Comparative survival and growth performance of European lobster Homarus gammarus post-larva reared on novel feeds

Received: 4 August 2019 | Revised: 2 September 2019 | Accepted: 18 September 2019

DOI: 10.1111/are.14351

ORIGINAL ARTICLE

Aquaculture Research WILEY

Comparative survival and growth performance of European lobster *Homarus gammarus* post-larva reared on novel feeds

James Hinchcliffe[1,2] | Adam Powell[1] | Markus Langeland[3] | Aleksandar Vidakovic[3] | Ingrid Undeland[2] | Kristina Sundell[1] | Susanne P. Eriksson[1]

[1]Department of Biological and Environmental Sciences - Kristineberg, University of Gothenburg, Fiskebäckskil, Sweden

[2]Department of Biology and Biological Engineering - Food and Nutrition Science, Chalmers University of Technology, Gothenburg, Sweden

[3]Department of Animal Nutrition and Management, SLU, Uppsala, Sweden

Correspondence
James Hinchcliffe, Department of Biological and Environmental Sciences - Kristineberg, University of Gothenburg, Kristineberg 566, SE-451 78 Fiskebäckskil, Sweden.
Email: James.Hinchcliffe@bioenv.gu.se

Funding information
Mistra, Grant/Award Number: Dnr DIA 2103/75

Abstract

One approach to ongrow juvenile European lobster, *Homarus gammarus*, is to utilize land based rearing systems, incorporating automated feeding, individual culture and provision of stable pelleted feeds, preferably using sustainable ingredients. We initiated three feeding experiments to investigate the general suitability of ingredients produced from seafood by-products as novel feeds for *H. gammarus*, in terms of promoting survival, development and growth of post-larval lobsters from post-larvae (PL) stage IV to the first juvenile stage (stage V). The first experiment was designed to screen an array of candidate, locally produced, novel protein sources on growth performance parameters. This initial experiment revealed that PL reared on a raw (i.e. wet, unprocessed shrimp) feed used as a reference showed superior performance to those reared on experimental feeds containing fishmeal, herring protein isolate or mussel meal; however, a novel type of shrimp meal, produced by flocculation from waste water, promoted the best PL performance of any experimental feed. A second experiment was designed to test the effect of drying method and to optimize the form of a wet shrimp reference feed used by lobster hatcheries. This showed that the performance of PL reared on experimental freeze-dried shrimp feed was not significantly different to those reared on the wet, unprocessed shrimp used as a reference feed. However, lobsters offered experimental oven-dried shrimp feed (with or without an immune supplement) resulted in significantly lower survival or growth performance. A third and final experiment was designed in an attempt to improve a candidate herring-based protein source, by supplementing with nutrients found in shrimp. However, the results showed that PL reared on the wet reference shrimp feed still showed superior growth and survival than those reared on a herring feed alone, or supplemented with additives found in shrimp meal (either glucosamine, astaxanthin or both supplements combined). The high survival and growth, low incidence of moulting problems and high availability of waste shrimp material, suggest that non-heat-treated shrimp products are a promising feed ingredient for post-larval European lobsters.

KEYWORDS
aquaculture, composition, homarid, moulting, nutrition

Hinchcliffe and Powell have contributed equally to this manuscript.

1 | INTRODUCTION

Cultivation of the European lobster (*Homarus gammarus*) currently operates at modest scales. Following larval metamorphosis through three pelagic Zoeal stages in upwelling tanks, post-larval lobsters may be ongrown in communal or separate benthic rearing systems (reviewed by Nicosia & Lavalli, 1999). The aim of farming this species could be divided into two complimentary routes: the improvement or remediation (restocking and stock enhancement) of the lobster capture fishery by releasing juvenile lobsters into the wild (Ellis et al., 2015) or the emerging subsector of commercial lobster farming (e.g. Drengstig & Bergheim, 2013). Long-term ongrowing of cannibalistic *Hommarus* spp. juveniles has proved challenging to realize and operate at the technical levels and scales necessary for individual rearing, threatening economic viability (Aiken & Waddy, 1995). One approach may follow extensive sea-based culture, in which juvenile lobsters obtain nutrition from natural food such as plankton and fouling organisms (e.g. Daniels et al., 2015; Powell & ELCE, 2016). An alternative approach may be to improve the design of land-based rearing systems by reducing costs and benefitting from economies of scale (Drengstig & Bergheim, 2013; Powell & ELCE, 2016). Alongside consistent and optimal composition and price, a physically stable dry feed (suitable for automated feeding) would also permit cheaper storage and labour costs (Cho, 1990; Fiore & Tlusty, 2005). With recent interest in expanding *H. gammarus* hatcheries (Drengstig & Bergheim, 2013), future lobster feeds could include a wide range of alternative ingredients to fishmeal (Glencross, Booth, & Allan, 2007), whilst the use of local raw materials (e.g. seafood industry by-products) would also improve sustainability (Arnason et al., 2015).

Formulated feeds for juvenile *H. gammarus* are proprietary, confidential within hatcheries and have yet to enter commercial production (European Lobster Centre of Excellence, ELCE, *pers. comm*). Indeed, most contemporary juvenile lobsters, destined for release into the sea, are generally reared for several weeks in Aquahive systems, using live or sterilized copepods (e.g. Daniels et al., 2015; Shellfish Hatchery Systems Ltd, 2017). Prior to this, juvenile lobsters were ongrown in small compartments (e.g. 'Orkney Cells') and were variously fed sterilized mysids, euphausids or *Artemia salina*, wet feed such as mussels, squid or periwinkles and commercially available aquaculture feeds (e.g. Burton, 2003; Schmalenbach, Buchholz, Franke, & Saborowski, 2009). Formulated, dry pelleted feeds are widely used in established crustacean sectors, such as Penaeid shrimp hatcheries and ongrowing facilities (Wickins & Lee, 2002). However, these feeds are species-specific, produced with a wide knowledge of nutritional requirements. Total or partial replacement of live or wet feed has been proven for American lobster, *Homarus americanus* larvae and post-larval stages (Fiore & Tlusty, 2005; Tlusty, Fiore, & Goldstein, 2005), using alternative protein sources (Floreto, Bayer, & Brown, 2000). More recently, dry pelleted feeds have been used to successfully rear *H. gammarus* larvae (Powell, Hinchcliffe, Sundell, Carlsson, & Eriksson, 2017). However, it is challenging to understand the nutritional requirements via observations and changes in biochemical composition, occuring during periods of nutritional and environmental stress, which can change nutrient demand (Anger 1998, Torres et al., 2002). Suboptimal feed can cause a variety of challenges when rearing lobsters, for example 'Moult death syndrome' (MDS), which causes mortality by entrapment in the exuviae. Prior studies with *Homarus* spp. juveniles have shown that the incidence of MDS could be reduced by including a source of phosphatidylcholine in the diet, such as lecithin (e.g. Kean, Castell, Boghen, D'Abramo, & Conklin, 1985). Supplementation of a simple fish based feed with powdered crustacean exoskeleton or a chitin source has also reduced gut bacterial load and increased survival in crabs and shrimp (Niu et al., 2013; Powell & Rowley, 2007). The addition of astaxanthin into formulated feed has also increased growth and survival in crustaceans, including lobsters (Lim, Yusoff, Shariff, & Kamarudin, 2017).

In the present study, we aimed to examine the growth, moulting and survival success of recently metamorphosed lobster larvae, reared through post-larval (PL) stage IV to first juvenile stage V, and fed novel feeds through a series of objectives, which were formulated as experiments. Objective one compared feeds, which incorporated novel types of feed ingredients produced from commercial seafood by-products, sourced from local industry and processed by predefined methods (mussel, shrimp and herring processors). Objective two was designed to optimize the form of raw shrimp, which was the best performing feed from objective one. Finally, objective three was designed to increase the suitability of other feed protein sources (namely, herring by-products) by supplementing with nutrients abundant in crustacean (shrimp) exoskeleton, such as the chitin monomer glucosamine and the carotenoid astaxanthin.

2 | MATERIALS AND METHODS

2.1 | Broodstock and larval rearing

Adult gravid *Homarus gammarus* broodstock was sourced and maintained as described in Powell et al., (2017). Larvae were collected and reared to post-larval (PL) stage IV as described in Powell et al., (2017) with modifications. Larvae were procured from one female per experiment to reduce variation and were stocked sequentially into four cylindro-conical hoppers (70L) over 2–3 days at an initial density of 1000–5000 larvae per hopper. Larvae were fed with 1 g of 'B1' Otohime feed (Marubeni Nisshin Feed Company Ltd) every 3 hr (8 g/day) and supplemented with *ca.* 2 g wet weight, Planktonic AS feed (700-1000 μm grade) three times per day. After 14 days, late stage Z3 larvae were placed into floating Aquahive trays (Shellfish Hatchery Systems Ltd), with PL (and any remaining moult) randomly but equally recruited (i.e. according to age and specific hopper origin) across 4–5 discrete Orkney Cell matrices (Shellfish Hatchery Systems Ltd) on the day of metamorphosis (n = 50). Recruited PL were limited to those that possessed both chelae and exhibited no obvious deformities, and which also metamorphosed within 6 days of being moved to Aquahive trays. PL that died within 24 hr of recruitment, or 24 hr of subsequent T_0 measuring, were replaced with

PL from the same brood. Recruitment across an experiment was completed within 8–9 days.

2.2 | Ethics statement

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to and the appropriate ethical review committee approval has been received.

2.3 | Post-larvae experimental system and experimental design

The same flow through system was used to provide water quality and lighting as described in Powell et al. (2017). For each feed treatment, Orkney Cell matrices (5 × 10 blocks) were labelled alphanumerically and placed inside circular tanks (*ca.* 100 L volume) with an external standpipe of sufficient height to permit *ca.* 100 ml volume of water in each Orkney cell, and *ca.* 30-cm depth of water underneath the matrix. Inflowing water (19°C, 2 L/min across two inflows per tank) from a single header tank was provided equally to all tanks and monitored every 15 min using a Sensdesk sensor and online recording system (HW group s.r.o., Czech Republic). Each circular tank was also aerated gently from the base (*ca.*1 L/min). The insides of Orkney cells were individually cleaned daily with a large pipette to remove uneaten feed, exoskeletons and dead PL, and were additionally gently flushed from above with excess water, twice per day (09:00 and 17:00). Concentrations of nitrite and ammonium were maintained below 6 and 2.5 µmol/L respectively. Every week, the undersides of the matrix were cleaned using a scrubbing brush, and tank bottoms syphoned to remove debris. PL were fed to apparent excess (up to 2 × 2 mm experimental pellets per day, or *ca.* 2 × 3 mm cube of defrosted shrimp *Pandalus borealis* abdomen) so that feed particles were always available, and a quantity remained uneaten upon cleaning. The duration of all experiments was designed to rear stage IV PL to juvenile stage V within a 30-day test period. After moulting to stage V, exoskeletal material was retained for 24 hr, to allow sufficient time for the lobster to ingest the moult. The following three experiments and associated test feeds were conducted.

2.4 | Experiment one - screening of by-product-derived ingredients

Post-larvae were offered excess wet shrimp abdomen (R, wet shrimp reference feed), and four additional treatments: isocalorific and isonitrogenous commercial fishmeal (F), or experimental shrimp meal (S; spray-dried), herring meal (H; freeze-dried) or mussel meal (M; oven-dried) based feeds (Table 1).

2.5 | Experiment two – effect of drying method

Post-larvae were offered shrimp abdomen (R, wet shrimp reference feed), fed ad libitum, and three additional experimental shrimp-based treatments: freeze-dried (FD), oven-dried (OD) and oven-dried with a Bio-Mos® (Mannan Oligosaccharide), a prebiotic with immunostimulant properties (ODS). The latter two feeds were included to ascertain any benefits from a prebiotic, by comparing performance strictly between OD and ODS.

2.6 | Experiment three – supplement assessment

Post-larvae were offered shrimp abdomen (R, wet shrimp reference feed) and four additional experimental treatments: isocalorific and isonitrogenous freeze-dried herring meal (H), herring meal with Astaxanthin additive (HA), herring meal with Glucosamine additive (HG) and herring meal with both additives (HAG; Table 1c).

2.7 | Feed production

For experimental feed treatments used in Experiments 1 and 3, isocalorific and isonitrogenous pellets were formulated and produced (Table 1). Three novel protein sources (shrimp by-product meal, herring by-product meal and mussel meal) were used as a replacement for fishmeal and added at an inclusion rate that contributed towards 70% of the total crude protein of the formulated feeds. Shrimp meal was produced on site at a shrimp boiling and peeling company by flocculation of shrimp boiling water with carrageenan according to the principle of Forghani, Bordes, Ström and Undeland (2020). Flocs were separated by flotation and subsequently spray dried (Anhydro Lab S3 spray dryer, Forghani et al. in manuscript). Herring by-product meal was produced by the pH-shift process (see Undeland, Kelleher and Hultin, 2002; Hinchcliffe, Carlsson, Jönsson, Sundell, & Undeland, 2019) followed by freeze-drying. Mussel meal was produced from a confidential method by Musselfeed AB (Sweden), comprising an oven-drying process. For control (reference) feeds and material for experiment 2, prior observations showed that juvenile and adult lobsters survived well on an *ad lib* diet of shrimp, *Pandalus borealis*, for *ca.* 1 year. A single batch of freshly caught local shrimp (Gullmarsfjorden, Sweden) was frozen at −20°C, and individual shrimp were defrosted daily prior to feeding. The cephalothorax, telson and any eggs were discarded, and small cross sections of abdomen, including both muscle and carapace, were removed. These were offered as wet (reference feed), freeze-dried or oven-dried (100°C for 24 hr) material, fed directly to PL for experiment 2. For experiments 1 and 3, defrosted shrimp was fed as a wet reference diet only, to allow comparison with growth data across the three experiments. For experiment 3, feeds were formulated using the herring meal, additional ingredients (Table 1) and experimental additions of supplements were then added (astaxanthin, glucosamine, both supplements and neither supplement). Levels of added astaxanthin were based on an extensive review by Lim et al., (2017), in this case, a high dose (350 mg/kg^{-1}) was chosen in order to observe a maximum effect since there has been no previous study on astaxanthin in a formulated diet of *H. gammarus* (Table 2). Similar doses have been used to obtain significantly higher survival in the diets of crustaceans (Yamada, Tanaka, Semeeshima, & Ito, 1990). Glucosamine addition was based on the previous study of Nui et al., (2013). For

TABLE 1 Composition of feeds in experiments 1, 2 and 3. Figures provided to two decimal places. Shading shows ingredient not used in particular experiment

Experimental diets														
	Experiment 1					Experiment 2				Experiment 3				
Ingredient g/100 g^{-1}	Reference	F	M	S	H	Reference	FD	OD	ODS	Reference	H	HA	HG	HAG
Raw shrimp	100	0	0	0	0	100	0	0	0	100	0	0	0	0
Freeze-dried raw shrimp						0	100	0	0					
Oven-dried raw shrimp						0	0	98	96					
Fish meal	0	58	8	6	10					0	8	8	8.25	6.25
Herring meal	0	0	0	0	56					0	56	56	56	56
Shrimp meal	0	0	0	63	0									
Mussel meal	0	0	68	0	0									
Wheat starch	0	3	1	2	6					0	6	1	6	1
Fish oil	0	7	2	2	3					0	3	3	3	3
Gelatine	0	6	5	6	6					0	6	6	6	6
Vitamin mineral premix	0	2	1	2	2					0	2	2	2	2
Cellulose	0	3	1	3	5					0	5	2	4	1
Monocalcium phosphate	0	4	2	4	4					0	4	4	4	4
Alginate						0	0	2	2					
Biomos						0	0	0	2					
Wheat gluten		15	10	10	6					0	8	6	8	8
CMC binder		1	1	1	1					0	1	1	1	1
Soybean lecithin		1	1	1	1					0	1	1	1	1
Glucosamine										0	0	0	0.75	0.75
Haematococcuspluvialis (dried powder)										0	0	10	0	10
Total inclusion	100	100	100	100	100	100	100	100	100	100	100	100	100	100

TABLE 2 Chemical composition of feeds utilized in experiments 1, 2 and 3. Figures provided to two decimal places. Shading shows ingredient not examined in particular experiment.

Experimental diets	Experiment 1					Experiment 2				Experiment 3				
Composition g/ 100 g^{-1}	Reference	F	M	S	H	Reference	FD	OD	ODS	Reference	H	HA	HG	HAG
DM- dry matter	22.00	92.69	93.61	92.12	94.27	22.00	99.00	99.00	99.00	22.00	91.95	92.32	91.73	92.47
Ash	5.50	10.47	12.45	11.35	3.88	5.50	25.00	29.40	28.85	5.50	3.56	3.72	3.56	3.44
GE MJ/kg	3.98	17.96	18.48	18.85	18.86	3.98	18.10	16.73	16.41	3.98	18.75	17.84	18.75	17.78
CP-crude protein	14.96	58.53	58.99	58.93	59.66	14.96	68.00	66.64	65.78	14.96	59.71	59.37	59.71	59.60
Lipid	0.88	10.09	9.97	13.67	11.56	0.88	4.00	6.99	6.88	0.88	11.51	14.48	11.51	14.40
Calculated phospholipid		1.72	1.10	1.07	1.12						1.00	1.00	1.00	1.00
Ca	0.50	2.36	0.96	1.36	1.44	0.50	2.27	3.77	3.71	0.50	1.40	1.40	1.40	1.36
Calculated glucosamine											0.00	0.00	0.75	0.75
Calculated astaxanthin											0.00	0.35	0.00	0.35
Essential AA %	5.49	24.94	26.42	27.04	31.72	6.73	30.57	30.52	29.94	6.25	28.42	27.76	28.42	27.81
Arginine	0.60	2.73	3.45	3.31	3.29	1.26	5.71	5.61	5.49	0.72	3.29	3.21	3.29	3.23
Histidine	0.26	1.19	1.07	1.27	1.42	0.31	1.39	1.32	1.30	0.31	1.42	1.38	1.42	1.40
Isoleucine	0.59	2.67	2.22	2.33	2.60	0.65	2.94	3.09	3.02	0.57	2.60	2.53	2.60	2.54
Leucine	0.81	3.67	3.47	3.98	4.48	1.06	4.84	4.91	4.81	0.99	4.51	4.39	4.51	4.43
Lysine	1.09	4.97	4.09	4.20	5.11	1.23	5.58	5.19	5.13	1.11	5.06	4.96	5.06	4.93
Methionine	0.30	1.36	1.23	1.31	1.80	0.39	1.76	1.84	1.81	0.39	1.78	1.76	1.78	1.75
Phenylalanine	0.49	2.23	2.09	2.53	2.35	0.61	2.78	2.78	2.73	0.53	2.39	2.30	2.39	2.34
Threonine	0.37	1.68	2.14	1.90	2.40	0.56	2.53	2.62	2.56	0.52	2.38	2.35	2.38	2.34
Valine	0.55	2.49	2.36	2.52	3.01	0.67	3.04	3.16	3.09	0.67	3.03	2.95	3.03	2.97

Abbreviations: AA, amino acids; Ca, calcium; CP, crude protein; DM, dry matter; GE, general energy content.
Experiment 1, reference = wet shrimp diet, F = fishmeal-based, M = mussel meal-based, S = Shrimp meal-based, H = herring-based.
Experiment 2, reference = wet shrimp diet, FD = Freeze-dried shrimp, OD = Oven-dried shrimp, ODS = Oven-dried shrimp with supplement.
Experiment 3, reference = wet shrimp diet, H = herring-based, HA = Herring +Astaxanthin, HG = Herring + Glucosamine, HAG = Herring + Astaxanthin + Glucosamine.

experiments 1 and 3, each diet was made in a single batch using standard feed ingredients (see Table 1) and mixed using a kitchen mixer (Hugin Titanium, Kenwood), with water added dropwise to reach the desired consistency. The resulting paste was processed through a meat grinder (Nima Maskinteknik AB, Örebro, Sweden) to produce 1.5-mm pellets, which were dried (forced air oven; 40°C, 24 hr until no further change in mass) in a drying cupboard. All dry feed used in the three trials was stored in air tight containers at 4°C and used within 7 days.

2.8 | Post-larvae measurements

Post-larvae were observed at least twice daily (09:00 and 17:00) to record mortalities and moulting to stage V with relation to stocking day, that is age in days since metamorphosis and immediate recruitment. For each treatment, this enabled calculation of survival to stage V and the time taken to moult (intermoult duration). Alternatively, mortality was recorded. Any moulting complications were also noted upon moulting to stage V (defined as stage IV PL surviving the moulting process, but moulting was incomplete, chelae were lost or other minor deformities were observed). Carapace length (CL) was measured 24 hr after recruitment, and again within 48 hr following moult to stage V, in order to calculate moult increment (percentage increase in CL from stage IV to stage V). For CL measurement, lobsters were imaged at *ca.* × 20 magnification using a stereomicroscope (Leica Wild M8, Leica Mikrosysteme Vertrieb GmbH). Measurements of carapace length (CL) were taken along the midline from the back of the eyesocket to the posterior margin of the carapace, using Dino-Lite software (AnMo electronics Corporation). Lobster wet weight (WW) was also recorded 24 hr after recruitment and again at a known age towards the end of an experiment (30 ± 5 days after metamorphosis). WW recording was advanced or delayed if individuals had moulted and were not fully calcified. Lobsters were blotted dry and weighed on a balance (Mettler Toledo XP205) to calculate WW increase, and thus growth rate (percentage increase in wet weight per day) and specific growth rate (see below).

2.9 | Feed composition

All test ingredients were analysed to determine their nutritional profiles before incorporation into experimental diets. Biochemical analysis was conducted as described in Powell et al., (2017), with the exception of energy content, which was determined through bomb calorimetry (Parr 6300; Parr Instrument Company) according to AOAC, 1995, with values expressed as MJ/kg.

2.10 | Statistical analysis and parameter definitions

Lobster performance data generated from different feed treatments were analysed and compared, within discrete experiments, using GraphPad-Prism (GraphPad Software Inc San Diego). Lobster survival is displayed as percentage alive following moult from stage IV to stage V. Similarly, moulting complications are shown as a percentage of affected as a proportion of surviving stage IV lobsters. These data were analysed using raw data between feed treatments using Fisher's Exact (i.e. Stage IV moulted vs. those that did not; or stage V expressing complications vs. those unaffected). All other parameters shown are mean ± 1 *SEM* and were tested for normality and homogeneity of variances (Kolmogorov–Smirnov test; Bartlett's test respectively) prior to analysis. All percentage data values were arcsine square root transformed prior to analysis (i.e. moult increment, the percentage CL increase between stage IV and stage V; and growth rate, the percentage increase in wet weight per day, between start [WT_0] and end [WT_1]). In addition to moult increment and growth rate, intermoult duration (number of days required to moult from stage IV to stage V), longevity (number of days required to die prior to successfully moulting to stage V) and SGR ([ln WT_1 – ln WT_0]/production period * 100) were compared between feed treatments, using ANOVA and Tukey post hoc test if data were parametric, or alternatively Kruskal-Wallace and Dunns post hoc test if data resisted transformation and did not meet parametric assumptions. Individual PL were occasionally checked to ascertain CL increase and were removed from calculations for average intermoult duration if a moult to stage V had been missed and not been recorded. The incidence of this was n = 0–3 per treatment. Feed analytical data are shown for reference only and are not qualitatively compared.

3 | RESULTS

3.1 | Observations

All feed pellets and raw shrimp feed were negatively buoyant, and sank provided water surface tension was broken and subsequently appeared physically stable following 24 hr immersion. Stage IV PL inspected and manipulated all feeds soon after introduction of feed items to individual cells, although recently metamorphosed individuals occasionally required *ca.* 48 hr for apparent weaning to occur. Although manipulation was initially only a few minutes duration, individuals were often seen returning to pellets throughout the day. PL also partially ate moulted exoskeletons in all feed treatments. Feed ingestion was confirmed by the appearance of a dark spot situated in the cephalothorax, posterior to the eyes, approximating to the location of the stomach and hepatopancreas. Towards the end of an experiment and during weighing, lobsters offered feeds containing shrimp meals (S, FD, OD, and ODS), and wet shrimp reference feed (R), generally appeared to have a more robust and colourful (green-blue) carapace, and also appeared more aggressive during handling (weighing) compared with most lobsters in the other feed treatments. However, HA and HAG feeds with added astaxanthin (experiment 3) also influenced lobster colour (orange–red colour).

3.2 | Experiment one – screening of by-product-derived ingredients

Homarus gammarus showed significant differences in survival and moulting success between the five different feed treatments in

experiment 1 (Table 3, Figure 1a). Survival was significantly lower for lobsters offered mussel feed (M), compared with all other treatments other than fishmeal feed (F; Fisher's Exact, $p < .001$). Mean intermoult duration was significantly shorter for lobsters offered wet shrimp reference feed (R) compared with all other treatments, other than the shrimp feed (S; Kruskal-Wallace, $p < .001$). Stage IV PL offered wet shrimp reference feed (R) moulted to juvenile stage V more quickly than those offered any other feed (i.e. first moult occurred on day 11), and all survivors had completed moult to stage V earlier than other treatments (i.e. all moulted by day 20; Figure 1a).

Lobster growth and development were also significantly different between feeds (Table 3). Moult increment was significantly higher for lobsters offered wet shrimp reference feed (R), compared with those offered mussel (M) or fishmeal (F) feeds (ANOVA, $p < .05–0.01$). Growth rate and SGR were also significantly higher for lobsters offered wet shrimp reference feed than in all other treatments, other than those offered shrimp meal feed (S; Table 3, Kruskal-Wallace, $p < .05–0.001$). Lobsters offered mussel (M) and herring (H) meal feed showed the lowest growth rate and SGR. Whilst the prevalence of moulting problems across treatments was not significantly different, they occurred in over 5% of lobsters offered herring and fish meal feed and two of mortalities in the herring feed treatment were due to MDS. In contrast, lobsters offered mussel (M), wet shrimp reference (R) and shrimp meal (S) feed showed zero, or very few moulting problems. Results of proximate composition of all experimental feeds are shown in Table 2 for comparison purposes. The reference wet shrimp feed (R) used in the present study had a moisture content of 78% compared with all dry experimental diets (*ca.* 7%) Analysis of dry matter showed that all dry experimental feeds were isonitrogenous and isocalorific, however, the reference shrimp diet contained higher protein (*ca.* 68% on a dry weight basis). The total ash content of the herring meal experimental diet was lower, *ca.* 4%, compared with the other experimental dry diets (*ca.* 11%).

3.3 | Experiment two - dehydration method

Lobster survival was very high in experiment 2. The majority (over 90%) of individuals successfully moulted to stage V in both reference and all experimental feed treatments, with no apparent mortality due to MDS. There were almost zero moulting complications seen across the experiment (Table 4, Figure 1b). However, lobsters fed both the wet shrimp reference (R) and experimental feeds containing freeze-dried shrimp (FD) showed improved performance, in terms of growth and development parameters, when compared to either of the oven-dried shrimp treatments (OD and ODS), as intermoult duration was significantly shorter, whilst moult increment, growth rate and SGR were significantly higher (Table 4, Kruskal-Wallace, $p > .001$). Lobsters offered wet shrimp reference feed (R) were not significantly different to those offered freeze-dried shrimp feed (FD) in any performance parameter. Similarly, lobsters offered either oven-dried shrimp feeds (OD and ODS) were not significantly different from each other in any parameter. Analysis of proximate composition in the diets utilized in the present experiment showed that nutritional characteristics presented little variation amongst the three experimental dried shrimp feeds.

3.4 | Experiment three – supplement assessment

Lobsters offered wet shrimp reference feed (R), and herring (H) meal feeds containing one additive only (Astaxanthin, HA, or Glucosamine, HG), showed high survival to stage V and were significantly higher than the Herring (H) only diet and Herring containing both supplements (Astaxanthin and Glucosamine combined, HAG). Apparent MDS caused mortality in four and seven individuals in the H and HAG treatments, respectively. Other moulting complications were significantly higher in lobsters offered the three experimental feeds (H, HA and HAG; Fisher's Exact, $p < .05$) compared with the shrimp reference (R). Compared with the shrimp reference, moulting duration was significantly prolonged for lobsters offered all experimental feeds other than HA (Kruskal-Wallace, $p < .01–0.001$). Lobsters reared on herring (H) meal feed showed the longest intermoult duration compared with the other treatments (Table 5, Kruskal-Wallace, $p < .001$). Lobster moult increment was significantly greater for those offered raw shrimp reference feed (R) than for any of the experimental feeds containing herring meal (Table 5, ANOVA, $p < .001$), however, there was no difference amongst lobsters offered any experimental herring feed. Similarly, growth rate and SGR for lobsters offered wet shrimp reference diet (R) were significantly greater than experimental feeds (Kruskal-Wallace, $p < .001$). Slowest growth rate

TABLE 3 Experiment one. Screening of by-product-derived ingredients. Comparison of survival and growth parameters for *Homarus gammarus* post-larvae. Data shown as basic survival percentage, or mean average ± 1 *SEM*. Different superscript letters denote statistically significant difference inside column values at $p < .05$ or less. Survival measured by Fishers exact. Intermoult duration, SGR and growth rate measured by Kruskal-Wallace and moult increment measured by ANOVA

Treatment	Survival to survival to stage V (%)	Moulting problems at stage V (% of survivors)	Intermoult duration (d)	Moult increment (% CL increase)	Percent growth/day	SGR
Shrimp feed (S)	78^{b} (0)	2.78^{a}	16.56 ± 0.74^{ab}	15.01 ± 0.54^{ab}	3.67 ± 0.22^{ab}	2.30 ± 0.12^{ab}
Mussel feed (M)	44^{a} (0)	0.00^{a}	17.75 ± 0.64^{b}	13.71 ± 0.65^{b}	1.93 ± 0.24^{d}	1.41 ± 0.13^{d}
Herring feed (H)	80^{b} (2)	5.13^{a}	17.38 ± 0.44^{b}	15.32 ± 0.46^{ab}	2.12 ± 0.15^{cd}	1.62 ± 0.09^{cd}
Fishmeal feed (F)	64^{ab}(0)	6.25^{a}	17.22 ± 0.39^{b}	14.63 ± 0.53^{b}	3.06 ± 0.24^{bc}	2.01 ± 0.12^{bc}
Wetshrimpreference (R)	80^{b} (0)	0.00^{a}	14.05 ± 0.37^{a}	17.01 ± 0.65^{a}	4.09 ± 0.20^{a}	2.49 ± 0.09^{a}
n	50	22–40	20–39	22–40	20–39	20–39

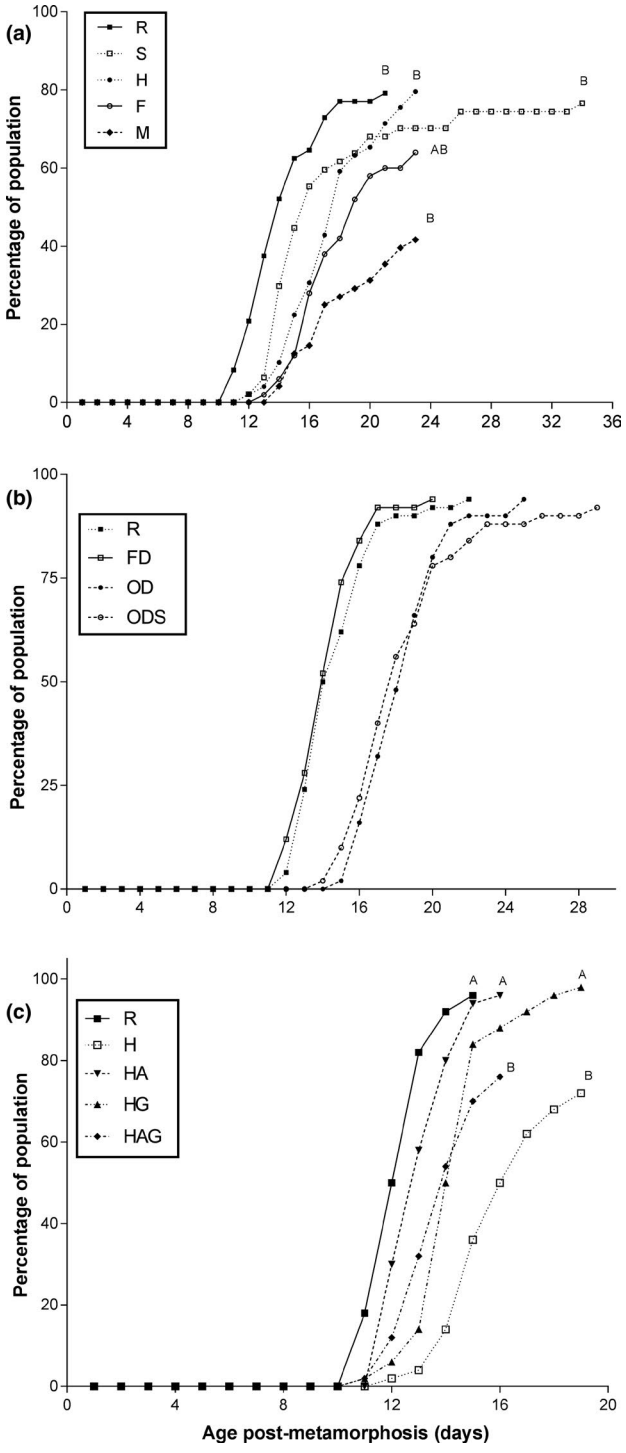

FIGURE 1 *Homarus gammarus* post-larvae. Cumulative survival and intermoult duration of postlarval stage IV successfully moulting to juvenile stage V, across three feed experiments. (a) Experiment one, R = Reference shrimp diet, F = fishmeal-based, M = mussel meal-based, S = Shrimp meal-based, H = herring-based. (b) Experiment two, FD = Freeze-dried, Wet = Raw shrimp, OD = Oven-dried, ODS = Oven-dried with immune supplement. (c) Experiment three, H = Herring without supplement, HA = Herring with astaxanthin, HG = Herring with glucosamine, HAG = Herring with astaxanthin and glucosamine. Graph lines end on the day of the last PL to moult or die, according to specific feed treatment

and SGR were observed in lobsters reared on herring meal feed (H) without any supplements. Growth rate of lobsters reared on astaxanthin supplemented feed (HA) was significantly higher than herring feed alone (H; Kruskal-Wallace, $p < .01$) and the SGR of lobsters reared on supplemented feed (HA and HAG) were also significantly higher than herring feed alone (H; Kruskal-Wallace, $p < .01$). Analysis of composition between the dry experimental feeds in experiment 3 showed that lipid levels in all herring-based diets containing the astaxanthin supplement (HA, HAG) were elevated to *ca.* 14% compared with herring-based feeds, which did not contain astaxanthin, which had a lipid profile of *ca.* 11%.

4 | DISCUSSION

The present study details satisfactory performance of stage IV PL reared on shrimp feeds, using the described experimental set-up. Despite differences in species, temperature, feed and ration, similar survival and growth parameters were achieved in comparison with related studies rearing juvenile *H. americanus* (e.g. Fiore & Tlusty, 2005).

4.1 | Experiment one

The results of experiment one suggest that a shrimp meal-based feed promoted an improved growth rate compared with feeds containing mussel meal, herring meal and standard fish meal and improved survival compared with fish meal and mussel meal-based feeds. Experimental feeds that included a source of crustaceans or crustacean meal have also tended to improve performance in juvenile *H. americanus* reared on increasing proportions of *Artemia* (Tlusty et al., 2005) krill meal (Floreto, Brown, & Bayer, 2001) and for adult animals, crab waste (Skonberg, Donahue, Bayer, Riley, & JG., 2001). Tlusty et al. (2005) suggested that poorer performing lobster feeds may be lacking in essential nutrients, compared with *Artemia* controls. Indeed, Floreto et al. (2001) correlated better performing feeds containing krill with higher proportions of carotenoids, n-3 PUFA fatty acids and arginine following carcass analysis. Nevertheless, Floreto et al., (2000) successfully reared *H. americanus* on 50% soybean meal dry diets without crustacean raw ingredient inclusion; however, no crustacean based diet was used as a reference. In the present study, all experimental feeds contained satisfactory arginine levels, but were lower compared with the reference shrimp diets (Table 2). Barrento, Marques, Teixeira, Vaz-Pires, and Nunes (2009) investigated the tissue of wild European lobster and found that arginine composition was 0.5%–2%, wet weight. For fatty acids, a significant PUFA source was provided by assuring similar levels of fish oil inclusion in all diets to avoid potential deficiency.

Phospholipids, such as phosphatidylcholines, with feed incorporating crab extract have been observed to improve survival and growth in *H. americanus* (Kean et al., 1985). An increased phospholipid content in the shrimp diets, compared with the other experimental sources, may be a reason that MDS was rarely observed (Coutteau, Geurden, Camara, Bergot, & Sorgeloos, 1997). Overall, the shrimp meal-based

TABLE 4 Experiment two. Effect of drying method. Comparison of survival and growth parameters for *Homarus gammarus* post-larvae. Data shown as raw percentage survival, or mean average ± 1 *SEM*. Different superscript letters denote statistically significant difference inside column values at $p < .05$ or less. Survival measured by Fishers exact. Intermoult duration, SGR and growth rate measured by Kruskal-Wallace and moult increment measured by ANOVA

Shrimptreatment	Survival to stage V (%)	Moulting problems at stage V (% of survivors)	Intermoultduration (d)	Moult increment (% CL increase)	Percent growth/ day	SGR
Freezedried (FD)	94	0.00^{a}	14.40 ± 0.24^{a}	20.87 ± 0.39^{a}	5.25 ± 0.35^{a}	3.10 ± 0.13^{a}
Ovendried (OD)	94	2.17^{a}	18.60 ± 0.32^{b}	17.47 ± 0.58^{b}	2.31 ± 0.06^{b}	1.77 ± 0.04^{b}
Oven dried plus supplement (ODS)	92	0.00^{a}	18.50 ± 0.43^{b}	16.89 ± 0.58^{b}	2.27 ± 0.08^{b}	1.74 ± 0.05^{b}
Wetshrimpreference (R)	94	0.00^{a}	14.87 ± 0.29^{a}	20.91 ± 0.59^{a}	4.86 ± 0.34^{a}	2.94 ± 0.14^{a}
n	50	46–47	46–47	46–47	45–47	45–47

TABLE 5 Experiment three. Supplement assessment. Comparison of survival and growth parameters for *Homarus gammarus* post-larvae. Data shown as basic survival percentage, or mean average ± 1 *SEM*. Different superscript letters denote statistically significant difference inside column values at $p < .05$ or less. Numbers in brackets denote number of mortalities caused by MDS. Survival measured by Fishers exact. Intermoult duration, SGR and growth rate measured by Kruskal-Wallace and moult increment measured by ANOVA

Treatment	Survival to stage V (%)	Moulting problems at stage V (% of survivors)	Intermoult duration (d)	Moult increment (% CL increase)	Percent growth/ day	SGR
Herring negative control (H)	72^{b} (1)	11.11^{bc}	15.86 ± 0.30^{d}	16.30 ± 0.65^{b}	1.72 ± 0.10^{c}	1.43 ± 0.07^{c}
Herring + Astaxanthin (HA)	96^{a} (4)	14.58^{c}	13.23 ± 0.16^{ab}	18.31 ± 0.51^{b}	2.27 ± 0.08^{b}	1.80 ± 0.05^{b}
Herring + Glucosamine (HG)	98^{a} (0)	2.04^{ab}	14.55 ± 0.20^{cd}	16.83 ± 0.54^{b}	2.01 ± 0.08^{bc}	1.63 ± 0.05^{bc}
Herring + Astaxanthin + Glucosamine (HAG)	76^{b} (7)	18.42^{c}	13.76 ± 0.20^{bc}	17.06 ± 0.69	2.40 ± 0.13^{bc}	1.87 ± 0.08^{b}
Shrimp reference (R)	98^{a}.(0)	0.00^{a}	12.55 ± 0.17^{a}	22.51 ± 0.57^{a}	5.08 ± 0.26^{a}	3.25 ± 0.11^{a}
n	50	36–49	36–49	36–49	25–48	25–48

feed promoted an improved growth rate compared with other protein sources; however, we believe care must be taken when utilizing a raw crustacean diet. It is possible that storage and transport conditions can degrade essential phospholipids (Fiore & Tlusty, 2005). For example, Wickins, Beard and Child (1995) observed that *H. gammarus* larvae offered frozen mysids had a higher rate of moulting problems compared with those offered a similar diet supplemented with live *Artemia*. The low ash content displayed by the experimental diet based on herring meal provided an interesting insight into a parameter that is often neglected and originates from a production step utilized in the pH-shift process (Hinchcliffe et al., 2019). The pH-shift process used to produce the protein was identified as a promising technique to produce high-quality fishmeal from bone rich by-products by the removal of ash during a separation step (Hinchcliffe et al., 2019).

4.2 | Experiment two

Experiment two, in which all feeds contained raw or processed dried shrimp, resulted in high survival, growth, no MDS and a low incidence of moulting complications. However, intermoult duration was much shorter for lobsters offered wet reference shrimp and freeze-dried shrimp feed only, whilst growth rate and SGR were also significantly higher. The nature of processing an ingredient prior to formulation and subsequent incorporation into a commercial feed often has important consequences (Glencross et al., 2007). For instance, differences in the digestibility of nutrients were observed with increasing heat exposure in canola meal, which caused lower digestibility (Glencross, Hawkins, & Curnow, 2004). It is well known that protein damage can be sustained during ingredient processing when an intensive heat treatment is applied, for example via Maillard reactions, cross linking/and polymerization. This in turn can lower digestibility and affect feed pellet palatability (Moskness, Rosenlund, & Lie, 1995). Previous research has also demonstrated that cuttlefish *Sepia officinalis* offered frozen or freeze-dried grass shrimp (*Palaemonetes varians*) grew faster than those fed oven-dried or boiled shrimp (Domingues, Marquez, Lopez, & Rosas, 2009). The authors suggested that the latter preparation techniques likely impacted upon heat labile components and denatured protein and oxidised fatty acids. Similarly, Gabaudan, Pigott, and Halver (1980) found that protein digestibility and metabolizable energy of krill and brine shrimp were reduced in oven-dried, but not freeze-dried samples. In our study, compared with freeze-dried or raw shrimp controls, lobsters offered oven-dried shrimp feeds required a longer duration to moult to stage V and did not grow so quickly, suggesting suboptimal digestion and presumably reduced nutrient assimilation. Digestibility or feed intake studies with small crustaceans which eat tiny feed particles intermittently are technically challenging, and potentially, studies

with adult lobsters could be performed to determine feed digestibility and palatability. These results may also suggest that other feeds tested in our study (i.e. oven-dried mussel meal supplied as an industrial by-product used in experiment one) could be improved if an alternative drying technique was used.

Finally, the comparison of lobsters offered oven-dried feed with or without Bio-Mos® suggests that an immune supplement conferred no direct advantage to *H. gammarus* PL in terms of survival or growth in this experiment. Since no immune parameters were measured, it is not possible to state how the immune status, and hence any related lobster performance, may have changed. However, recent studies (Daniels et al., 2015; Middlemiss, Daniels, Urbina, & Wilson, 2015) have incorporated probiotics (*Bacillus* spp.) and prebiotics (mannan oligosaccharides) into larval feeds (*Artemia salina*) and culture water of *H. gammarus*. Daniels et al., (2015) found improvement in survival, growth and stress tolerance of communally reared larvae in experimental treatments, which used pro- and prebiotics (including Bio-Mos®) in a green water system (mesocosm). Our study does differ, as we not only used a different life stage, but also reared individually in a 'clear water' system without live feeds. Hence, the development of the immune system between larval and postlarval lobsters, and bacterial loading between experimental systems, is likely to have differed. Thus, further studies investigating immune competence or bacterial loading in PL lobsters should be performed, to investigate its potential impact for long-term ongrowing operations.

4.3 | Experiment three

Experiment 3 was designed to investigate whether a herring meal-based feed could be improved by supplementing with glucosamine (chitin monomer) and/or astaxanthin at high doses, based on the results of experiment 1, which showed that shrimp-based feeds promoted better lobster performance compared with a basic herring meal. Crustacean diets are a source of astaxanthin (Lim et al., 2017) and chitin (Niu et al., 2013), which have both been shown to enhance growth, survival and stress tolerance in crustacean diets (Lim et al., 2017; Niu et al., 2013). Whilst survival of lobsters offered HA and HG feeds were significantly increased compared with those fed herring alone (H), in general survival in all four herring-based feeds were inferior to the wet shrimp reference diet regardless of supplementation. In particular, the incidence of MDS or moulting complications at stage V was not eliminated by any of the supplements. Furthermore, PL fed HAG feed, which contained both supplements, was one of the poorest performing diets in terms of survival and development, indicating that a combination of both supplements at the high doses may have created an antagonistic effect on lobster performance. The observation that most lobsters ate their moult within 24 hr (and indeed assumed a different colour in HA and HAG treatments) suggests that the glucosamine and astaxanthin supplements are capable of being digested and metabolized. Surprisingly, the results in the current study do not support the hypothesis that supplementation with glucosamine and astaxanthin improve lobster performance.

Previous studies have observed that *H. americanus* colour is influenced by the addition of carotenoids in the diet (see review by Lim et al., 2017), although in the spiny lobster *Panulirus ornatus* such supplementation did not markedly improve survival or growth (Barclay, Irvin, Williams, & Smith, 2006). The addition of crustacean-derived chitin to a basic fish diet improved survival in adult shore crabs *Carcinus maenas* (Powell & Rowley, 2007). Earlier studies demonstrated that the chitin or glucosamine supplements were not as effective as whole shrimp meal (Conklin, Devers, & Bordner, 1977) suggesting that our herring feed with added supplements was still deficient, compared with the shrimp reference diet. Niu et al., (2013) tested the addition of chitin, chitosan and glucosamine on the growth and stress performance on the black tiger shrimp, *Penaeus monodon* at inclusion levels of 0.4% and concluded that dietary intake of chitin or chitosan could enhance growth performance and resistance to stress in *P. monodon*, but not the inclusion of glucosamine. In contrast to this, the substitution of glucosamine with equal amounts of chitin or chitosan did not produce the same growth promoting response in shrimp (Kanazawa, Shimaya, Kawasaki, & Kashiwada, 1970; Kitabayashi, Kurata, Shudo, Nakamura, & Ishikawa, 1971; Clark, Lawrence and Swakon, 1993). Clearly, therefore, there is further research is needed to understand digestion and assimilation of exoskeletal nutrients in crustaceans.

4.4 | Future scope

Whilst the nutritional requirements of *Homarus gammarus* have not yet been established, reported optimum protein levels for *H. americanus* fed artificial formulated feeds have varied widely in the literature (Conklin, 1995). Yet, there still remains a paucity of research testing various protein levels in diets for *H. gammarus* and *H. americanus*. For our study, we designed feeds with a high inclusion level of protein (60%) to compare with raw shrimp reference feed, and the maximum suggested for *H. americanus* (Castell & Budson, 1974) to avoid potential malnutrition in low-protein commercial diets (Fiore & Tlusty, 2005). Future consideration should also be paid to the interaction between phospholipid requirements and the protein source in aquaculture feeds (See review by Coutteau et al., 1997). In juvenile *H. americanus*, diets based on casein showed high levels of mortality due to MDS, which were alleviated by supplementation with dietary soybean lecithin (Conklin et al., 1977). However, no phospholipid requirement was found for lobsters when purified crab protein rather than casein was used as the primary protein source (Kean et al., 1985). Schmalenbach et al., (2009) reared juvenile *H. gammarus* on *Artemia salina*, Brown Crab *Cancer pagurus* and the isopod *Idotea emarginata* and achieved a very high survival rate. Brown Crab was considered cost effective for *H. gammarus* and *H. americanus* to utilize due to locally abundant fishery discards (Schmalenbach et al., 2009; Skonberg et al., 2001). Therefore, the interaction between protein source and phospholipid levels may have important implications for formulation of practical diets. A comparative study using similar phospholipid sources added to both the commercial fishmeal, experimental diets and crustacean-based diets would allow a better interpretation of the results we observed in the present study.

The high protein content of the reference shrimp compared with experimental dry diets also suggests a need for a comparative study investigating differing protein concentrations in diets based on crustaceans and fishmeal. Overall, the results of the present study suggest that the shrimp processing sector represents an undervalued resource that can be upgraded to feed ingredients, which may not require the addition of valuable supplements. Further development could likely investigate the differences between freeze-dried abdomen (i.e. a potential human grade food unsuitable for animal feed), shrimp meal created from steaming water (experiment 2) and other by-products such as head and carapace waste resulting from a 'peeled' product.

In conclusion, our study confirms the usefulness of the method of Tlusty et al. (2005) to screen an array of candidate feeds relatively quickly, studying young lobsters. However, we would advocate longer term trials, greater than a few months, to proceed using the best performing feeds. This study also provides a breakdown of lobster feed composition, and a method to make satisfactory dry feed (e.g. freeze-dried feed, experiment 2) which gave identical performance to raw shrimp feed, and may assist home aquarists and the restocking subsector. Although it is challenging to understand the ecological and nutritional needs of juvenile *H. gammarus*, the results of our study show that a diet containing a proportion of shrimp, created from local industry by-products, was the best source of a sustainable lobster feed for the emerging lobster aquaculture sector.

ACKNOWLEDGMENTS

This research forms part of the 'NOMACULTURE' project 2013-1961-27044-74 funded by FORMAS, MISTRA and the NoVaqua project funded by Nordic innovation (Project Mar 14322). The authors would like to thank all colleagues at the Sven Lovén Centre for Marine Infrastructure—Kristineberg for their technical support (particularly Fayez Alsaleh, Bengt Lundve and Linda Svanberg), the crew of the fishing vessel *Tärnö* (supply of broodstock) and Royne Robertsson (supply of raw shrimp). Feed ingredients were provided by the Swedish university of agricultural sciences (SLU), Astaxanthin samples were a kind gift of Linkan feed ingredients AB, Sweden. Mussel meal was provided by Musselfeed AB, Sweden.

CONFLICT OF INTERESTS

None.

AUTHOR CONTRIBUTIONS

JH and AP wrote the manuscript, performed statistical analysis and were responsible for data collection and experimental designs. ML, AV and IU assisted in diet design and feed manufacture. KS, IU, ML and SE assisted with experimental design. All authors have read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

James Hinchcliffe https://orcid.org/0000-0003-0165-0462
Markus Langeland https://orcid.org/0000-0002-2473-790X
Aleksandar Vidakovic https://orcid.org/0000-0002-8362-1974
Kristina Sundell https://orcid.org/0000-0002-7643-2083

REFERENCES

Aiken, D. E., & Waddy, S. L. (1995). Aquaculture. In J. R. Factor, (Eds.), *Biology of the lobster* Homarus americanus (pp. 153–176). San Diego, USA: Academic Press, Inc.

AOAC (1995). *Official methods of analysis of AOAC international*, 16th (eds). Washington, DC: Association of Official Analytical Chemists.

Arnason, J., Larsen, B. K., Björnsson, B. T., Sundell, K., Hansen, A.-C., Lindahl, O., … Bjornsdottir, R. (2015). *Local fish feed ingredients for competitive and sustainable production of high-quality aquaculture feed, LIFF*. Nordic Innovation Publication, 2015:02. Retrieved from: http://nordicinnovation.org/Global/_Publications/Reports/2015/NI_LIFF_report_DEF_NOV2015.pdf.

Barclay, M. C., Irvin, S. J., Williams, K. C., & Smith, D. M. (2006). Comparison of diets for the tropical spiny lobster *Panulirus ornatus*: Astaxanthin-supplemented feeds and mussel flesh. *Aquaculture Nutrition*, *12*, 117–125. https://doi.org/10.1111/j.1365-2095.2006.00390.x

Barrento, S., Marques, A., Teixeira, B., Vaz-Pires, P., & Nunes, M. L. (2009). Nutritional quality of the edible tissues of European lobster *Homarus gammarus* and American lobster *Homarus americanus*. *Journal of Agricultural and Food Chemistry*, *57*(9), 3645–3652. https://doi.org/10.1021/jf900237g

Burton, C. A. (2003). Lobster hatcheries and stocking programmes: An introductory manual. Sea Fish *Industry Authority Aquaculture Development Service. Seafish Report*, SR552.

Castell, J. D., & Budson, S. D. (1974). Lobster nutrition: The effect on *Homarus americanus* of dietary protein levels. *Journal of the Fisheries Board of Canada*, *31*(8), 1363–1370.

Cho, C. Y. (1990). Fish nutrition, feeds and feeding: With special emphasis on salmonid aquaculture. *Food Reviews International*, *6*, 333–357. https://doi.org/10.1080/87559129009540876

Clark, D. J., Lawrence, A. L., & Swakon, D. H. D. (1993). Apparent chitin digestibility in penaeid shrimp. *Aquaculture*, *109*(1), 51–57.

Conklin, D. E. (1995). Digestive physiology and nutrition. In J. R. Factor (Eds.), *Biology of the lobster* Homarus americanus (pp. 441–458). San Diego, USA: Academic Press.

Conklin, D. E., Devers, K., & Bordner, C. (1977). Development of artificial diets for the lobster, *Homarus americanus*. *Journal of the World Aquaculture Society*, *8*, 841–852. https://doi.org/10.1111/j.1749-7345.1977.tb00165.x

Coutteau, P., Geurden, I., Camara, M. R., Bergot, P., & Sorgeloos, P. (1997). Review on the dietary effects of phospholipids in fish and crustacean larviculture. *Aquaculture*, *155*(1–4), 149–164. https://doi.org/10.1016/S0044-8486(97)00125-7

Daniels, C. L., Wills, B., Ruiz-Perez, M., Miles, E., Wilson, R. W., & Boothroyd, D. P. (2015). Development of sea based container culture for rearing European lobster (*Homarus gammarus*) around South West England. *Aquaculture*, *448*, 186–195. https://doi.org/10.1016/j.aquaculture.2015.05.026

Domingues, P. M., Marquez, L., Lopez, N., & Rosas, C. (2009). Effects of food thermal treatment on growth, absorption, and assimilation efficiency of juvenile cuttlefish, *Sepia officinalis*. *Aquaculture International*, *17*, 283.

Drengstig, A., & Bergheim, A. (2013). Commercial land-based farming of European lobster (*Homarus gammarus* L.) in recirculating aquaculture system (RAS) using a single cage approach. *Aquacultural Engineering*, *53*, 14–18.

Ellis, C. D., Hodgson, D. J., Daniels, C. L., Boothroyd, D. P., Bannister, R. C. A., & Griffiths, A. G. F. (2015). European lobster stocking requires comprehensive impact assessment to determine fishery benefits. *ICES Journal of Marine Science*, *72*, 35–48. https://doi.org/10.1093/icesjms/fsu196

Fiore, D. R., & Tlusty, M. F. (2005). Use of commercial *Artemia* replacement diets in culturing larval American lobsters (*Homarus americanus*). *Aquaculture*, *243*, 291–303. https://doi.org/10.1016/j.aquaculture.2004.10.009

Floreto, E. A. T., Bayer, R. C., & Brown, P. B. (2000). The effects of soybean-based diets, with and without amino acid supplementation, on growth and biochemical composition of juvenile American lobster. *Homarus Americanus Aquaculture*, *189*, 211–235. https://doi.org/10.1016/S0044-8486(00)00363-X

Floreto, E. A. T., Brown, P. B., & Bayer, R. C. (2001). The effects of krill hydrolysate-supplemented soya-bean based diets on the growth, colouration, amino and fatty acid profiles of juvenile American lobster, *Homarus americanus*. *Aquaculture Nutrition*, *7*, 33–43. https://doi.org/10.1046/j.1365-2095.2001.00154.x

Forghani, B., Bordes, R., Ström, A., & Undeland, I. (2020). Recovery of a protein-rich biomass from shrimp (Pandalus borealis) boiling water: A colloidal study. *Food chemistry*, *302*, 125299.

Gabaudan, J., Pigott, J. M., & Halver, J. E. (1980). Effect of processing on protein ingredients for larval diets: Biological evaluation. *Journal of the World Aquaculture Society*, *11*, 424–432.

Glencross, B. D., Booth, M., & Allan, G. L. (2007). A feed is only as good as its ingredients–a review of ingredient evaluation strategies for aquaculture feeds. *Aquaculture Nutrition*, *13*(1), 17–34. https://doi.org/10.1111/j.1365-2095.2007.00450.x

Glencross, B., Hawkins, W., & Curnow, J. (2004). Nutritional assessment of Australian canola meals. I. Evaluation of canola oil extraction method and meal processing conditions on the digestible value of canola meals fed to the red seabream (*Pagrus auratus*, Paulin). *Aquaculture Research*, *35*(1), 15–24.

Hinchcliffe, J., Carlsson, N. G., Jönsson, E., Sundell, K., & Undeland, I. (2019). Aquafeed ingredient production from herring (*Clupea harengus*) by-products using pH-shift processing: Effect from by-product combinations, protein solubilization-pH and centrifugation force. *Animal Feed Science and Technology*, *247*, 273–284. https://doi.org/10.1016/j.anifeedsci.2018.07.014

Kanazawa, A., Shimaya, M., Kawasaki, M., & Kashiwada, K. (1970). Nutritional requirements of prawn-I. Feeding on artificial diet. *Bulletin of the Japanese Society of Scientific Fisheries*, *36*(9), 949–954.

Kean, J. C., Castell, J. D., Boghen, A. G., D'Abramo, L. R., & Conklin, D. E. (1985). A re-evaluation of the lecithin and cholesterol requirements of juvenile lobster (*Homarus americanus*) using crab protein-based diets. *Aquaculture*, *47*, 143–149.

Kitabayashi, K., Kurata, H., Shudo, K., Nakamura, K., & Ishikawa, S. (1971). Studies on formula feed for kuruma prawn. I. On the relationship among glucosamine, phosphorus and calcium. *Bulletin of the Japanese Society of Scientific Fisheries*, *65*, 91–107.

Lim, K. C., Yusoff, F. M., Shariff, M., & Kamarudin, M. S. (2017). Astaxanthin as feed supplement in aquatic animals. *Reviews in Aquaculture*, *10*, 738–773.

Middlemiss, K. L., Daniels, C. L., Urbina, M. A., & Wilson, R. W. (2015). Combined effects of UV irradiation, ozonation, and the probiotic Bacillus spp. on growth, survival, and general fitness in European lobster (Homarus gammarus). *Aquaculture*, *444*, 99–107.

Moksness, E., Rosenlund, G., & Lie, Ø. (1995). Effect of fish meal quality on growth of juvenile wolfish, *Anarhichas Lupus L*. *Aquaculture Research*, *26*(2), 109–115. https://doi.org/10.1111/j.1365-2109.1995.tb00890.x

Nicosia, F., & Lavalli, K. (1999). Homarid lobster hatcheries: Their history and role in research, management, and aquaculture. *Marine Fisheries Review*, *61*, 1–57.

Niu, J., Lin, H. Z., Jiang, S. G., Chen, X. U., Wu, K. C., Liu, Y. J., … Tian, L. X. (2013). Comparison of effect of chitin, chitosan, chitosan oligosaccharide and N-acetyl-d-glucosamine on growth performance, antioxidant defenses and oxidative stress status of *Penaeus monodon*. *Aquaculture*, *372*, 1–8. https://doi.org/10.1016/j.aquaculture.2012.10.021

Powell, A., & ELCE, (2016). New developments in European lobster aquaculture. *Aquaculture Europe*, *41*(2), 5–12.

Powell, A., Hinchcliffe, J., Sundell, K., Carlsson, N. G., & Eriksson, S. P. (2017). Comparative survival and growth performance of European lobster larvae, *Homarus gammarus*, reared on dry feed and conspecifics. *Aquaculture Research*, *48*, 5300–5310. Online. (10.1111/are.13343)

Powell, A., & Rowley, F. (2007). The effect of dietary chitin supplementation on the survival and immune reactivity of the shore crab, *Carcinus maenas*. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, *147*, 122–128.

Schmalenbach, I., Buchholz, F., Franke, H. D., & Saborowski, R. (2009). Improvement of rearing conditions for juvenile lobsters (*Homarus gammarus*) by co-culturing with juvenile isopods (*Idotea emarginata*). *Aquaculture*, *289*, 297–303. https://doi.org/10.1016/j.aquaculture.2009.01.017

Skonberg, D. I., Donahue, D. W., Bayer, R. C., Floreto, E., & Riley, J. G., (2001). Quality evaluation of American lobsters fed diets containing crab processing waste. *Journal of Aquatic Food Product Technology*, *10*, 17–29. https://doi.org/10.1300/J030v10n02_03

Tlusty, M. F., Fiore, D. R., & Goldstein, J. S. (2005). Use of formulated diets as replacements for Artemia in the rearing of juvenile American lobsters (*Homarus americanus*). *Aquaculture*, *250*, 781–795. https://doi.org/10.1016/j.aquaculture.2005.05.025

Undeland, I., Kelleher, S. D., & Hultin, H. O. (2002). Recovery of functional proteins from herring (Clupea harengus) light muscle by an acid or alkaline solubilization process. *Journal of agricultural and food chemistry*, *50*(25), 7371–7379.

Wickins, J. F., Beard, T. W., & Child, A. R. (1995). Maximizing lobster, Homarus gammarus (L.), egg and larval viability. *Aquaculture Research*, *26*(6), 379–392.

Wickins, J. F., Lee, D. O'C., (2002). *Crustacean farming, ranching and culture* (p. 434). Oxford, England: Blackwell Science.

Yamada, S., Tanaka, Y., Semeeshima, M., & Ito, Y. (1990). Pigmentation of prawn (*Penaeus japonicus*) with carotenoids. I. Effect of dietary astaxanthin, b-carotene and cantaxanthin on pigmentation. *Aquaculture*, *87*, 323–330. https://doi.org/10.1016/0044-8486(90)90069-Y

How to cite this article: Hinchcliffe J, Powell A, Langeland M, et al. Comparative survival and growth performance of European lobster *Homarus gammarus* post-larva reared on novel feeds. *Aquac Res*. 2020;51:102–113. https://doi.org/10.1111/are.14351