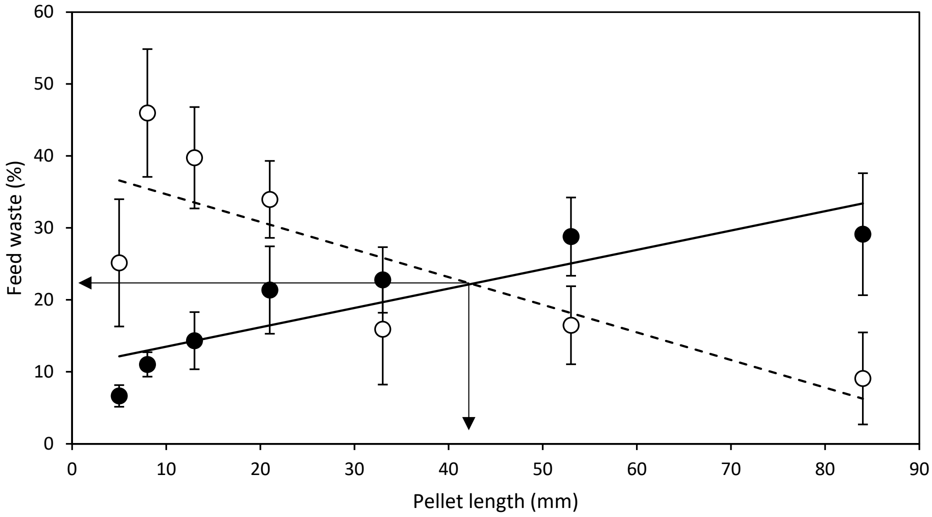

Figure 4. Effect of pellet length on hard and dry pellet (HDP) (1) non-feeding related waste (NFRW), white symbols and (2) feeding related waste (FRW), black symbols. The dashed line shows linear regression for NFRW y = −0.38x + 38.5, R^2 = 0.197, p = 0.001; the solid line shows linear regression for FRW y = 0.26x + 10.8, R^2 = 0.207, p = 0.000. Intercept of regressions, x = 42.4, y = 22.2. Values are average, error bars denote S.E.

The feeding efficiency was highest at the smallest length (Figure 5). Like pellet diameter and despite the significant effects of pellet length on feed waste type and feeding efficiency, the AFI was not significantly different (Table 2), indicating similar levels of the total waste produced. As with pellet diameter, the leaching of DM decreased with pellet length and showed significant differences in pairwise comparison, with the highest leaching in 5 and lowest in 84 mm length. The leaching data showed significant linear regression (Table 2).

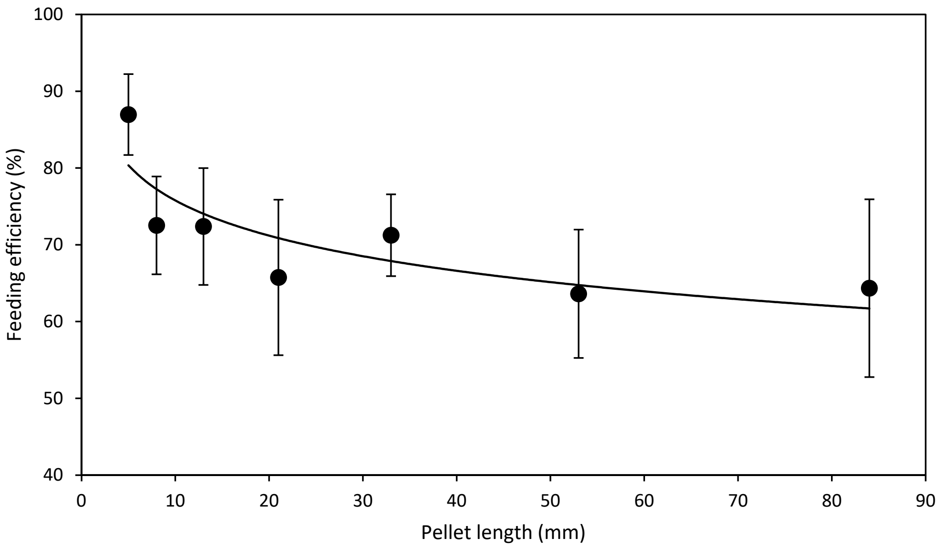

Figure 5. Effect of pellet length on hard and dry pellet (HDP) feeding efficiency, the line shows logarithmic regression y = −6.6ln(x) + 91.0, R^2 = 0.075, p = 0.041. Values are average, error bars denote S.E.

Table 2. Apparent feed intake (AFI) and feed leaching rate in juvenile *Sagmariasus verreauxi* when supplied varied feed lengths of HDP (hard dry pellet). Data represents mean ± S.E. (n = 8 for AFI; n = 3 for leaching rate), significant differences between means (ANOVA, $p < 0.05$) are marked with superscript and significant linear regressions ($p < 0.05$) are marked with asterisk (*). Survival was at 100%.

		Length (mm)													
Parameter	**Texture**	**5**	**8**	**13**	**21**	**33**	**53**	**84**	**Test**	**a**	**b**	**R^2**	**df**	**F/Chi-Sq**	***p***
FI (% DW)	HDP	71.4 ± 7.8	53.1 ± 8.1	56.2 ± 6.7	55.9 ± 7.0	68.7 ± 6.8	64.5 ± 6.5	70.1 ± 9.0	Anova				6,49	1.044	0.409
									Regression	0.1	58.9	0.026	1,54	1.427	0.238
Leaching rate (% DW * 6 h^{-1})	HDP	10.0 ± 0.3 ^{a}	8.9 ± 0.4 ^{ac}	7.7 ± 0.4 ^{bcd}	7.7 ± 0.3 ^{bcd}	8.1 ± 0.4 ^{abc}	6.2 ± 0.5 ^{bd}	6.1 ± 0.4 ^{d}	Anova				6,49	12.365	0.000 *
									Regression	−0.04	9.1	0.605	1,19	29.109	0.000 *

4. Discussion

The feed intake of formulated feeds by spiny lobsters has been described as "messy" due to the breakdown of feed into smaller particles while manipulating and macerating pellets [2,20,21], leading to high amounts of feeding related waste (FRW). For spiny lobsters, particularly *J. edwardsii*, it was estimated that up to 50% of formulated feed was wasted by inefficient feeding [1]. However, there were some indications that FRW may be reduced by optimising feed dimensions for *P. argus* [4], *P. ornatus* [7], and *J. edwardsii* [1]. Thus, optimizing feed dimensions, may improve feeding efficiency and perhaps increase feed intake in spiny lobsters. The present study is the first to provide a thorough account of the relationship between different feed physical characteristics and feeding efficiency by considering the nature of the feed waste produced by the spiny lobster, *S. verreauxi*.

Here we show that feed diameter and feed length of HDP affected the type of feed waste produced by *S. verreauxi*. An increase in FRW irrespective of texture, suggested a reduced feeding efficiency as pellet diameter increased, as was observed for feed length with HDP. However, the increase in feeding efficiency due to low FRW for small diameter pellets did not improve feed intake as the total amount of feed waste was not reduced, i.e., improved FRW was offset by a corresponding increase of NFRW. Overall feed waste varied from 32 to 57% irrespective of tested dimension (diameter or length) or texture. The minimal FRW was observed for the smallest pellet diameters (SMP and HDP) and lengths (HDP) indicated that lobsters were efficiently consuming these pellets whole after locating them. Similarly, for *J. edwardsii* it was observed that lobsters could also sweep up multiple small pellets dispersed on the tank floor with the pereiopods and pass them to mouthparts for consumption [1]. Similarly, for *P. ornatus*, FRW was a function of pellet diameter and less FRW was produced when juvenile lobsters (50–60 g) were fed small 3 mm diameter HDP, when compared to 9 mm diameter HDP [7].

At the lowest diameter (1.3 mm—HDP and 1.5 mm—SMP) investigated in the current study, the set ration of 0.5% BW consisted of ~150 pellets and the highest diameter (9.5 mm—HDP and 10.2 mm—SMP) consisted of 4 pellets. In the L expt., the 0.5% BW rations consisted of ~43 pellets for lowest length (5 mm) and 4 for highest (84 mm). The expectation that the higher number of pellets for the smallest feed diameter or length would favour encounter and therefore more feeding, did not occur. The effect of feed encounter was probably offset by the fact that small pellets lose attraction at a faster rate than larger pellets because of the higher relative surface area exposed to leaching. This is supported by the general observed pattern of faster dry matter loss to leaching by smaller size pellets. In addition, the smaller pellets would require more handling, specifically to grasp and hold with first pair of walking legs and III maxillipeds for ingestion [3,6]. It is highly likely that the combined effect of extended feed handling time and rapid attractant leaching in small diameter/length pellets may have led to a decrease in motivation to feed and in consequence to an increase in NFRW. The higher NFRW for small HDP in both the diameter and length experiments, supports the argument that while feed encounter is higher with small pellets, the duration of attraction to the feed is shorter. A high number of small pellets to consume in a limited time frame of attraction, inevitably leads to more NFRW. However, there were no clear pattern for the NFRW for SMP of different diameters, indicating that feed diameter did not influence the amounts of NFRW produced with SMP. The less pronounced results for NFRW in SMP may be the outcome of different SMP pellets characteristics. For example, it may be possible that the leaching rates of attractants in SMP is different to HDP, which requires further investigation. For both SMP and HDP in the D expt., it was clear that optimising feed diameter and for HDP in the L expt., optimising feed length, improves feeding efficiency; however, it did not result in improvement of feed intake due to an increase in uneaten feed (NFRW).

Lobsters were fed at 0.5% lobsters BW to exclude the possibility of overfeeding; thus, it is highly unlikely that lobsters were fully satiated [18]. However, a significant amount of this ration was not consumed, irrespective of feed size and texture. At one extreme, a less than optimal feed intake as observed by the reduction in feeding efficiency with increase in feed size suggest the need to standardize feed size with respect to lobster size. At the other extreme, the loss of attraction to feed and/or poor gustatory stimulation provides a strong valid explanation for the lack of improvement in feed intake when feeding efficiency was optimised. For example, it is well known that after immersion in water, attractants quickly leach out feed and consequently, lobsters lose interest in consumption [3,4]. The complex nervous and sensory system of spiny lobsters dictates wide behavioural repertoire. Their feeding behaviour includes detection, distinguishing, search and location of the feed. To stimulate this response and in consequence feed intake, odour signal must be attractive [22,23]. Another important aspect is spiny lobsters learning abilities, meaning that they can modify their reaction to attractants based on previous experiences [3,5,24]. Future research in feed development for juvenile lobsters should investigate solutions to improve feed intake by prolonging the attractiveness of feeds. Although, utilising multiple feeding frequencies of the feed ration may represent a good strategy to keep feed attractive over time and thus, promote feed intake [25].

5. Conclusions

Supported with significant patterns from regression analyses, we found some evidence to suggest that feeding efficiency may be optimised through manipulating feed dimensions, although feed intake was unaffected. This finding suggests that currently a counteractive interaction exists between pellet size and feed attractiveness and suggests improving attractiveness would further enhance feeding. Feed waste categorisation as FRW and NFRW is a path for indirect observations of *S. verreauxi* feeding behaviour, although in the present study, we were unable to provide an ideal pellet size. Future research should aim at optimising feed dimensions simultaneously to support efficient feeding whilst enhancing prolonged attraction/gustatory stimulation. However, a multiple feeding frequency strategy may be an alternate strategy to overcome the loss of feed attraction encountered in feeds with high feeding efficiencies.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fishes8110553/s1, Table S1: L expt. feeding randomisation for fourteen consecutive days; experimental feeds included seven diameters (Ø) HDP (hard dry pellet) and seven diameters (Ø) SMP (soft moist pellet). Table S2: D expt. feeding randomisation for seven consecutive days; experimental feeds included seven lengths HDP (hard dry pellet).

Author Contributions: Conceptualization, K.K.-K., Q.P.F., M.B.C., A.J.T., C.G.C. and G.G.S.; Methodology, K.K.-K., Q.P.F., M.B.C., A.J.T., C.G.C. and G.G.S.; Software, K.K.-K.; Validation, K.K.-K., Q.P.F., M.B.C., A.J.T., C.G.C. and G.G.S.; Formal analysis, K.K.-K.; Investigation, K.K.-K., Q.P.F., M.B.C., A.J.T., C.G.C. and G.G.S.; Resources, Q.P.F., M.B.C., A.J.T., C.G.C. and G.G.S.; Data curation, Q.P.F. and M.B.C.; Writing—original draft preparation, K.K.-K.; Writing—review and editing, Q.P.F., M.B.C., A.J.T., C.G.C. and G.G.S.; Visualization, K.K.-K., Q.P.F., M.B.C., A.J.T., C.G.C. and G.G.S.; Supervision, Q.P.F., M.B.C., A.J.T., C.G.C. and G.G.S.; Project administration, Q.P.F., M.B.C., A.J.T., C.G.C. and G.G.S.; Funding acquisition, Q.P.F., C.G.C. and G.G.S. All authors have read and agreed to the published version of the manuscript.

Funding: Rock Lobster research at IMAS is supported by the Australian Research Council Industrial Transformation Research Hub (project number IH12100032).

Institutional Review Board Statement: Ethical review and approval are not required for research study with lobsters in Australia.

Data Availability Statement: Data are contained within the article and Supplementary Materials.

Acknowledgments: We thank the staff at the Australian Research Council Industrial Transformation Research Hub for assistance in the culture of lobsters and construction of systems.

Conflicts of Interest: The authors declare no conflict of interest.

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