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REVIEWS IN Aquaculture

REVIEW

Barriers in European spiny lobster (*Palinurus elephas*) aquaculture: What we know so far?

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Abstract

Palinurids, also known as spiny lobsters, are high-value seafood, which is economically important for many European and Asian seafood trades. However, the reduction of wild European spiny lobster populations produces a need for developing alternative renewable strategies to meet current and future demands. Aquaculture of spiny lobsters has the potential to become of major economic importance in the coming years with growing markets in Asia, Europe, and America, with *Palinurus elephas* being a promising candidate species for use in the commercial culture and stock enhancement of natural fisheries. This is due to its shorter larval periods and rapid growth to the critical puerulus stage compared with other spiny lobster species. While we have a basic understanding of the lifecycle and biology of *P. elephas*, much of this is based on work undertaken on similar species globally. There are many gaps in our knowledge that need to be addressed to make its aquaculture viable with appropriate feeds being an immediate issue as well as many other husbandry-related factors. Previous studies act as a platform providing a baseline for further research and highlighting constraints. Developments in the use of *P. elephas* are promising due to realistically bridgeable knowledge gaps, the likelihood of producing sustainable food and the high commercial value of spiny lobsters. This review identifies our present state of knowledge and outlines the scope for further research and necessary technological developments to make it a viable contribution towards crustacean aquaculture in Europe.

KEYWORDS
disease, hatchery, larval development, lifecycle, production, spiny lobster

1 | INTRODUCTION

Farmed decapods such as prawns, crabs and lobsters are economically important seafood that supplied over 9 million tonnes to the international market in 2019.[1] Lobsters and, in particular, the high-value spiny lobsters within the *Palinurus* genus, account for >700 tonnes in capture fisheries.[1] The European spiny lobster (*Palinurus elephas*) is commercially important for many European coastal communities with individuals selling for €40–120 kg^{-1}.[3] The species can be found in the Mediterranean Sea, from the West of Turkey to the North-East Atlantic Ocean, and from Morocco to Scotland.[4] European spiny lobster adults are typically found from the littoral zone to a depth of ~200 m, while post-larvae settle at shallower depths of 5–15 m. Off the Irish Atlantic Ocean coastline, typical increments in the growth of 12 mm per moult were observed.[5] After 2–3 years at 200 m depth, inhabiting rocky and coralligenous substrates that provide holes and crevices for protection, carapace lengths (CL) of ~86 mm have been estimated for wild European spiny lobster (*P. elephas*), with males weighing 0.455 kg and females 0.510 kg.[3] When individuals are 8–9 years old, females have been reported to be 158 mm CL weighing 2.35 kg, while males are 160 mm CL and weigh 2.68 kg. This is slightly larger in size and growth rate than observed in the Mediterranean Sea.[6] Adults tend to be solitary, in pairs or small groups living around rocks and boulders with gravel beds. They are more active at night when foraging occurs. Juveniles, on the other hand, leave their crevices infrequently perhaps due to their vulnerability to predation on the reefs.[7] In the wild, *P. elephas* are typically found in water temperatures between 13 and 18°C, with mortalities reported at temperatures above 24°C.[8]

The high demand and pricing of the European spiny lobster can be ascribed to low wild stocks, a result of past fishing pressures.[9,10] Consequently, this has led the species to be listed as a 'vulnerable' species on the International Union for Conservation of Natures (IUCN) Red List.[11] Another indication of fishing pressure is shown in historical catch records where, for example, spiny lobster weight landed in Spain has decreased from an average of 2.0 to 0.6 kg per individual since the 1900s.[12] Moreover, the impact of the predicted increase in sea temperatures caused by climate change will reduce the survival of spiny lobsters. A past study has shown that energy demand from swimming would double with a temperature increase from 17 to 24°C, while migration time of pueruli is predicted to lengthen as temperature increases resulting in more predation opportunities.[13]

Attempts to conserve and protect vulnerable wild lobster stocks (including *P. elephas*) have led to national legislative fishing management requirements on limiting the type of fishing gear being used and prohibiting the taking of undersized, berried females (gravid), and v-notched females. The latter being a predominately volunteer-based approach relying on buy-in by fisherman, where for any berried females caught, a notch in the shape of a 'v' is removed from the tail. The female is released to prevent future removal until the notched tail segment is grown back, thereby protecting reproductive females and boosting egg release rates. This method has led to an increase in the mean reproductive value of American clawed lobsters (*Homarus americanus*) of 18%.[14] The effects of V notching in tank-based setting found no effect on the growth and health of individuals; however, temperature stress resulted in reduced survivability.[8]

A more sustainable and long-term strategy to meet growing market demands is to farm spiny lobsters.[15] Furthermore, the production of farmed juveniles could be used to restore wild populations through stock enhancement programmes, such as schemes being carried out using the common European lobster (*H. gammarus*).[16] To date, there is no equivalent European spiny lobster (*P. elephas*) restocking programme or commercial aquaculture venture for this species. Much of this is due to the lack of biological knowledge (e.g., complex larval stages) and underdeveloped farming practices for the species and not due to a lack of demand.[6] The lack of knowledge on European spiny lobsters has required that the authors draw parallels with research undertaken on similar species. The insight provided by research on related spiny lobster species such as those from southern rock lobster (*Jasus edwardsii*),[17] western rock lobster (*P. cygnus*),[18] and ornate lobster (*P. ornatus*)[19] could be extremely valuable.[20] The caveat to this is that although parallels are drawn from published studies on similar species, species differences exist, and further research will be required to define the optimum requirements/parameters relevant for *P. elephas*. This review will focus on the potential of farming European spiny lobster (*P. elephas*) and evaluate the knowledge gaps in the animal's lifecycle, nutritional requirements and potential production bottlenecks, such as diseases. The review will also discuss the economic viability of culturing European spiny lobsters as a commercially farmed species and creating a viable stock enhancement programme. To the authors' knowledge, the last extensive review carried out on European spiny lobster (*P. elephas*) was by Goni and Latrouite,[6] which evaluated its biology, ecology and fisheries. The present review will seek to go beyond the previous review by examining the spiny lobster as a potential farmed species to meet consumer demand but also for wild stock enhancement.

2 | BIOLOGY AND LIFECYCLE OF EUROPEAN SPINY LOBSTER

2.1 | Reproductive behaviour and mating

In the Atlantic Ocean, pre-reproductive onshore migration occurs in spring and post-reproductive offshore migration in late autumn.[5] The size at which sexual maturity is reached in European spiny lobster is unclear for either sex with various studies suggesting sizes ranging from 76–95 mm CL.[21] Mating occurs between June and October in the Atlantic Ocean, which takes place between the intermoult of individuals, a few weeks after the female has moulted. The male places two white gelatinous spermatophores below the female reproductive openings found on both sides of the sternum at the base of the third pair of pereiopods.[22] The spermatophores do not harden as seen in other palinurids and only remain for a maximum of 10 days.[5,7] Shortly after mating oviposition occurs, the eggs are released over the spermatophores on the female's sternum, the female uses the fifth pereiopod to scratch open the spermatophores releasing the spermatozoids and the eggs are fertilised (Figure 1).[5,7] The eggs are then held at the pleopods by a protein matrix, where embryonic development occurs until hatching.

2.2 | Egg incubation and larval stages

Egg incubation duration can vary in the wild and span over 9 months in the Atlantic Ocean and 5 months in the Mediterranean Sea. The eggs hatch in the summer and spring, respectively. The difference in egg development is most likely due to the temperature difference between the coastal regions. This is consistent with the water

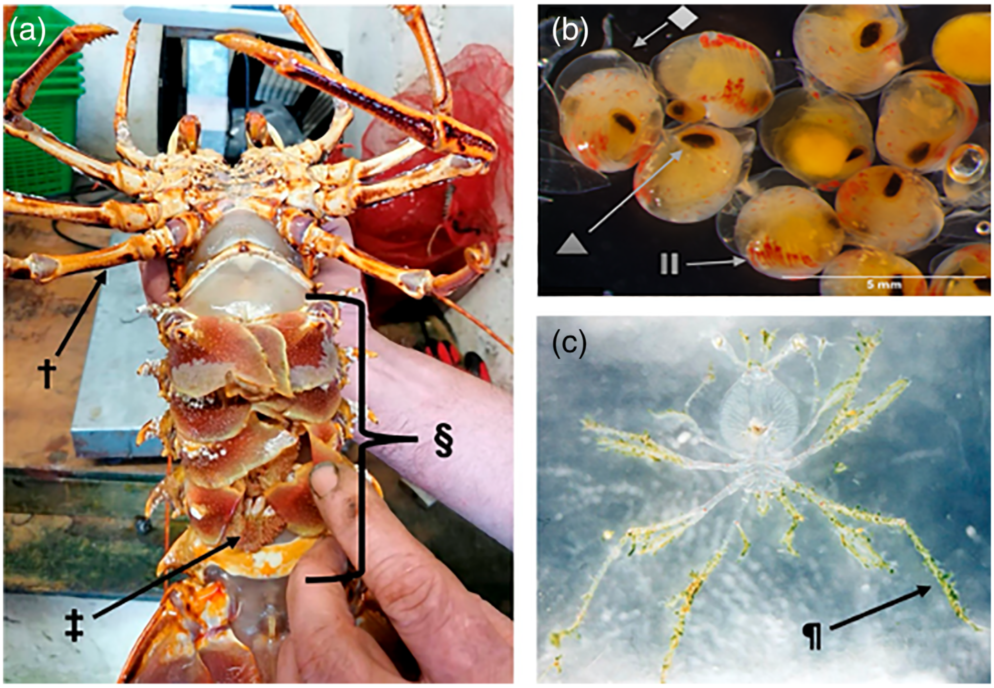

FIGURE 1 (a) Female berried European spiny lobster (*Palinurus elephas*) at the later stage of egg maturation. ‡Indicates the eggs, §—abdomen, †—5th pereiopod. (b) Well developed *P. elephas* eggs prior to hatching. Indicates egg envelope, —eye spot, II—pigment. Magnification 0.75×. (c) *P. elephas* phyllosoma 2–9.5 mm (John Mercer/Carna Research Station image library, size from Kittaka & Ikegami[23]). ¶indicates fouled setae

temperature effect on embryo development in the ornate spiny lobster (*Panulirus ornatus*), where embryonic development to the point of hatching was ~14 days shorter at 30°C than 24°C.[24] An indication of temperature effect was also observed in artificially reared conditions. For *P. elephas*, hatching can be completed within 24 h[5]; however, Karlovac (1965) reported hatching to take as long as 8 days.[25]

The *P. elephas* larvae are larger than other similar *Palinuridae* species and hatch at a length of 2–3 mm[23] (Figure 1). The number of *P. elephas* phyllosoma (the distinct larval form of spiny, slipper and coral lobsters) instars is not known, between six and nine instars is generally accepted[23,26] (Figure 2). At the pueruli phase, the lobsters possess developed pleopods, abdomen and carapace. The pueruli moult become juveniles, which are visually comparable to the settled adult stage. From the hatching to the juvenile stage typically takes 5–6 months in the Mediterranean Sea and can be as long as a year in the Atlantic Ocean.[6,7,27] This could be the result of higher average sea temperatures in the Mediterranean Sea compared with the Atlantic Ocean, which would allow development to advance more rapidly. An effect of temperature in shortening the development stages would be beneficial for future farming efforts as an effective husbandry application so long as it does not lead to deformities or decreased survival.[28]

Once hatched, the planktonic European spiny lobster (*P. elephas*) larvae are transparent, apexed oval shape and relatively well developed.[29] Under aquaria conditions, at least six larval instars before metamorphosis into pueruli, in this case taking 65–69 days (Figure 2).[26] Although this differs from the earlier estimates of nine instars being observed.[23] Other comparisons cannot be drawn due to limited published or peer-reviewed information on the instar stages. Most recently, research carried out on *P. elephas* larval development found a similar time frame, where it took 83 days to develop from post-hatching to juveniles and there was a 50% survival rate to the final larval stage.[30]

The early stage larvae are often found near the coast due to larvae hatching happen inshore.[3] As the larvae are planktonic, they are subject to ocean currents, which affect the distribution of the European spiny lobsters and the gene flow between populations. The long planktonic stages allow the larvae to travel thousands of kilometres in the currents before settling to the seafloor.[31] There are known genetic differences in European spiny lobster populations from the Atlantic Ocean and the Mediterranean Sea. The cause of this has been attributed to restricted gene flow through the Strait of Gibraltar. Other differences between Brittany and Ireland-Scotland populations are believed to be due to the Gulf stream dividing into a northern and southern flow south of Ireland.[27] The understanding of *P. elephas* larval dispersal is challenging as it is near impossible to decipher where the larvae originate or follow their movement for months at sea.[31]

3 | THE POTENTIAL OF FARMING EUROPEAN SPINY LOBSTER

To the authors' knowledge, there are no known commercially operated European spiny lobster farms in service. However, in Asia, the ornate spiny lobster species are commercially grown and in Vietnam, the aquaculture of spiny lobster (*Panulirus spp*, inc. *P. ornatus*) was 631 tonnes in 2010 rising to 1100 tonnes in 2018, with a value of

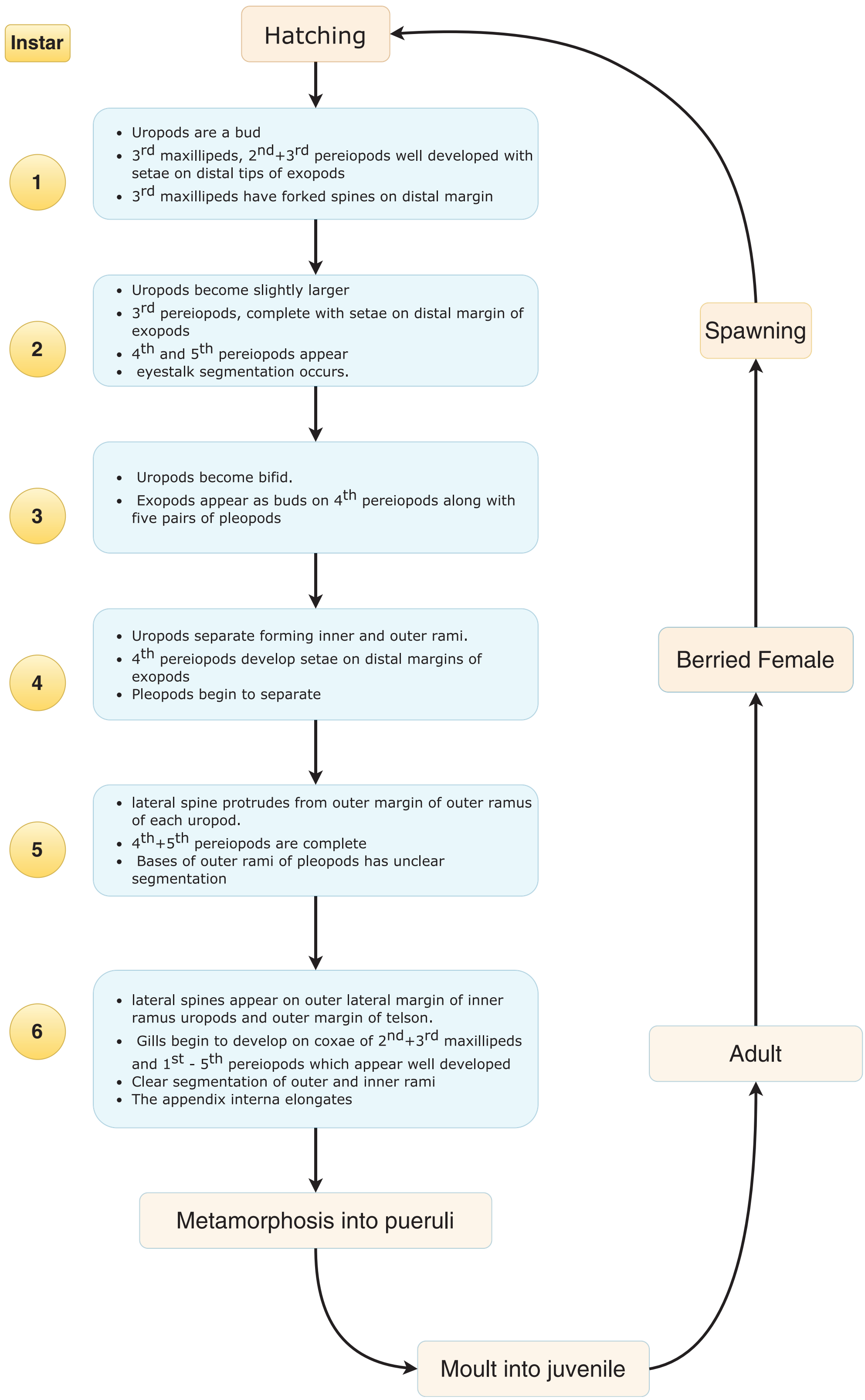

FIGURE 2 Key morphological changes during the larval instar stages of European spiny lobster (*Palinurus elephas*, adapted from Kittaka et al.[26])

USD 30.9 million.[1] The comparative absence of European spiny lobster farms is not due to a lack of technology transfer or economic drive to produce lobsters but is based on specific farming practices. For instance, all farmed ornate spiny lobsters (*P. ornatus*) are wild-caught at their post settling stage, rather than reared from eggs. They are subsequently placed in sea cages for on-growing (except for an

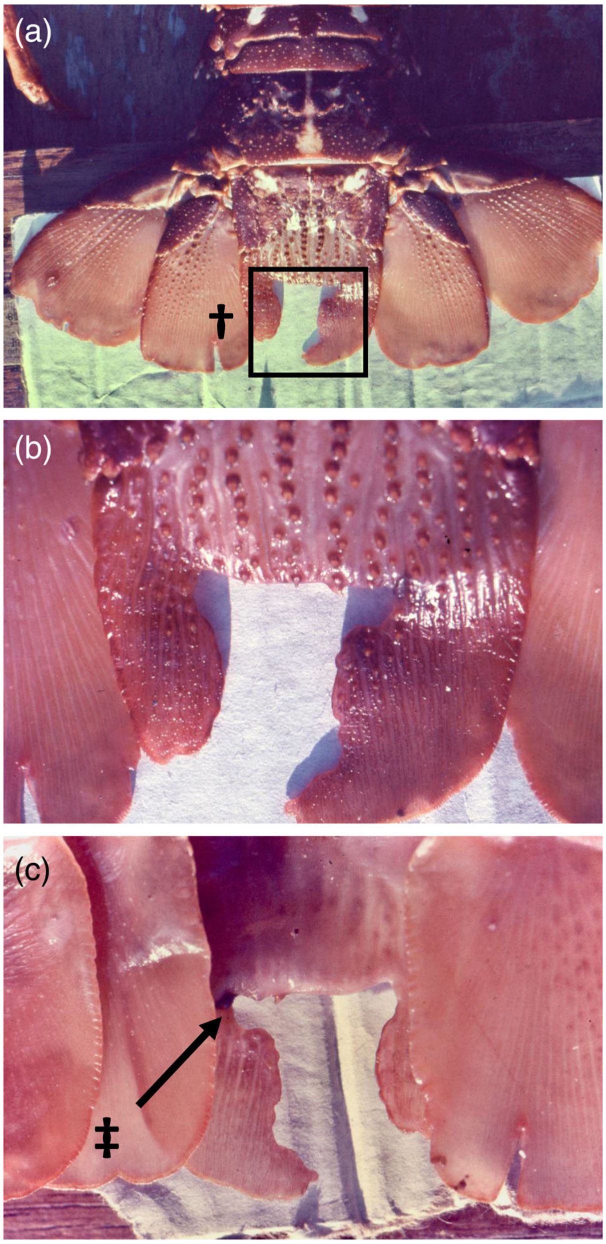

FIGURE 3 External clinical signs of tail fan necrosis in *Palinurus elephas* (a) Dorsal view of the tail fan, †Indicates considerable erosive lesion on the telson. (b) Close up of erosive lesion, dorsal view. (c) Ventral view of telson, ‡Indicates initial melanisation on the affected area (John Mercer/Carna Research Station image library)

Australian farm, ornatas.com.au). This is only possible in countries like Vietnam, the Philippines, India, and Indonesia, as they have an abundance of naturally settling lobsters (Figure 3b).[32,33] Although collecting wild ornate spiny lobster seedstock is currently successful in Vietnam, it might not be a sustainable practice or desirable due to disease risk associated with wild stocks, lack of quality, quantity (variation in lobster settlement), and price variability of the annual seedstock.[34] Furthermore, there is also the risk of legislative changes on wild seed stock collection. For example, in 2015, Indonesia introduced a minimum landing size (>200 g) legislation to all lobster (inc. *P. homarus* and *P. ornatus*) species which consequently led to 95% reduction in grow-out productions.[35]

In European spiny lobster (*P. elephas*), post-settling and early juvenile stages are rarely seen and caught from the wild.[4] Therefore, a farmed hatchery supply of pueruli should be developed to ensure a sustainable source for the development of spiny lobster captive rearing. With *P. ornatus* this has been achieved in Australia as recent developments in methods and equipment have closed the *P. ornatus* life cycle from broodstock through to juvenile production.[36] Furthermore, a larval diet has been produced along with mass culture systems, this may enable the aquaculture of other species like *P. elephas* to be rapidly developed using these new technologies.[37]

Based on FAO Fisheries and Aquaculture data,[1] the market price of a lower quantity of fished *P. elephas* can be seen to match the price of a larger quantity of cultured *Panulirus sp*. This suggests that the aquaculture of *P. elephas* has a large margin for the expenses associated with aquaculture while remaining profitable (Table 1). The major economic costs of spiny lobster production that should be considered are hatchery production of juveniles, which includes feed, labour, the establishment of water filtration and treatment to maintain high water quality, and culture infrastructure to produce large pueruli volumes. While grow-out cost includes infrastructure, feed, labour, and managing cannibalism/stocking density to achieve an optimal and viable business enterprise. These costs would be present from the hatchery through to the on-growing of the product. With increased production from aquaculture, the value of *P. elephas* might drop as it becomes more available; however, the demand is very high allowing this to remain a lucrative industry. Aquaculture production of *Panulirus* lobster species has not been shown to have an impact on the production from fisheries, at least as far as the global catch figures (Table 1). This could be due to legislative restrictions on their landing sizes from fisheries and bottlenecks remaining in their rearing in farms (e.g., Asian ornate lobster farms relying on wild seedstocks with only one known farm in Australia utilising hatchery-produced seedstocks).

4 | DIETARY REQUIREMENTS OF EUROPEAN SPINY LOBSTER

4.1 | Natural diets

The diet of wild larvae is largely unknown. However, it is believed that they are omnivorous, and their mouthpart morphology and appendages have allowed them to adapt to feeding on soft-bodied prey items found in the water column, such as fish larvae, jellyfish, bivalves, and polychaetes.[9] Further evidence was found by Jeffs et al.,[17] where southern rock lobster (*J. edwardsii*) prey items were predominantly gelatinous zooplankton. Adult European spiny lobster (*P. elephas*) are benthic omnivores, they prey primarily on molluscs, echinoderms, and crustaceans. While hard-shelled organisms are their main prey, they also feed on ophiuroids and coralline algae and are opportunistic feeders that alter their preference based upon prey abundance.[39] It is possible to infer that this species is adapted to high dietary protein, low in lipids, and

TABLE 1 Total global wild fisheries production of European spiny lobster (*Palinurus elephas*) in comparison with aquaculture spiny lobsters (inc. *Panulirus ornatus*) in the past decade.

	European spiny lobster *Palinurus elephas*			*Panulirus sp*			
	Fisheries			Aquaculture		Fisheries	
Year	Min. (USD)[a]	Max. (USD)[a]	Production (tonnes)	Value (USD)[a]	Production (tonnes)	Value (USD)[a]	Production (tonnes)
2018	16,198	48,595	363	46,164	1694	704,806	25,912
2017	19,590	58,770	439	60,800	3035	721,371	26,521
2016	18,162	54,486	407	34,047	1619	685,521	25,203
2015	17,225	51,675	386	30,064	1563	600,739	22,086
2014	16,466	49,399	369	30,607	1563	746,966	27,462
2013	11,825	35,476	265	29,139	1632	887,182	32,617
2012	13,119	39,358	294	25,200	1329	785,753	28,888
2011	16,912	50,737	379	22,668	1035	678,150	24,932
2010	22,446	67,338	503	23,086	1031	606,832	22,310
2009	25,792	77,378	578	14,014	1406	431,609	15,868
2008	17,492	52,478	392	11,084	1084	541,388	19,904

Note: European spiny lobster (as 'common spiny lobster' in the FAO statistics) value was determined using the values ranges €40 (min) and 120 kg^{-1} (max),[3] 1 tonne = 907 kg, Euro to USD exchange rates from 1999 to 2021 were used,[38] 1:1.23, all values were rounded down to the nearest thousand.
Note: European spiny lobster price per tonne is USD$ 44,600–133,800.
Note: Global *Panulirus sp* inc. *ornatus* (excluding Europe) price per tonne is USD 27,200.
[a]$\times$10.[3] Statistical data collected from FAO 2022.[1,2]

medium-high in carbohydrate foods. The latter can be based upon glycogen being the major store of energy in molluscs, making up 14–24% of the ash-free dry matter.[15] A potential route towards gaining fundamental knowledge in animal nutrition includes stable isotope analyses for determining trophic relationships and dietary patterns in wild stock. This approach was successfully applied for both wild and captive *P. elephas* specimens, where relative nutrient assimilation rates were related to a differential enrichment ratio of ^{13}C and ^{15}N isotopes.[40] The authors found evidence in both captive and wild *P. elephas* of tissue-specific composition and function independent of diet history. Leg muscle appeared to be the best tissue for analysing tropho-dynamics in this species as it can regenerate after sampling offering scope for continuous feeding studies under captive environments.

4.2 | General nutrient requirements based on fundamental investigations

4.2.1 | Proteins, carbohydrates, and lipids

Published dietary requirement trials in lobster species suggest that a feed composed of ~50% crude protein and 6–10% lipid would likely be the best dry diet for recently settled European spiny lobster (*P. elephas*). However, specific requirements for this species remain to be established. Analysis of the total composition, amino acid composition, and the macro minerals present in the muscle of adult market size *P. vulgaris* (*P. elephas* synonym) has been conducted.[41] The total composition of *P. elephas* was 77.13 ± 0.08% moisture, 0.63 ± 0.03% lipid, 19.95 ± 0.68% protein, and 0.15 ± 0.01% carbohydrate and 2.14 ± 0.01% ash. The essential amino acids phenylalanine (2.321 g 100 g^{-1}), and lysine (1.439 g 100 g^{-1}) were found in the highest concentrations.[42] These findings were within a small sample size of only four individuals therefore a small amount of inaccuracy can be expected.

It has been reported that the optimal dietary carbohydrate to lipid ratio for *J. edwardsii* should ideally be 2:1 in their post-larval stages.[43] While studies on the American clawed lobster (*H. americanus*) confirmed its ability to utilise some dietary carbohydrates.[42] with European clawed lobsters (*H. gammarus*), a ratio of 50:25:12, protein, carbohydrate and lipid were suggested for formulated diets in order to yield optimum growth. It is likely that a similar ratio will exist for the European spiny lobster, although further research is required to identify this. Lipids are utilised for energy purposes in the early larval stages as shown for wild western rock lobster (*P. cygnus*), and lipid reserves become depleted as larvae progress in development from phyllosoma to juveniles.[18] This is the case for most crustacean species as they transition to a predominantly protein mode of nutritional dependency. The bioenergetic significance of this was reported in the juvenile stage of green rock lobster (*Sagmariasus verreauxi*) primarily utilising protein for energy to drive maintenance and growth requirements and protein accretion.[44] It was found that 50% dietary protein was optimal for reducing protein catabolism for energy purposes while allowing maximum retention. Post-prandial measurements relating to routine metabolism and specific dynamic action associated with protein catabolism and biosynthesis provided an insight into this complex use of nutrients and could be applied to *P. elephas*.

Lipids are the major sources of essential fatty acids in storage fats and as phospholipids within cell membranes of tissues. Crustaceans have been shown to have a dietary dependency with regards to lipids such as essential fatty acids, phospholipids, and sterols.[45] It was reported that radiolabelled eicosapentaenoic acid (C20:5n-3) and docosahexaenoic acid (C22:6n-3) were primarily incorporated into phospholipids rather than neutral glycerides in the tissues of the Japanese spiny lobster (*P. japonicus*). In comparison, analysis of lipids and fatty acid profile in zooplankton that is a likely food source for *J. edwardsii* larvae was predominantly polar lipids (phospholipids), with triacylglycerols, free fatty acids and sterols following in descending order.[46] Furthermore, the major fatty acids measured were C22:6n-3 (docosahexaenoic acid), C16:0 (palmitic acid), C18:1n-9c (oleic acid) and C20:5n-3 (eicosapentaenoic acid). Fatty acid profiles shifted from predominantly saturated (i.e., C16:0 and C18:0) and monounsaturated (i.e., C16:1n-7 and 18:1n-9c) to polyunsaturated fatty acid dominate profile (i.e., C20:5n-3 and C22:6n-3) as the larvae developed into the settled juvenile form. In a recent study on wild European spiny lobster (*P. elephas*), the fatty acid profile was somewhat different,[47]with saturated (i.e., C16:0 and C16:0) and monounsaturated (i.e., C16:1n-7, C18:1n-9, and C18:1n-7) the dominant fatty acids in the muscle tissue comprising 42.67% and 32.30%, respectively of the total measured. Only 25.38% of the fatty acids were made up of polyunsaturated fatty acids with omega 6 (23.14%) being more dominant than omega 3 fatty acids (2.24%). However, the study did not specify what size class or sex the lobsters were but presumably from the collection gear stated these were mature adult individuals.

4.2.2 | Cholesterol

Like many other decapods, cholesterol is an important dietary required nutrient in spiny lobsters, as they cannot synthesise it de novo. This vital micronutrient is used as the precursor to produce ecdysteroid, a hormone that is primarily responsible for moulting, growth development and survival.[48] Earlier work in juvenile American clawed lobsters (*H. americanus*) showed that ∼0.5% cholesterol was the optimum level for this species in giving the highest growth and survival.[49] More recent work on the dietary cholesterol requirement of juvenile and sub-adult *P. ornatus* lobsters indicated that a dietary level of 0.35% cholesterol in the presence of 2.5% phospholipid is adequate for optimal growth and high survival.[50] Noted in the study, phospholipid plays a key role in the nutritional uptake of cholesterol as it acts as an emulsifier and facilitates transport in the body. It will be important to define the precise cholesterol requirements for *P. elephas*, especially during its critical juvenile stages of development to reduce mortalities.

4.2.3 | Macro and trace element requirements for spiny lobsters

The macro and trace element requirements for most lobster species have not been fully elucidated due to the difficulties in undertaking effective investigations to date. Consequently, we have very limited knowledge in this area that could apply to larval diets and on-growing stages of *P. elephas* culture. The earlier review by Allen and Gatlin[51] provides a good basis for fundamental nutritional requirements, including the function of macro and trace elements for crustaceans in general. Although, this is mainly for marine shrimp, such as those in the *penaeid* species.

In seawater, significant transient mineral uptake may be expected from gill and intestinal routes apart from dietary contributions. Calcium, phosphorus and trace metals, such as zinc, copper, iron, molybdenum, manganese and iodine, are essential for growth and metabolic function in decapods. Much could be learned from comparative tissue analysis of *P. ornatus* during key stages in the life cycle and profiling these tissues would provide indicative data on the nutritional requirement of key elements.[40]

The analysis of metal content in the European spiny lobster found that selenium and iodine were present in concentrations of ∼0.805 and ∼0.086 mg kg^{-1}.[42] The inclusion of selenium in the diet is crucial as it is an antioxidant and important in enzyme functions.[52] From the muscle tissue content, it can be assumed that the diet will need to consist of reasonable levels of the essential minerals as they cannot be synthesised, therefore, they must be ingested from the environment and food.[53] Further experiments are required using specific diets to ascertain the base level mineral requirements of the European spiny lobster.

4.2.4 | Vitamins

There is no known definitive vitamin requirement information available for *P. elephas*, and data are scarce for the full water-soluble and fat-soluble vitamins for most lobster species. There is little, if any, direct information on the vitamin requirements of spiny lobsters, but requirements determined for marine shrimp will be a useful guide until more specific information is available for lobsters.[54] All classes of vitamins will be required as essential cofactors for cellular metabolism and must be supplied in the diet. These include the B-complex, vitamin C (ascorbic acid) and vitamins A, D, E and K. The various phases of production from larval, grower and brood stock will need to be investigated but will pose significant research challenges.

4.2.5 | Carotenoids

Carotenoids are a necessary part of the diet in crustaceans and are utilised in important metabolic function and behavioural adaptations.[55] Among these are their important capacity for colouration, antioxidant role protection against oxidative reactive species in cell metabolism and photo-protection. They are typically deposited in the carapace and underlying epithelium esterified to proteins (carotenoproteins and crustacyanin) and lipids as a storage source for transportation to other tissues and organs (epithelial chromatophores) and particularly translocated to the gonads and ova during maturation. However, crustaceans are unable to synthesise carotenoids *de novo* and therefore are dependent on their diet to meet their demands but may transform specific carotenoids into other forms.

In decapods, astaxanthin is the predominant carotenoid and is more efficiently used by crustaceans than β-carotene. For Japanese spiny lobster (*P. japonicus*), these carotenoids (i.e., astaxanthin, adonixanthin, and pectenolone) are found as fatty acid esters form.[56] It is worth noting that in most crustaceans, β-carotene can be converted to astaxanthin and may be regarded as a precursor molecule to retinal (vitamin A).[15,57] Algae, and in particular microalgae, can be a dietary source of these natural carotenoids. For instance, *Dunaliella salina* is a microalga that is high in β-carotene and has been incorporated into crustacean aquafeeds.[57] Likewise, microalgae such as *Chlorella* and *Haematococcus* are also high in astaxanthin and used by commercial aquafeeds.[58] Nevertheless, astaxanthin was seen to have no impact on the growth or survival of juvenile *P. ornatus*.[34] However, it improved both parameters in juvenile black tiger prawn (*Penaeus monodon*).[59] It seems more likely that the European spiny lobster will respond similarly to *P. ornatus*. Although, it is possible that the lack of dietary carotenoids could reduce the growth and survival in *P. elephas*. Additionally, a diet without astaxanthin supplementation may result in a lack of shell pigmentation, this could reduce the market value of the product. Furthermore, astaxanthin is an important antioxidant, its presence improves recovery to thermal and osmotic stress in crustaceans and appears to be involved in immunocompetence.[15,60] As a parallel, the suggested dietary astaxanthin level is 50 mg kg^{-1} (dry weight) for the common European lobster (*H. gammarus*).[61] A dietary level of 50 mg kg^{-1} free astaxanthin (equivalent to ~80 mg kg^{-1} of carotenoid) was also found to be optimum in juvenile ornate lobsters (*P. ornatus*) which gave good carapace colouration.[32] From a commercial point of view, the inclusion of carotenoids may add to the cost of the feed; however, the benefits would outweigh the economic costs and should be added into the diets of spiny lobsters.

4.3 | Diets used in captivity

4.3.1 | Larval diets

To the author's knowledge, there are no published formulated diets suited for spiny lobster larvae or juveniles. However, there has been a bespoke diet kept under commercial confidentiality for *P. elephas* larvae between stages 1 and 5[62] and another for the Moreton Bay bug (*Thenus australiensis*[36]). These bespoke diets are stated in reports rather than cited in validated peer-reviewed scientific publications to date.[63] The *P. elephas* feed is claimed to possess an attractiveness duration of >15 h with pellets at an optimal size that is nutritionally appropriate for *P. elephas*.[62] The mouthpart morphology and its interpreted use in respect to diet are consistent between scyllarids-slipper lobsters (e.g., *Thenus australiensis*) and palinurids (e.g., *P. elephas*), which may allow for developed feeds to be applicable in both species.[9]

An appropriate feeding regime for larval European spiny lobsters (*P. elephas*) has yet to be determined. In previous cultivation studies, Kittaka[23] trialled *Artemia* nauplii during the larval stages and used blue mussel (*Mytilus edulis*) when the lobster larvae were more advanced in their development.[64] The author noted that there were high mortality rates due to the deterioration in water quality and particulate interference from the mussel flesh on the pereiopods, i.e., fouling. In later studies, Japanese sandfish (*Arctoscopus japonicus*) larvae and blue mussel (*M. edulis*) gonads were used as larval diets for many spiny lobster species, due to their high essential amino acids and fatty acids levels.[9,26] In particular, the use of Japanese sandfish (*A. japonicus*) larvae, which are high in lipids, reduced the time for *P. elephas* to reach puelurus from 132 days to 65–72 days. Long-chain polyunsaturated fatty acids, such as eicosapentaenoic (C20:5 n-3) and docosahexaenoic acid (C22:6 n-3), are 8 and 500 times, respectively, higher in Japanese sandfish larvae than those found in *Artemia* nauplii.[26] The survival to puerul was 0.005% using Japanese sandfish larvae, whereas it was 0.001% using mussel gonads. In comparison, in the earlier *P. elephas* study by Kittaka and Ikegami the survival rate was less than 1%.[23] However, it is worth noting that larval feed technologies have advanced substantially due to the demands in fish aquaculture with many commercial enrichment diets available in classically used larval live feeds, i.e., rotifers and artemia.

A previous investigation conducted by Limbourn & Nichols[18] has collated the research on the nutritional requirements of the larvae in several spiny lobster species. Although this work did not include *P. elephas*, it could allow parallels to be drawn. This study also analysed the protein content of *P. cygnus* at three developmental stages, i.e., newly metamorphosised puerulus, pigment developing pre-moult puerulus and post-moult juvenile. The subsequent protein contents were found to be ~80, ~100 and ~70 mg g^{-1} (dry weight), respectively. The protein decrease during development has been attributed to the production of a new exoskeleton post-moult. Furthermore, the study investigated the lipid content of the final stage phyllosoma of *P. cygnus*. The levels were reported as 238.5 ± 11.1 mg g^{-1} of lipid (dry weight), which decreased to 121.4 ± 4.3 mg g^{-1} after metamorphosis into puerulus, and further reduced to 53.6 ± 2.7 mg g^{-1} when moulting to the juvenile stage. These phases include intermoult periods where there is a cessation of feeding. However, late stage phyllosoma must attain a specific polar lipid (phospholipid) content and composition to facilitate growth and survival through the puerulus phase to a first feeding juvenile phase. These larval lipid profiles are expected to be similar in *P. elephas*. Therefore, a diet supplying these nutrient levels will be a prerequisite when considering larval rearing strategies in the hatchery.

4.3.2 | Juvenile diets

Similarly, little is known about the specific nutritional requirements of juvenile European spiny lobster (*P. elephas*). Studies on the protein and lipid requirements of similar species, such as *P. cygnus*,[65] *P. ornatus*[66] and *J. edwarsii*,[67] have been undertaken (Table 2). These experiments consisted of trialling dry pelleted feeds of 35–

TABLE 2 Protein and lipid requirements of juvenile lobster species and their impact on specific growth rates using dry and fresh feeds

	Western rock Lobster		Ornate spiny lobster		Southern rock lobster		European lobster	
	Panulirus cygnus		*Panulirus ornatus*		*Jasus edwardsii*		*Homarus gammarus*	
	Optimum dry feed	Mussel	Optimum dry feed	Kuruma shrimp diet	Optimum dry feed	Mussel	Optimum dry feed	Krill
Mean starting weight; g	0.54	0.56	3.80	3.90	3.58	3.60	0.86	0.86
Mean Final weight; g	0.93	2.00	5.10	6.60	7.11	10.28	–	–
Trial length; days	42	–	84	–	84	–	32	–
SGR[a]	2.78	6.11	1	2	0.82	0.92	~0.65[b]	~1.20[b]
FCR	2.50	–	–	–	3.76	2.46	–	–
Optimum level								
Protein (%, dw)	≥55	–	53	–	47	–	54.37	69.36
Lipid (%, dw)	6	–	10	–	9	–	9.38	11.44
References	65		66		67		68	

Note: Food conversion ratio (FCR) = g dry feed consumed / g wet weight gain.
[a]Specific growth rate (SGR) = ([ln final weight - ln initial weight] × 100 days^{-1}). Mussel, *Mytilus edulis*; Krill, *Euphausia superba*.
[b]Approximations are due to interpretation of the figure results.

60% crude protein in increasing amounts, with either 6 or 10% total lipid content on early juvenile lobsters. A diet of either opened/cracked blue mussels (*M. edulis*), or commercial kuruma shrimp (*Marsupenaeus japonicus*) feed (Lucky Star, Taiwan Hung Kuo Industrial Co., I-Lan, Taiwan), was used as a comparison against formulated pelleted feeds. Overall, these studies indicate that the ideal protein level ranges between 47 and 55%, and an ideal lipid level at 6–10% in formulated diets. The trial carried out on *P. cygnus* did not yield an optimum dietary protein requirement because the highest specific growth rate occurred in the treatment with the highest protein content. It is worth noting that these lobster trials were carried out in different temperature ranges (i.e., 18–28°C) which can affect feed digestibility and thus the optimal requirement of proteins and lipids.

In addition, Williams[15] speculated that (1) each species of spiny lobster may have different lipid and protein requirements, requiring species-specific feed; and (2) the optimum feeds produced less growth than the mussel/shrimp, and less than observed in nature. Therefore, these experiments may not provide an accurate insight into the dietary requirements of the lobster.

4.4 | Improving nutrition and feeding technologies

The greatest cause of mortalities in many spiny lobster cultures is nutritional deficiencies.[9] For any form of stock enhancement or aquaculture to be successful, an appropriate diet is needed that provides all the essential nutrients throughout all developmental stages. To develop a successful feed for spiny lobsters, other attributes besides nutritional content need to be considered including palatability, hardness, rate of degradation (durability), size, shape and digestibility. There are several artificial diets available on the market that serve the needs of shrimp, and in particular penaeid shrimp, from the hatchery to grow-out and especially for the Pacific white legged (*L. vannamei*). There are also bespoke diets for various species of crab and crayfish. Recent work by Hinchcliff et al. presented a novel European claw lobster (*H. gammarus*) dry feed developed from the flocculation of shrimp wastewater, this dry feed yielded the greatest SGR when compared with other experimental diets while performing marginally worse to the control wet feed consisting of shrimp.[69] Such commercial diets may suffice, but to the authors' knowledge, these have not been investigated for *P. elephas*. While feed studies have been conducted in other Palinurids species, this is not guaranteed to meet the same nutritional specifications for this European species. To bridge some fundamental knowledge gaps in *P. elephas* nutrition, baseline studies of the nutrient composition of the various larval and juvenile stages should also be addressed in parallel studies. In the meantime, propriety diets should be considered as a preliminary route to achieving feasible *P. elephas* production in any farmed system. This will aid in developing a suitable dietary regime by elucidating essential nutritional requirements. Such studies are typically based on a linear dose–response design, i.e., increasing nutrient level or an ingredient in the feed that would yield an ideal or highest favourable response. However, mixture design studies could offer an alternative method in finding the optimum nutrition requirement that would both reduce study time and resources being expended. This would involve several nutrients of interest being included within the same feed. By testing different permutations of the various nutrient inclusion levels, it is possible that response surface statistics could discern the ideal nutrient requirements.[70] Such studies have been carried out on fish species in the past, for instance, Hamre and Mangor-Jensen[71] investigated the potential of optimising the dietary requirement of protein, lipid and carbohydrate in Atlantic cod weaning diets using a three-component feed study design (*Gadus morhua*).

4.4.1 | Improving larval nutrition

It has been suggested that dry diets are unsuitable for the phyllosoma stages of spiny lobsters. As a more suitable alternative, a gelatinous diet with 60–80% moisture content may be more appropriate and better represent natural prey.[63] Furthermore, diets with high moisture content are believed to release more chemo attractants than dry feed and this could lead to a higher feeding response and less fouling of the water column. This has certainly been observed with stage 1 southern rock lobster (*J. edwardsii*), where high moisture diets did not foul their maxillae as seen in the dry diets.[72] Past research has shown that xanthan gum, acacia and even gelatine could be used to provide a gelatinous texture to diet but also give higher moisture content without affecting palatability.[63] A neutrally buoyant feed would be preferable as this would increase the availability of the food in the water column. This is especially important during their phyllosoma stage, while a more negatively buoyant feed is needed for their settled stages to reduce leaching time in the water column. The use of microencapsulation can be used to limit leaching in dry diets. However, with moist diets, double encapsulation could also be used to increase nutrient bioavailability.[73] Ultimately, microencapsulation feed technology can reduce the deterioration in water quality by stabilising the nutrients and lead to higher survival rates through lower incidences of disease outbreaks and fouling.

The diets that have been used in early *P. elephas* larval rearing have consisted primarily of *Artemia* nauplii,[64] although a later study had shown sailfin sandfish (*A. japonicus*) larvae and mussel gonads were also possible (*M. edulis*).[26] Feeding copepods could be a means by which to deliver the necessary nutrients such as *Acartia tonsa* nauplii that are <100 μm to the lobster larvae and easily digestible.[74] Furthermore, copepods have a higher content of polyunsaturated fatty acids such as eicosapentaenoic (C20:5n-3) and docosahexaenoic acid (C22:6n-3), which are potentially responsible for reducing the time to puerulus in *P. elephas* from 132 days to 65–72 days.[26,75] It should be noted that these lipids are stored in the form of wax esters rather than triglyceride as found in fish oils. Therefore, in terms of the enrichment of artemia and other live foods, wax esters are better assimilated in the larval stages of most marine organisms by using copepod.[76] As such, the nutritional value of copepods can be altered based on the microalgae fed to them, and in turn, delivering the necessary nutritional requirement of the lobster larvae.[77] In addition, there are a number of copepod species that are commercially used in larval feeding.[78] Specifically, *Apocyclops royi* is believed to be promising species as population density is not limiting a factor, where culturing densities can be brought up to 10,000 individuals per litre.[79] Researchers and hatcheries should be mindful that even though live feeds can deliver the necessary nutritional requirements to the phyllosoma larvae, they can also be a source of bacterial contamination that could lead to production losses. As such, the long-term goal for any commercial larval production units would be to develop and use formulated feeds that are free from this issue.

4.4.2 | Improving juvenile nutrition

Improving feed intake in culture systems will mitigate the impact of waste feed degradation, thereby, reducing costs and water quality deterioration. It has been observed that *J. edwardsii* handling and maceration of pellet feeds can result in up to 50% in food wastage, however, presenting an appropriate size pellet can reduce this wastage by 19%.[80] For juvenile *P. ornatus* with a body weight of 2 g, a pellet 10–15 mm long with a diameter of 1 mm is most suitable. While 60 g individuals, a pellet of 10–20 mm long with a 3 mm diameter was found to be optimal at reducing wastage.[19] In comparison, Hoang and Huong[81] found 60 g *P. ornatus* juveniles had the lowest mortalities when fed with noodle-shaped pellet feeds with a diameter of 1.5 mm diameter. Another method to optimise formulated feeds is to use stoichiometric bioenergetics to determine metabolic energy substrate use, this will improve feeding regimes and therefore protein-sparing and growth performance. Stoichiometric bioenergetics consist of measuring nitrogenous excrement and respiratory gas levels, this can then be used to determine metabolic energy substrate use.[82]

Furthermore, the inclusion of krill meal has been favourable when incorporated into *P. ornatus* feeds. Krill has high levels of carotenoid pigments and high free amino acids and peptides content that increase the visual attractiveness of the feed. Moreover, krill have similar fatty acid and amino acid profiles to *P. ornatus*, therefore, providing essential nutrients.[83] Similarly, the use of probiotics, prebiotics and symbiotics need to be investigated for the beneficial effects they can provide. Their inclusion in *H. gammarus* diets has been extremely positive with significant increases in growth, survival and stress resistance.[84]

4.5 | Nutrient digestibility

The consumption of formulated feed by juvenile southern rock lobster (*J. edwardsii*) is seemingly limited by the small foregut found in many spiny lobsters, the expansion of feeds post-immersion and the long digestion time. These limitations result in a daily food consumption amounting to a single foregut which is approximately 2–3% of the lobsters' body weight.[20] If this physiological trait is similar in *P. elephas*, improving the digestibility and utilisation of proteins, carbohydrates and lipids will be vital in producing an effective feed. Protein solubility has been suggested as a key factor in *J. edwardsii* protein digestion, with methods such as freeze-drying or low-temperature drying (<60°C) to increase fish meal solubility also proposed. The initial assessment of carbohydrate suitability in formulated feeds for spiny lobsters should be the postprandial glycaemic response as it is a quick method for obtaining nutritional information on carbohydrates.[85] The carbohydrates most digestible in *J. edwardsii* are carboxymethyl cellulose and the polysaccharides dextrin, mussel glycogen and gelatinised starches.[86] This suggests carboxymethyl cellulose could be used as a binding agent in spiny lobster formulated feeds.[87] Although developing an appropriate feed has been the major barrier to successful spiny lobster aquaculture, there are also other areas (e.g., health, stocking conditions, tank designs) that require attention to maximise survival and growth rates.

5 | HEALTH AND WELFARE MANAGEMENT OF *PALINURUS ELEPHAS*

Maintaining the health and welfare of farmed animals is necessary for meeting legislative requirements and consumer demands. Poor farming practices often manifest themselves as physical damages and/or disease outbreaks in the animals. Unlike other species (e.g., fish and shrimps), lobsters, in general, are traded as a live food source. Physical damages, deformities and discolouration on the shell can often impact consumer acceptability and market value. Correct stocking densities can reduce these issues, especially in lobsters that exhibit cannibalism and aggressive behaviour in a social environment.[88] For *P. elephas*, individuals can naturally live in solitary or in small groups,[6] which differs from the locally found clawed lobster, *H. gammarus*. This trait could allow for greater stocking densities with *P. elephas*, with less risk of cannibalism or physical damage as seen in *H. gammarus*.[89]

5.1 | Infectious diseases

Most of the infectious diseases identified in the different life stages of spiny lobsters are opportunistic infections (Table 3). It is also possible that pathogens could be conveyed into a production facility by wild specimens, such as establishing a brood stock or collections of seedstock, e.g., ornate lobsters with latent infections. These diseases occur when lobsters are either injured during moulting, post-moulting, inadequately fed, poor nutrition or/and under stress.[86] The latter include poor water quality, sudden temperature change, salinity, handling, transportation, sound and high stocking densities.[90,91] To avoid the onset of infectious conditions, it is important to provide good water quality during the rearing process, but also minimise chronic and acute sources of stress. In addition, disease surveillance as part of the hatchery and on-growing facilities' shellfish health management plan and meeting the nutritional requirement of the reared lobster will further prevent disease outbreaks.[92]

5.1.1 | Bacterial infections

Bacterial infections are commonly reported in farmed operations and can lead to high mortalities.[93] The early stages in lobster development are often the most susceptible to bacterial infections, particularly to *Vibrio* and *Aquimarina* pathogen species.[92,94]

Hatchery vibriosis

Vibriosis refers to any infectious disease caused by the genus *Vibrio* (Table 3). It is mainly observed in early life stages and adversely impacts the survival rate during the hatchery phase. Opportunistic pathogens, including *Vibrio* sp., have been described as the causative agents of phyllosoma vibriosis in Palinurid lobsters.[95,96] A significant proliferation of potential pathogens in the hatchery may result in phyllosoma vibriosis.[97] There are four main compartments from the larval rearing system that contribute to bacterial growth, including pathogenic *Vibrio* species: water column in the tank, biofilm formation, the use of live feeds such as *Artemia*, and the phyllosoma themselves.[95] Phyllosoma vibriosis can occur in all the six larval instars of *P. elephas*.[26] The disease occurs fast as *Vibrio* grows inside the phyllosoma, leading to larval death.[98] Transmission routes include cannibalism of infected larvae and ingestion of contaminated food sources.[92] It has been reported that high mortality rates of ∼90% have been observed 2 to 4 days post-infection.[99]

Tail fan necrosis

Tail fan necrosis, also known as tail infection, is a common form of shell disease in both juvenile and adult spiny lobsters, including *P. elephas* (Table 3). This condition was predominantly described in an aquaculture research facility by Mancuso et al. (2010). It starts with a lesion or abrasion on the carapace caused by an injury.[100] The infection is characterised by the appearance of melanised and erosive lesions on the tail fan (Figure 3). Microscopically, an inflammatory response occurs associated with melanisation, as well as pseudomembrane formation.[100,101] The natural microbiota of the lobster body is believed to be responsible for causing shell diseases, acting as opportunistic pathogens.[101] Chitinolytic bacteria are recognised as causative agents of this shell disease.[93,100] Mild cases of tail fan necrosis commonly do not lead to death. However, secondary infections increased the chance of mortality and morbidity. The unattractive aspect of a damaged carapace negatively affects its market price. Whereby rather than being sold as a live animal, the damaged animal is classed as a lower grade for prepared meals, preserved or canning.[102]

Other bacterial infections

Despite not being described in *P. elephas*, other bacterial infections may be a potential health risk for farmed European spiny lobster. Surveillance programmes and good health practices should be in place to avoid the spread of potential pathogens in the European spiny lobster.

Milky haemolymph disease (MHD) has affected tropical, juvenile and adult spiny lobster species, particularly in *P. ornatus*, *P. homarus* and *P. stimpsoni*.[103] Four rickettsia-like bacteria species has been recognised as the causative pathogens.[104] High turbidity and milky appearance of the haemolymph of infected animals can be observed when a high loading of the pathogen invades the haemolymph.[103,104] Affected lobsters often become lethargic and anorectic, and individuals soon die after the clinical signs are displayed.[103] Although the disease has so far been reported in farmed lobsters in Vietnam. Other diseases may also lead to milky haemolymph, e.g., *Panulirus argus* virus 1 and protozoan infections.[93,105]

TABLE 3 Main infectious diseases identified in Palinurid and homarid lobsters

Disease and affected life stage	Infectious agent	Known susceptible lobster	Clinical signs	Possible treatment	References
Hatchery vibriosis (spiny lobster larvae)	*Vibrio alginolyticus*,	Palinurid lobsters, inc.	Darkness of midgut gland	Mannan oligosaccharide dietary supplementation 0.4% diet, 60 days	95
	Vibrio campbellii	*Panulirus ornatus*	Enteritis	Sodium nifurstyrenate 10 mg L^{-1} 3–5 h day^{-1}	91
	Vibrio harveyi	*Palinurus elephas*	Erosion of gut epithelium	Green water technology (*Nannochloropsis* spp.)	96
	Vibrio jasicida		Septicaemia		26
	Vibrio natriegens		Larval death		119
	Vibrio owensii				
	Vibrio parahaemolyticus				
	Vibrio proteolyticus				
	Vibrio rotiferanus				
	Vibrio tubiashii				
Tail fan necrosis (juvenile and adult)	Chitinolytic bacteria, inc.	Spiny lobsters, inc.	Lesion inflammation	Formalin (10 mg L^{-1})	120
	Aeromonas hydrophila	*Palinurus elephas*	Erosive tail fan lesion	Malachite green (5 mg L^{-1})	100
	Shewanella spp.		Melanisation of tail fan lesion	(bath)	101
	Vibrio alginolyticus		Darkness of carapace		93
	Vibrio anguillarum		Pitting	Vaseline	121
	Vibrio parahaemolyticus		Uropod ulceration	(topic)	
	Vibrio vulnificus		Autotomy		
Milky haemolymph	*Rickettsia-like bacteria*	*Panulirus ornatus*	Lethargy	Oxytetracycline (10 mg kg^{-1})	104
disease		*Panulirus homarus*	Anorexia		
(juveniles >3-month-old, adult)		*Panulirus stimpsoni*	Milky appearance of haemolymph	(Intramuscular injection)	103
			Death soon after clinical signs		
Gaffkemia	*Aeroccocus viridans*	Homarid lobsters, inc.	Weakness	Oxytetracycline (1 g lb^{-1})	122
(larvae)	(var.) *homari*	*Homarus americanus*	Anorexia	(by feed)	96
		Homarus gammarus	Reddish discoloured carapace		123,124
			Pink haemolymph		
		Palinurid losbters, inc.	Pink abdomen		
		Panulirus argus[a]	Bleeding disorder		
		Panulirus interruptus[a]	Heavy mortality due to septicaemia		

TABLE 3 (Continued)

Disease and affected life stage	Infectious agent	Known susceptible lobster	Clinical signs	Possible treatment	References
Panulirus argus virus 1 infection (juvenile & adult)	*Panulirus argus* virus 1	*Panulirus argus*	Lethargy	NA	109
			Milky appearance of haemolymph		125
			Not clotting haemolymph		108
			Pale, fouled carapace		107
			Energy depletion		
			Dysbiotic gut microbiota		
			High mortality (up to 100%)		
			Adults are asymptomatic		
White spot syndrome (juvenile and adult)	White spot syndrome virus	*Palinurus homarus*[a]	Asymptomatic carrier	NA	110
		Panulirus longipes			96
		Panulirus ornatus			
		Panulirus penicillatus[a]			
		Panulirus polyphagus			
		Panulirus versicolor			
Fusariosis (adult)	*Fusarium solani*	Spiny lobsters, inc.	Anorexia	NA	91
		Panulirus cygnus	Melanised lesions		93
		Panulirus ornatus	Eroded, dark, thick lesions on carapace, abdomen and appendages		116
			Brownish discolouration of gills		
			Autotomy of damaged appendage		
			High mortality during moulting		
Oomycetes infection (eggs, larvae, low occurrence in adults)	*Aphanomyces astaci*	*Palinurus japonicus*	Anorexia	Formalin (20 mg L^{-1})[b]	126
	Atkinsiella panulirata		Lethargy	Malachite green (0.05–0.1 mg L^{-1})[b]	127
	Haliphthoros mildfordensis		Mortality	(bath)	116,128
Microsporidiosis	Microsporidians	*Panulirus argus*	Coagulative necrosis	NA	117
	Ameson-like microspodidians	*Panulirus cygnus*	Milky muscle appearance		116
		Panulirus ornatus	Muscle loss		118

Abbreviation: NA: not available.
[a]Experimental infection observations.
[b]Pre-treatment trial required to avoid overdosing.

The so-called Gaffkemia (or red tail disease) is a systemic infection that has primarily been reported in homarid lobsters (e.g., *H. americanus* and *H. gammarus*, Table 3).[93] The condition is caused by the bacterium *Aerococcus viridans* (var.) *homari* and is associated with the low health status of the larvae, inadequate water quality and high stocking densities.[106] Palinurid lobster species are believed to be highly resistant to *A. viridans* (var.) *homari* infections, as observed in challenge infections in the Caribbean (*P. argus*) and California spiny lobsters (*P. interruptus*).[93,96]

5.1.2 | Viral infections

Viral diseases in Palinurid lobsters are rarely reported. It has been suggested that the limited viral diseases found in lobsters including Palinurid are because it is receiving limited research attentio.[93] Although so far, two viruses are known to infect Palinurid lobsters.

Panulirus argus virus 1

The *P. argus* virus (PaV1) is a lethal, naturally occurring pathogen in juvenile and adult Caribbean spiny lobster (*P. argus*). The virus can be found widespread on the Western coast of the Atlantic Ocean, from Bermuda to Brazil, with a prevalence ranging from 5 to 37%.[107,108] The infection has been reported in two culture facilities in the state of Florida, USA. The disease is observed in benthic juveniles, which die due to metabolic exhaustion after 5 to 7 days displaying the clinical signs.[108] After 30 to 80 days post-infection, mortalities can reach up to 100%.[109] Although the virus pathogen affects spiny lobsters, it has been reported that adult lobster individuals in different species are commonly asymptomatic carriers.[108] It has been identified that disease transmission primarily occurs through direct contact, waterborne, ingestion of infected tissue and inoculation. Avoidance behaviour can be observed in uninfected lobsters, which chemically detect and avoid proximity to diseased lobsters. Such avoidance behaviour occurs as soon as a lobster individual becomes infectious.[93]

White spot syndrome

Spiny lobsters, including *P. elephas*, are not a natural host to the white spot syndrome virus (WSSV). Nevertheless, WSSV has been identified in different organs (inc. epidermis, gills, hepatopancreas, stomach) in experimentally infected Palinurid lobster species including *P. homarus*, *P. longipes*, *P. ornatus*, *P. penicillatus* and *P. versicolor*.[93] Natural infections have been described in *P. longipes*, *P. ornatus*, *P. polyphagus* and *P. versicolor*.[110,111] Infected lobster individuals did not present clinical signs of disease for over 70 days.[110] As such, both European Food Safety Authority (Council Directive 2006/88/EC) and the World Organisation for Animal Health-OIE[112] declared that all decapod crustaceans are susceptible host species. Furthermore, it has been suggested that Palinurid lobsters (inc. *P. elephas*) may be a reservoir of the virus and an asymptomatic carrier.[93]

5.1.3 | Fungal infections

Despite few studies devoted to marine fungi, this group of potential pathogens are found in all marine habitats, and their biomass is hypothesised to surpass even the level of bacterial biomass in the wild.[113,114]

Fusarium sp.

Fusarium sp. is a terrestrial fungal genus with opportunistic pathogenic species (e.g., *F. solani*) that can infect adult spiny lobsters, leading to death just before or during moulting.[91] The fungus invades the lobster body through damaged cuticles or dead tissues.[91,115] The condition is mostly observed in farmed lobsters; however, it has also been described in wild individuals, e.g., *P. cygnus*.[91,116] Proximity to wood and poor water quality especially in high organic load is believed to induce the disease.

Oomycetes

Oomycetes are saprophytic fungus-like eukaryotic microorganisms that are widespread in different ecosystems. A small number of pathogenic marine oomycetes are known to infect palinurid lobsters. They mainly infect the lobster eggs and larvae and are rarely reported in adult animals.[93] One of these pathogens, *Haliphthoros mildfordensis*, has been associated with mortalities in spiny lobster aquaculture facilities.[116] To the authors' knowledge, oomycetes have not been reported infecting the European spiny lobster (*P. elephas*).

Microsporidiosis

Microsporidians have been found in wild spiny lobsters, e.g., *P. argus*, *P. cygnus* and *P. ornatus*.[116,117] The microsporidians can infect the muscle tissue. The typical clinical sign of the disease is a milky muscle with a cooked appearance due to the heavy microsporidia infection. For this reason, the condition is also known as 'white tail' or 'cotton disease'.[117,118]

5.2 | Farming welfare

5.2.1 | Farming-related stressors

Farm machinery and equipment such as tank circulation pumps, protein skimmers, air blowers or aeration paddles can all emit an array of sounds and vibrations into the water column and rearing tanks. This could potentially have implications on farmed animals' growth performance, health and survival. For instance, it has been observed that lobsters have a higher locomotive activity when exposed to the boat and other underwater noises.[129] Subsequent analysis on noise-exposed animals' total haemocyte counts (e.g., hyalinocytes, semigranulocytes and granulocytes) showed these were up to 30% lower than non-audio stimuli animals. The embryonic development in spiny lobsters was not affected by the noise or vibrations.[130] Nevertheless, sensitivity to underwater noise in the on-growing of

P. elephas means that farms will need to be strategically designed and built to minimise or even eliminate noise and vibrations-induced stresses.

Similarly, photoperiods, light intensity, nutrient loading, temperature and other water parameters, e.g., dissolved oxygen will need to be optimised to maintain a health and welfare status in the farmed populations. For example, at a low temperature of 10.5°C, the early stage of *J. edwardsii* development did not progress beyond phyllosoma stage II.[131] Juvenile southern rock lobster (*J. edwardsii*) exposed to constant light or darkness suppressed animal activity and lower food consumption rates compared with a lighting regime of 12:12, light: dark photoperiod.[132]

5.2.2 | Stocking density and rearing conditions

Another aspect of good animal husbandry is achieving the optimal stocking density and stocking conditions for the specific species. This includes stocking density management, as well as providing an environment in which animals feel safe and free from threat.

Spiny lobsters can be reared at high densities; however, it is advised that suitable habitat is set up within tanks to ensure peaceful and stress-free cohabitation. The optimum stocking density of spiny lobsters is unknown for many spiny lobster species, including the European spiny lobster. For the ornate spiny lobsters, they can tolerate high stocking densities with ~80 adult individuals being reported in a single sea cage (4 × 4 m).[133] Furthermore, communal rearing has even been seen to increase the specific growth rate in juvenile ornate spiny lobsters.[79] Trials have also shown that under farm raceway conditions, ornate lobsters can tolerate densities from 14 to 43 kg m^{-2}, without compromising survival rates.[78,134]

It is widely accepted that in the wild, *P. elephas* favours a habitat with an abundance of holes, crevices and overhangs in which to take shelter. Díaz et al. (2001) monitored the preferred substrate of juvenile spiny lobsters after settlement in the western Mediterranean Sea.[4] Results indicated that recently settled juveniles were primarily found in holes carved into the rock by date mussels (*Lithophaga lithophaga*) on surfaces that were either vertical or had a significant overhang. As individuals grew, however, the size of date mussel holes made them a less suitable shelter, thus it has been reported that adult lobsters upgrade from small holes to larger spaces for shelter (e.g., under rocks and boulders). European spiny lobsters have also shown a strong preference to shelter shape and size. It was found that 55% of captive juvenile spiny lobsters favoured a semi-circular shelter shape, compared with 16.5% for square and 11% for circular shelters.[135] Further tests found a positive linear trend between the diameter of the favoured shelter and carapace length. The study also determined that 63% of individuals favoured a shelter inserted into an overhang of 35° vs. a shelter inserted into a vertical structure. It may be of benefit to incorporate natural substrate to mimic a wild environment. For *P. homarus* juveniles, there was a preference for triangular-shaped shelter over PVC piping, square and tube-shaped shelters.[136] Other studies have shown that shelters suspended in the water column at open-water sea sites significantly increased survival rates in spiny lobsters.[17,137,138] Adding shell and sand into the rearing systems of European claw lobster (*H. gammarus*) has been shown to aid their claw development during stages 5–7.[139] This technique of environmental enrichment could also be applied to *P. elephas* resulting in healthier and hardier individuals.

High mortalities have been observed in captive crustaceans subjected to unsuitable handling and housing conditions.[140] Thus, a suitable shelter must be available in the rearing environment of both the correct shape and size to facilitate wild type behaviour and reduce the potential for stress on housed individuals. This could be achieved by providing hides made from plastic piping and earthenware,[141] which would not only provide shelter but also create an artificial reef habitat by enabling microflora to settle.[142] In addition, sufficient space should be left clear for individuals to carry out foraging behaviour.

5.2.3 | External shell fouling

Shell fouling typically affects lobster larvae, including Palinurid's phyllosoma stage. For example, the filamentous marine bacterium *Leucothrix mucor* is recognised as one of the main agents for shell fouling. Other microorganisms may be associated with the condition, such as the protists (*Zoothamnium* sp., *Vorticella* sp. and *Acinata* sp.), filamentous bacteria (e.g., *Thiothrix* sp.) mesomycetozoeans, cyanobateria (e.g., *Lyngbya* sp.), parasites and eco-symbionts (e.g., *Lepas* sp., cestode larvae, copepods, nematodes, worms), and fungi.[116,118,143,144] Fouling organisms are typically evident in the gill chamber of lobsters before moult occurs or at the terminal moulting stage (Figure 1C).[118] The consequences of fouling are lower oxygen uptake and increased energetic demand for swimming.[91] Additionally, the condition impairs the phyllosoma feeding ability by interfering with food capture and the mastication process. Overall, this has a negative impact on the animal's nutrition, prolonged inter-moult stage, and favours the proliferation of opportunistic pathogens.[96]

In the wild, Palinurid lobsters live primarily in oligotrophic waters, with little dissolved organic matter or suspended solids. Thus, if there is an increase in the particulate organic matter (e.g., due to low feed quality) or silt in the water column, this could potentially foul the setae on the thoracic appendages during larval stages.[96] Consequently, a heavy bloom of fouling organisms would impact larval locomotion and their ability to stay in the water column, leading to the phyllosoma slowly sinking and ultimately death. Fouling organisms can be commonly found in seawater systems and phyllosoma cultures. As such, it has been suggested that appropriate system water treatment (e.g., seawater pasteurisation for algal cultures, UV, or ozonation) and effective system designs are used to prevent bloom formation.[92]

As particulates can foul the setae during phyllosoma stages, water low in particulates should be used in the aquaculture of this species such as that achieved through microfiltration membranes.[145] The use of ozonation as water treatment has been reported to have detrimental effects by causing deformities in *P. elephas* larvae and subsequent mortalities. It has been suggested that this is maybe due to a reduction in essential nutrients, e.g., oxidation of unsaturated fatty acids and vitamins.[63]

To reduce biofouling and settlement of the early larval stages, it is imperative that the larvae remain suspended in the water column, but more importantly, that contact with other larval individuals is reduced as they are prone to cannibalism and their appendages clumping together. At least six different tank designs have been examined for their suitability for phyllosoma rearing, including:

(a) Horizontal gyre,

(b) Vertical upweller – cone,

(c) Vertical upweller – column,

(d) Vertical kreisel,

(e) Raceway and,

(f) Parabolic tank.

These designs have incorporated different directions of water flows, current speeds, flow rates, recirculation and flowthrough provision of water, static and periodic bulk water exchange.[96] The primary aims of these system parameters are (1) increasing the availability of food, (2) maintaining larval suspension in the water column, (3), and ensuring larvae separation to avoid cannibalism. The horizontal gyre has a circulating water flow maintained by airlift pumps, this keeps feeds suspended in the water column and larvae evenly dispersed.[146] The use of aeration may not be beneficial as it can damage larvae while not providing enough circulation resulting in the larvae aggregating at the bottom of the tank.[147] It has been reported that *J. edwardsii* larvae have been reared in a vertical upweller—column with some success.[148] This design uses vertical water flow to maintain the larvae in suspension and is appropriate for live feeds, survival was >60% to late-stage larvae. Murakami et al.[149] used a vertical kreisel to rear *P. japonicus*, the advantage of which is that it increased the encounters of the larvae with the mussel gonad feed. Unfortunately, it also increases the contact between larvae. Compared with the bowl-shaped tanks previously used, the survival rate almost tripled but the number of larvae with damaged limbs also increased. Mass mortalities of *H. gammarus* have occurred for unknown reasons using parabolic tanks and therefore given there are other options their use in larval rearing seems ill-advised.[150]

5.2.4 | Gut health

The gut microbiome plays a critical role in the overall health of the host organism. This has major implications that include impacts on growth, digestion, immune response and resistance to pathogens.[94] The core gut microbiome of *P. ornatus* is dominated by Tenericutes and Proteobacteria, with *Vibrionaceae* also being commonly found in the intestinal tract, which likely plays a role in digestion.[151] In-depth studies on *P. elephas* gut microbiota are however limited, but inferences can be made with other species where data exists from recent investigations. Microbial colonisation of the gut is derived from the surrounding environment.[152] A recent study by Holt et al.[153] compared the microbial gut communities in *H. gammarus* cultured on land and at sea. The sea-based lobsters had gut microbiota with significantly higher species richness and diversity. Gut microbiota can notably affect the overall health of the host. *H. gammarus* individuals lacking diversity in gut microbiota were found to be more susceptible to the viral pathogen *H. gammarus* nudivirus (HgNV). This suggests that sea-based aquaculture could potentially be beneficial to the health of organisms and that for land-based systems providing a diverse diet for juveniles to seed the gut microbiota may be necessary.[154] We can also assume that more attention could be given in future to the use of functional feed additives such as prebiotics and probiotics in formulated diets, that may assist in promoting robustness and performance in the rearing to *P. elephas*. This is comparable to commercial shrimp farming where functional ingredients that act upon the gut health and microbiome structure are already being widely employed.

6 | CREATING A SUSTAINABLE LOBSTER FARMING MODEL

Ranching is the stocking of an organism with the explicit interest of removing the organisms after it has grown, this differs from stock enhancement that seeks to increase wild stocks.[154] The ranching of European spiny lobsters could be financially feasible, with current trading market prices potentially offsetting the time and resource investment in such commercial rearing. This method has been implemented with *H. gammarus* where released individuals were successfully recaptured above the no catch size limits.[155] The cost–benefit of ranching lobsters has been questioned, the primary concern being that overall recapture rates from these projects were below 5%.[156] Given the difficulties previously mentioned (wild juvenile availability etc), we believe the most sustainable option is to create a closed production model, requiring a hatchery to facilitate year-round production of eggs and larvae. For a hatchery to be successful it will require appropriate diets, suitably designed systems and the ability to maintain high water quality.

From this basis, a breeding programme could be formed. To develop a breeding programme for *P. elephas*, wild broodstock should be captured and on-reared in a hatchery facility. These should be screened to ensure there is a broad genetic base upon which to build the programme. The conditions in broodstock tanks (e.g., temperature, pH, salinity, dissolved oxygen, photoperiod, stocking densities, hides/shelters, male: female ratio) must be optimised to prevent stress. Furthermore, adult lobsters require conditioning (optimal nutrition over the period where gonads develop) to ensure optimal gonadal maturation, which must also be investigated to understand species-specific requirements. This should include evaluations of steroid hormones and fatty acids requirements.

In parallel, genetic samples should be taken to establish if production/harvest traits of economic value can be selected into the breeding line. These traits have been estimated, in crustaceans, to improve by up to 10% per generation through selective breeding.[157] Vijayakumaran et al.[158] developed a broodstock programme for *P. homarus*. By modifying the nutrition and rearing conditions, they were able to increase the average number of viable spawnings per female from <2 to 4 per year. Before selective breeding and genetic improvement can commence it will be necessary to:

(1) Produce F1 and F2 cohorts of lobster, i.e., close the production loop. F1 cohorts are lobsters bred from wild lobsters, F2 cohorts are bred from two F1 lobsters.

(2) Estimate genetic variation within the broodstock (to determine effective population size).

(3) Calculate heritability estimates of key traits.

Once these have been established it will be possible to selectively plan breeding cycles to produce genetically superior lobsters with the desired traits. This is an essential part of producing a sustainable aquaculture system as it does not rely upon extracting spiny lobsters from the natural environment, which is currently the norm in other parts of the world, to provide for the industry.[133]

To add further justification in creating a long-term farm broodstock for aquaculture is the fact that some European countries prohibit the capture of berried females. While others, like the UK, explicitly prohibit the landing of European spiny lobsters while the females are berried (UK Statutory Instrument 2000 No.874), except for exclusively used in research and restocking purposes.[159] This could ultimately have implications for countries that do not have the legal mechanism to allow wild individuals to be used as broodstock and a stock enhancement programme.

The production of settled lobsters from a hatchery operation will lead to the on-growing stage into market size adult lobsters. The technical challenge will be to grow the lobsters using an economically viable method, particularly feeding, as it takes 2–3 years to grow into the market size, such difficulties have been seen in *H. gammarus* on-growing.[161] With further information (e.g., on biology and economics), it will be possible to calculate specific growth rates and feed conversion ratio parameters to optimise cost-effectiveness and predict trajectories for attaining harvest-size spiny lobsters (Figure 4, 2b). On-growing of ornate spiny lobster in Vietnam typically uses 'trash' fish (e.g., trimmings or low-value fish) to feed the animals; however, this can have an impact on water quality, disease transmission risk and poor growth performance.[133] For low-value fish, the FCR was calculated between 12 and 25 depending on the year and affected by the nutrient variability/limitations in low-value fish being fed to the lobsters.[162] In addition to diet, the design of the production facility needs to be considered if the farming operation is to be economically viable, biosecure and overall fit for purpose. While it may also warrant

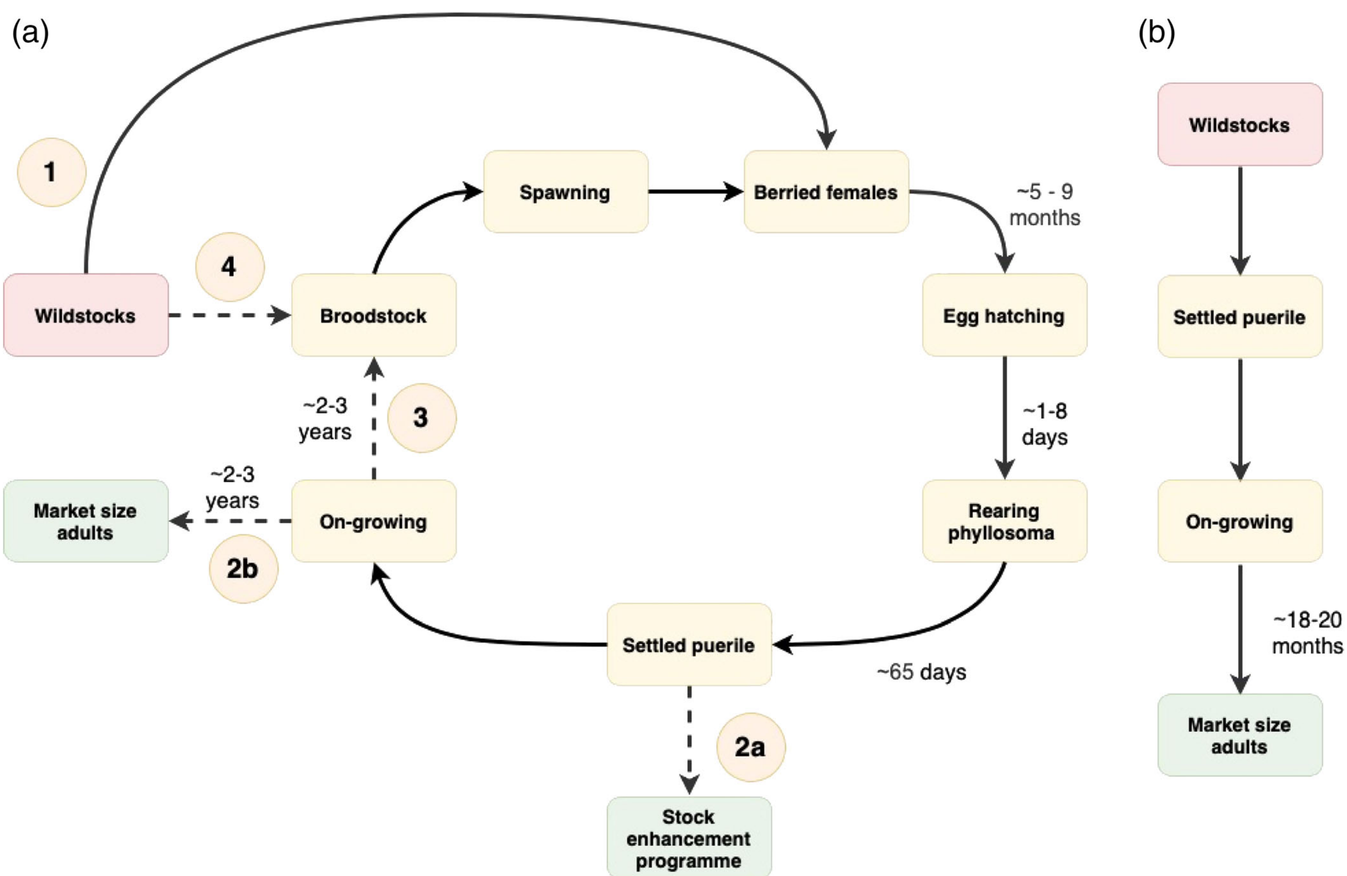

FIGURE 4 (a) The potential of European spiny lobster (*Palinurus elephas*,). Times were measured from the point of hatching, except for the egg incubation period. Duration of developmental stages taken from previous published studies.[5,6,23,26] The time to Market size adults and broodstock was based upon wild growth rates, average fecundity size[6,26] and minimum size legislation.[160] Production cycle; (b) in comparison with current farmed ornate spiny lobster (*Palinurus ornatus*). Time to market size adult is from on-growing in captivity.[133] Potential inputs (1 and 4) and outputs of this farming cycle (2a, 2b and 3) cultivating spiny lobster in a communal setting to improve growth performance and behaviour, as this was observed in *Sagmariasus verreauxi* spiny lobsters.[163]

The use of recirculating aquaculture systems (RAS) has been highly advocated as the future for the aquaculture industry, growing aquatic species in a controlled manner to mitigate disease risk, wastewater effluent impact, environmental impact through the potential of farming closer to the consumer demand (e.g., towns and cities) and an array of other benefits.[89,164] Overall, there is a higher degree of control for optimising the production system. However, the initial capital investment (e.g., capital RAS equipment and equipment consumables) and running cost (e.g., heating/chilling the water, electricity demand for circulation pumps, ozonation, ultraviolet light sterilisation) are typically higher than on-growing in sea cages.[165] The use of robotics and artificial intelligence could reduce labour costs and maximise feeding. In Norway, this has been put into practice with the production of European lobsters (*H. gammarus*). This technology is used for the feeding of individual lobsters, welfare control, tracking moulting rate and monitoring survival, growth, and harvest time.[166] This approach should guarantee a more uniform and consistent product at a more stable price than that of seasonal and unpredictable wild catches. Moreover, with continuing refinements such as the development of more efficient lobster production techniques and an increase in survival rate to market size, the farmed lobster wholesale price could be comparable or lower than wild fished individuals.

In contrast, farming lobsters out at sea could require less capital investment, but they would also be exposed to potential disease outbreaks, toxic algal blooms and reduced growth caused by lower seasonal sea temperatures during the winter months. An integrated multitrophic aquaculture (IMTA) system is the concept of co-rearing at least two trophic levels of aquatic organisms where there is intentionally managed energy exchange (i.e., food) within the same water body. There is a fed species (e.g., finfish) cultivated alongside extractive species such as suspension or deposit feeders.[167] IMTA can be coastal or offshore with suggestions that the latter has less concentrated environmental impacts.[168] The on-growing of lobsters at sea in an IMTA model could compensate for the reduced growth performance with several advantages. Subsequently, the potential rearing of spiny lobsters adjacent to fish sea cages (e.g., seabass, salmon and sea bream) could allow passive feeding of the lobsters with the fish waste, e.g., uneaten food and faecal matter. This is economically beneficial as the cost of feeding is reduced and lessens the environmental impact by transforming waste residues into a valuable co-product. This can be illustrated by a recent study where common juvenile European lobsters (*H. gammarus*) were held for 319 days close to salmon sea cages.[169] The study showed that the lobsters utilised the salmon waste residues as a food source through stable isotope analysis; however, growth performance was not improved or decreased by this farming strategy. The co-culture dependency would add to the production time scale to achieve the optimal harvest weight of lobsters and would likely be challenging in practice, e.g., disease outbreaks and treatments on the salmon and changing water temperatures. Ultimately, any uptake of technologies by the farmer such as a new method of cultivating practice will need to have a socio-economic consideration such as local support, acceptance and willingness to adopt the practice.[170]

7 | CONCLUSION

In summary, there is a clear justification for farming this species due to their higher economic value in comparison with many other shellfish found in Europe and beyond, but also there are limited wild stocks. There are more reported wild observation studies than aquaculture research for this species. Consequently, this has created knowledge deficits that would otherwise allow the full realisation of spiny lobster farming. To address this issue, future studies need to focus on advancing several crucial areas through the following descending priorities:

Fundamental understanding

1. A comprehensive understanding of *P. elephas* biology.
2. Closing the *P. elephas* life cycle, especially the larval stages.
3. Determining the fundamental nutrient requirements of *P. elephas* at all stages of the life cycle and applying this knowledge to formulating practical diets for their culture

Establishing commercial productions

4. Novel rearing methods of *P. elephas* to increase survival rates, welfare and animal robustness to disease and stress.
5. Creating a *P. elephas* broodstock that is optimised for farming conditions.

Improving production levels and sustainability

6. Employing novel technologies in culturing *P. elephas* to enhance survival, e.g., tank designs and time-release/microencapsulation of feed nutrients.
7. Use of IMTA and RAS technologies to sustainably rear *P. elephas*.

While the aquaculture of *P. elephas* is not currently feasible due to our incomplete knowledge base to date, targeted research into the aforementioned areas would progress this goal. Given the similar biological traits of *P. elephas* to *P. ornatus*, the authors are confident that the rearing improvements observed for *P. ornatus* in recent years can also be applied to *P. elephas*. This would result in the addition of a promising high-value crustacean species to Mediterranean, European and indeed global markets.

AUTHOR CONTRIBUTIONS

Adam Lien-Kym Yeap: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; visualization; writing – original draft; writing – review and editing. **Cecilia Souza Valente:** Conceptualization; methodology; project administration; supervision; validation; writing – original draft; writing – review and editing. **Finnian Hartnett:** Conceptualization; data curation;

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CONFLICT OF INTEREST

The authors would like to declare that there is no conflict of interest relating to the content of this review.

DATA AVAILABILITY STATEMENT

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

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