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REVIEW

REVIEWS IN Aquaculture

Addressing the welfare needs of farmed lumpfish: Knowledge gaps, challenges and solutions

Carlos Garcia de Leaniz[1] | Carolina Gutierrez Rabadan[1] | Sara I. Barrento[1] | Rebecca Stringwell[1] | Paul N. Howes[1] | Ben A. Whittaker[1,2] | Jessica F. Minett[1] | Robert G. Smith[1] | Craig L. Pooley[1] | Ben J. Overland[1] | Leigh Biddiscombe[1,3] | Richard Lloyd[1] | Sofia Consuegra[1] | Jake K. Maddocks[1] | Paul T. J. Deacon[1] | Ben T. Jennings[1] | Sonia Rey Planellas[4] | Amanda Deakin[5] | Amber I. Moore[6] | Daniel. Phillips[7] | Guillermo Bardera[8] | Maria F. Castanheira[9] | Maria Scolamacchia[10] | Nancy Clarke[11] | Ollie Parker[1,3] | John Avizienius[12] | Malcolm Johnstone[12] | Michalis Pavlidis[13]

[1]Centre for Sustainable Aquatic Research, Swansea University, Swansea, UK
[2]Department of Integrative Biology, University of Guelph, Canada
[3]Three-sixty Aquaculture, Swansea, UK
[4]Institute of Aquaculture, Stirling University, Stirling, UK
[5]FAI Farms, Oxford, UK
[6]MOWI Ireland, Cloghmore, Ireland
[7]Ocean Matters, Penmon, UK
[8]Moredun Scientific, Penicuik, UK
[9]University of Algarve, Faro, Portugal
[10]National Research Council, Torre Grande, Italy
[11]World Animal Protection, London, UK
[12]Royal Society for the Prevention of Cruelty to Animals, Horsham, UK
[13]Department of Biology, University of Crete, Greece

Correspondence
Carlos Garcia de Leaniz, Centre for Sustainable Aquatic Research, Swansea University, Swansea, UK.
Email: c.garciadeleaniz@swansea.ac.uk

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Abstract

Lumpfish (*Cyclopterus lumpus* L.) are increasingly being used as cleaner fish to control parasitic sea lice, one of the most important threats to salmon farming. However, lumpfish cannot survive feeding solely on sea lice, and their mortality in salmon net-pens can be high, which has welfare, ethical and economic implications. The industry is under increasing pressure to improve the welfare of lumpfish, but little guidance exists on how this can be achieved. We undertook a knowledge gap and prioritisation exercise using a Delphi approach with participants from the fish farming sector, animal welfare, academia and regulators to assess consensus on the main challenges and potential solutions for improving lumpfish welfare. Consensus among participants on the utility of 5 behavioural and 12 physical welfare indicators was high (87–89%), reliable (Cronbach's alpha = 0.79, 95CI = 0.69–0.92) and independent of participant background. Participants highlighted fin erosion and body damage as the most useful and practical operational welfare indicators, and blood parameters and behavioural indicators as the least practical. Species profiling revealed profound differences between Atlantic salmon and lumpfish in relation to behaviour, habitat preferences, nutritional needs and response to stress, suggesting that applying a common set of welfare standards to both species cohabiting in salmon net-pens may not work well for lumpfish. Our study offers 16 practical solutions for improving the welfare of lumpfish and illustrates the merits of the Delphi approach for achieving consensus among stakeholders on welfare needs, targeting research where is most needed and generating workable solutions.

KEYWORDS
cleaner fish, Delphi expert assessment, feeding rations, habitat preferences, operational welfare indicators, Salmon farming

1 | INTRODUCTION: THE NEED FOR WELFARE INDICATORS FOR LUMPFISH

There are ~250 species of fish farmed globally[1] which account for 52% of fish used for human consumption.[2] Yet, despite the scale of the fish farming industry—and evidence that fish are sentient, very little is known about the welfare needs of most farmed fish.[3-5] Specific welfare standards and Animal Health Codes have been developed for some intensively farmed species such as the Atlantic salmon (*Salmo salar*)[6-8] and the rainbow trout (*Oncorhynchus mykiss*),[9,10] but only generic guidelines exist for most farmed fish.[11,12] For most farmed fish, knowledge on their welfare needs typically lags behind advances on production.

The Atlantic lumpfish (*Cyclopterus lumpus* L.) is a case in point. Lumpfish are a novel species to marine aquaculture whose farming has increased exponentially over the last 10 years and represents one of the fastest-growing aquaculture sectors in Europe.[13] Unlike most farmed fish, lumpfish are not farmed for human consumption, but are used (along with some temperate wrasse) as cleaner fish to control parasitic sea lice (*Lepeophtheirus salmonis*).[13-15] Sea lice are one of the major threats to salmon farming [16] as it causes huge economic losses[17] and compromises the welfare of wild and farmed salmon alike,[18,19] tarnishing public's perception of salmon farming.[20,21] Sea lice have developed resistance to most anti-parasitic chemical compounds,[22] prompting an interest in the use of cleaner fish as a 'green' alternative to chemotherapeutants.[13] However, lumpfish survival in salmon net-pens is often poor, and there is increasing concern regarding their welfare.[23,24] Studies have shown that lumpfish mortalities can reach 27% or more shortly after deployment in salmon net-pens[25-31] although the reasons for this are not clear.[30] Emaciation, stress, diseases and poor knowledge of the specific nutritional and habitat requirements have been flagged as some of the main welfare challenges for the species.[32-34] Many of these problems stem from the fact that salmon farming has evolved to suit the needs of Atlantic salmon, not those of cleaner fish. For example, exposed sites that may be appropriate for salmon may have currents that are too strong for lumpfish.[35]

The soundness of using cleaner fish to control sea lice is also being questioned on efficacy grounds,[36,37] as delousing efficacy varies enormously among studies, from 9% to 97% in lumpfish.[37,38] Yet, until more powerful preventive methods are developed, ie vaccines, artificial selection,[39] the judicious use of cleaner fish will continue to offer the industry an attractive and cost-effective means of controlling sea lice,[38,40] but only if cleaner fish welfare is not compromised.[13]

Most Europeans (79%) want better welfare in the salmon farming industry[41] and are willing to pay more for the salmon they eat,[42] but it is essential that solving one problem for salmon farming (sea lice control) does not create a welfare problem for lumpfish. The cost of poor fish welfare in salmon farms has recently been estimated at $4.6 billion,[43] but sacrificing one species for another species' welfare cannot be the way forward.[44]

The welfare of lumpfish cannot be improved without welfare indicators. These need to be practical and easy to use, or they will not be used by fish farmers.[45,46] Operational welfare indicators (OWIs) are designed to address this practical need (as opposed to laboratory-based indicators) and should provide an objective assessment of the welfare of the fish that can easily be scored at the farm,[6,47] can be used to benchmark farming operations and can serve to identify areas in need of improvement and develop best practices, as done for Atlantic salmon,[6] ballan wrasse[48] and rainbow trout.[9] However, assessing the welfare of lumpfish poses particular challenges, caused mostly by the lack of agreed guidelines. Some welfare indicators have recently been developed for lumpfish,[27,49,50] but only a few have been validated and can easily be used by fish farmers.[49,51]

The benefits of having agreed welfare standards and guidance for improving the welfare of lumpfish are multiple. For example, operational welfare indicators are now stipulated in quality assurance schemes, without which certification cannot be made. Achieving high welfare makes economic sense, as fish with deformities and low welfare do not survive as well.[51,52] Reducing the incidence of lumpfish with deformed suckers, and skeletal deformities,[53] may improve delousing efficacy and consequently reduce the number of cleaner fish required by industry. Higher welfare should also result in less stressed lumpfish which might reduce the risk of pathogen cross-transmission from one species to the other.[13,54] Ultimately, improving the welfare of lumpfish will help increase the sustainability, social acceptance and reputation of the salmon farming industry, but only if agreed, evidenced-based welfare standards are used to demonstrate improvements.

2 | AIMS

The aims of this study were threefold: (1) to identify the main challenges and knowledge gaps surrounding lumpfish welfare, (2) to offer potential solutions and identify opportunities for improving lumpfish welfare and (3) to assess the degree of consensus among different stakeholders on the value of different welfare metrics.

3 | USING THE DELPHI APPROACH TO IDENTIFY CHALLENGES AND PRIORITISE SOLUTIONS

We hosted a workshop dedicated to Lumpfish Welfare (Swansea, 14 May 2019- https://www.welfareaquaculture.com/1st-symposium) with the participation of 53 experts from three main stakeholder groups: fish farming, academia and animal welfare. We employed a Delphi approach to identify the main challenges, opportunities and potential solutions for improving lumpfish welfare and for making their use in salmon farming more sustainable. The Delphi approach seeks to harness the value of expert judgment through consultation rounds and is based on the tenet that the views of a group are more authoritative (and thus more likely to gain support and become adopted) than the views of individuals. This approach is increasingly being used to prioritise knowledge needs in fields where opinions may differ among knowledge users, such as aquaculture[55] and animal welfare.[56] The classic Delphi approach is entirely anonymous, but we used a 'modified Delphi approach' that benefitted from group discussions, as in other applications to animal welfare.[56-58] Consultation followed by open discussion does not guarantee consensus, or can be a substitute for research, but it can help identify what experts consider important and reduce the risk that key issues are not being missed.

A three-step process was implemented (Figure S1), similar to that described in other prioritisation assessments.[55] In the first step, participants were divided into 10 pre-allocated tables consisting of 4–5 people representative of the three stakeholder groups, and a facilitator. Each participant was asked to write (in coloured notes and independently of each other) a list of the main knowledge gaps, opportunities and solutions for improving the welfare and sustainability of lumpfish. In the second step, each table was asked to find common answers and to reach a consensus on the three most common answers. In the third step, each table reported their answers to the whole group, all colour coded notes were displayed and the most popular answers were identified and compiled. Steps 2 to 3 were repeated for the three aspects pertinent to lumpfish welfare (knowledge gaps, main challenges and potential solutions), lasting 90 min in total.

We classified each challenge, solution and opportunity proposed by the expert group into broad semantic types (e.g. knowledge gap, husbandry, nutrition, health and disease, training, monitoring, etc.) and used their relative frequencies as measures of their relative importance. We then calculated the joint probability of occurrence for each challenge and solution identified by the focus group and used the *circlize* R Package [59] to visualise the relation between the most important challenges and solutions via a flow (chord) diagram.

4 | PERCEIVED UTILITY OF DIFFERENT WELFARE INDICATORS

To assess the perceived utility of different welfare indicators for lumpfish (i.e. their usefulness under farm conditions), a close-ended questionnaire was given to participants (Table S1) who were asked to (1) identify their background, (2) rank the utility of 5 behavioural and 12 physical welfare indicators for lumpfish and (3) specify which of the indicators (if any) were used at their facilities to assess the welfare of lumpfish. Participants were given five minutes to complete the form independently of each other. To estimate the perceived utility of each welfare indicator, we converted the responses to a 4-point Likert scale and used the *clmm2* cumulative link mixed model in the *ordinal* R package [60] to assess the degree of consensus among participants. We used the *psych* package [61] to calculate Cronbach's alpha as an indicator of the reliability of each welfare indicator separately, as well as globally.

5 | DIFFERENCES IN THE NICHE OF LUMPFISH AND ATLANTIC SALMON

Lumpfish are deployed with Atlantic salmon but conditions that may be suitable for one species may not be adequate for the other. We, therefore, compiled data on 23 traits that define the habitat niche and life history of the two species and calculated the specific absolute difference for each trait (%), on the assumption that the more different two cohabiting species are the more likely it is that conditions may become unfavourable for one of them. Information was compiled from FishBase[62] and the primary literature. We then examined the main differentiating traits of lumpfish, the potential welfare implications and the consequences for commercial production.

TABLE 1 Challenges (C), solutions (S) and opportunities (O) for improving the sustainability and welfare of farmed lumpfish identified by a focus group, weighted by their relative frequency (LF = lumpfish).

Challenges (*n* = 40)	Weight
Knowledge gaps—0.35	
C1. Unusual species, general biology	0.32
C2. Behaviour	0.23
C3. Extent and reasons for mortality	0.16
C4. Thermal preferences and maximum currents	0.13
C5. Welfare needs	0.10
C6. Genetics	0.06
Husbandry and Logistics—0.17	
C7. Grading	0.13
C8. Shelters and enrichment	0.13
C9. Breeding programme and domestication	0.13
C10. Separating LF from salmon and removal prior to cage treatment	0.13
C11. Appropriate light levels	0.07
C12. Anaesthetic	0.07
C13. Water quality (RAS, microbial loads)	0.07
C14. Better facilities for LF	0.07
C15. Working on remote sites	0.07
C16. Balance between welfare and efficiency/output	0.07
C17. Focus on salmon needs—little on LF needs	0.07
Nutrition—0.12	
C18. Poorly known nutrition requirements (including weaning on *Artemia*)	0.45
C19. Criteria for supplemental feeding in cages	0.36
C20. Lack of useful probiotics	0.09
C21. Limited knowledge on diet in sea cages	0.09
Health and Disease Management—0.12	
C22. Uncertainty on vaccine efficiency or need	0.27
C23. Transport stress	0.18
C24. High incidence of deformities	0.09
C25. Handling stress	0.09
C26. Lack of information on diseases and transmission	0.09
C27. Unknown stress basal values	0.09
C28. Disease screening for live broodstock	0.09
C29. Bacterial infectious diseases	0.09
Training and Staffing—0.08	
C30. Lack of SOPS and guidance for sampling	0.57
C31. Training, staff skills and dedication	0.43
Monitoring and Screening—0.07	
C32. Difficult to collect data, particularly in sea cages (morts., sea lice)	0.83
C33. Assessing body condition (Fulton's condition factor is unreliable)	0.17
Environment—0.06	
C34. Impact of noise pollution	0.20

(Continues)

TABLE 1 (Continued)

Challenges (*n* = 40)	Weight
C35. Poor water quality (microbial loads)	0.20
C36. High incidence of escapees	0.20
C37. Biosecurity risks of wild broodstock	0.20
C38. Reliance on wild broodstock and impact on natural populations	0.20
Knowledge Exchange and Communication—0.02	
C39. Communication between hatchery plants and sea farms	1.00
Economics—0.01	
C40. High cost	1.00
Solutions (*n* = 40)	**Weight**
Husbandry and Logistics—0.35	
S1. Acclimatisation before cage deployment (including feeding on sea lice)	0.16
S2. Closing the breeding cycle in captivity	0.10
S3. Better tank design, dedicated broodstock facilities	0.10
S4. Technology (eg basket under lifted kelp, non-stick surfaces)	0.10
S5. Recondition and reuse of broodstock	0.06
S6. Sperm bank and collecting sperm from live males non-destructively	0.06
S7. Lower densities	0.06
S8. Selective breeding (genetics)	0.06
S9. Deployment plans and fish of adequate size (currently too small)	0.06
S10. Appropriate husbandry (eg salinity adjustment for FW baths)	0.06
S11. Tank/cage enrichment	0.03
S12. Use of sterile fish to reduce the impact of escapees	0.03
S13. Combining wrasse with lumpfish	0.03
S14. Choice trials to establish thermal optima	0.03
S15. Disease challenges to advance disease management and vaccines	0.03
Training and Staffing—0.16	
S16. Welfare guidelines and indicators	0.50
S17. Training and practical guidelines (various)	0.36
S18. Guidelines for cage deployment	0.07
S19. Guidelines for transport	0.07
Knowledge Exchange and Communication—0.16	
S20. Marketing and public awareness	0.43
S21. More knowledge exchange and collaborations	0.36
S22. Better internal communication between hatcheries and sea-farms	0.21
R&D—0.15	
S23. Generic	0.38
S24. Basic research	0.15
S25. Applied research	0.08

(Continues)

TABLE 1 (Continued)

Solutions (*n* = 40)	Weight
S26. Morphology	0.08
S27. Vaccines	0.08
S28. Nutrition	0.08
S29. Impacts on wild stocks	0.08
S30. Sucker deformities	0.08
S31. Reuse of farmed lumpfish at end of the cycle (eg caviar)	0.08
Monitoring and Screening—0.13	
S32. Generic	0.36
S33. Disease screening	0.18
S34. Selection of broodstock for selective breeding	0.18
S35. Delousing efficacy	0.09
S36. Passive grading	0.09
S37. Better data collection	0.09
Nutrition—0.05	
S38. Improved feeding management	0.75
S39. Block feeds	0.25
Economics—0.01	
S40. More funding	1.00
Opportunities (*n* = 43)	**Weight**
R&D—0.54	
O1. Innovative reuse (biomedical/feed/fertiliser/release/broodstock)	0.23
O2. Closing breeding cycle, domesticate	0.12
O3. Habitat preferences, limiting parameters and rearing conditions	0.12
O4. Behaviour salmon-lumpfish, delousing variation	0.12
O5. Selective breeding for desirable traits (eg growth, welfare)	0.10
O6. Welfare research, legal protection (welfare/slaughter/transport)	0.08
O7. Alternative species for cleaning sea lice, other solutions to LF	0.04
O8. Health, disease prevention and diagnostics, better vaccines	0.04
O9. Better diets (insect-based protein feeds) and feeding methods	0.04
O10. More research—better understanding in all areas	0.04
O11. UK egg sourcing	0.02
O12. More research on wild stocks	0.02
O13. Big data and data mining	0.02
O14. Stress indicators	0.02
O15. Market demand research (consumer - research - production)	0.02
Technology—0.15	
O16. Monitoring technologies (tagging/loggers/sonar/cameras)	0.22
O17. Shelters and cage designs to facilitate natural behaviours	0.11

(Continues)

TABLE 1 (Continued)

Opportunities (*n* = 43)	Weight
O18. Use of renewable energies at sites	0.11
O19. Automated systems	0.11
O20. Efficient transport and deployment	0.11
O21. Integrated approaches	0.11
O22. More specialist hatchery equipment	0.11
O23. Quick and effective method to remove from cages prior to treatment	0.11
Knowledge Exchange and Communication—0.13	
O24. More networking and collaborations industry-academia	0.33
O25. Welfare indicators including certification and best practice	0.25
O26. Marketing and consumer awareness, emphasise good things	0.25
O27. Increase openness and transparency	0.17
Husbandry and Logistics—0.10	
O28. Adaptation to cages, optimise environment and husbandry	0.20
O29. Freshwater treatment for AGD	0.10
O30. Commercial scale research	0.10
O31. Link production and supply to production cycles	0.10
O32. Use of local stocks	0.10
O33. Behavioural welfare index	0.10
O34. Strategies for reducing mortalities	0.10
O35. Better grading practice - more often	0.10
O36. Training LF to feed on sea lice	0.10
Nutrition – 0.06	
O37. Better diets (incl. use of algae), based on nutritional requirements	0.50
O38. Better feeding methods	0.50
Monitoring and Screening—0.04	
O39. Improved monitoring of mortalities and LF health in sea cages	0.50
O40. Screening and identification of robust cleaners	0.25
O41. Better monitoring of cage escapees – impacts on wild populations	0.25
Training and Staffing—0.02	
O42. Improved recruitment of trained and experienced people	1.00
Economics—0.01	
O43. Funding for innovative and integrative research	1.00

6 | WELFARE GAP ANALYSIS

6.1 | Challenges

The 53 participants in the welfare workshop originated from four distinct backgrounds: animal welfare (*n* = 20; 38%), fish farming (*n* = 16; 30%), academia (*n* = 14; 26%) and other (*n* = 3; 6%). They identified 40 different challenges in relation to lumpfish welfare, spanning knowledge gaps, husbandry and logistics, nutrition, health and disease management, training and staffing, monitoring and screening, environment, knowledge exchange and communication, and economics (Table 1).

The most important knowledge gaps were thought to be in relation to the general biology, motivated by its unusual morphology and clinging habits,[63] the little information available on many aspects of its behaviour,[64-66] the extent and causes of mortality,[67] the preferences of the species in relation to temperature [30,68,69] and current velocity,[70] as well as its genetic structure[71,72] and specific welfare needs.[51] In terms of husbandry and logistics, participants highlighted problems surrounding the optimal timing and frequency of grading, the correct use of shelters[73] and tank enrichment, the development of a breeding programme[13] and the practical difficulties of separating lumpfish from salmon prior to cage treatment. Other, less pervasive challenges related to optimal light levels which are poorly known in lumpfish,[27,74] the choice and use of anaesthetics,[75] poor water quality and permissible bacteria loads,[76,77] lack of specific facilities for the rearing of the species, and the logistic constraints caused by working at remote sites. The challenge of balancing the welfare needs of lumpfish with efficiency in salmon production and a tendency to prioritise the needs of Atlantic salmon over those of lumpfish[44] were also flagged as particular issues.

The main challenges related to the nutrition of lumpfish were thought to be caused by limited knowledge on their nutritional requirements at all life stages, from uncertainties on the weaning of *Artemia*[13,78] to the specific dietary needs during the deployment stage,[79,80] lack of agreed criteria for supplemental feeding in cages (including specific diets for net-pens, feeding regime and mode of delivery) and limited availability of useful probiotics (but see[81]).

The main problems related to health and disease management included vaccine efficacy and needs,[32,82] uncertainty on basal cortisol stress values—which vary widely among studies[51,83-85] and makes it difficult to properly manage stress during handling and transport, a high incidence of sucker deformities in some egg batches, uncertainties on the incidence and transmission routes of infectious diseases[32] and disease screening of broodstock.[13,86,87] Selective breeding using novel genomics approaches has improved disease resistance and adaptation to captivity in Atlantic salmon and other farmed fish, and the same approach can be developed for lumpfish.[72]

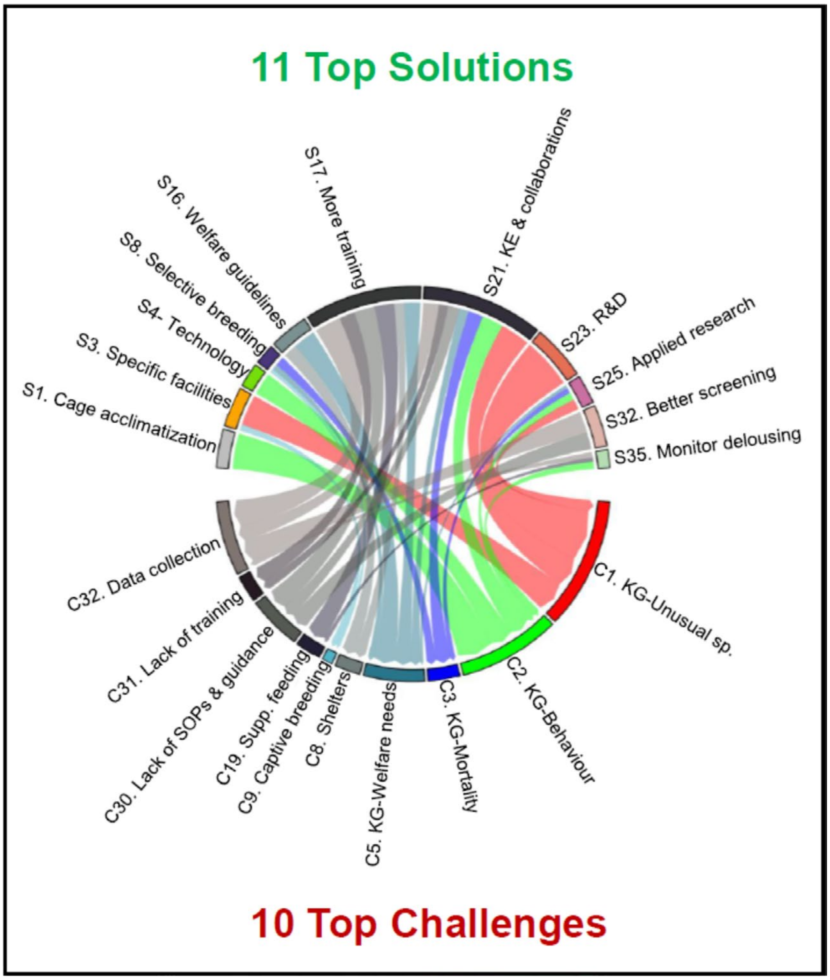

FIGURE 1 Flow diagram showing the relationship between the 10 most important challenges (C) for improving the welfare and sustainability of farmed lumpfish and the corresponding solutions (S) identified by the focus group. The width of the chords is proportional to the joint relative frequency of occurrence and the numbers refer to Table 1 (KG: Knowledge gap)

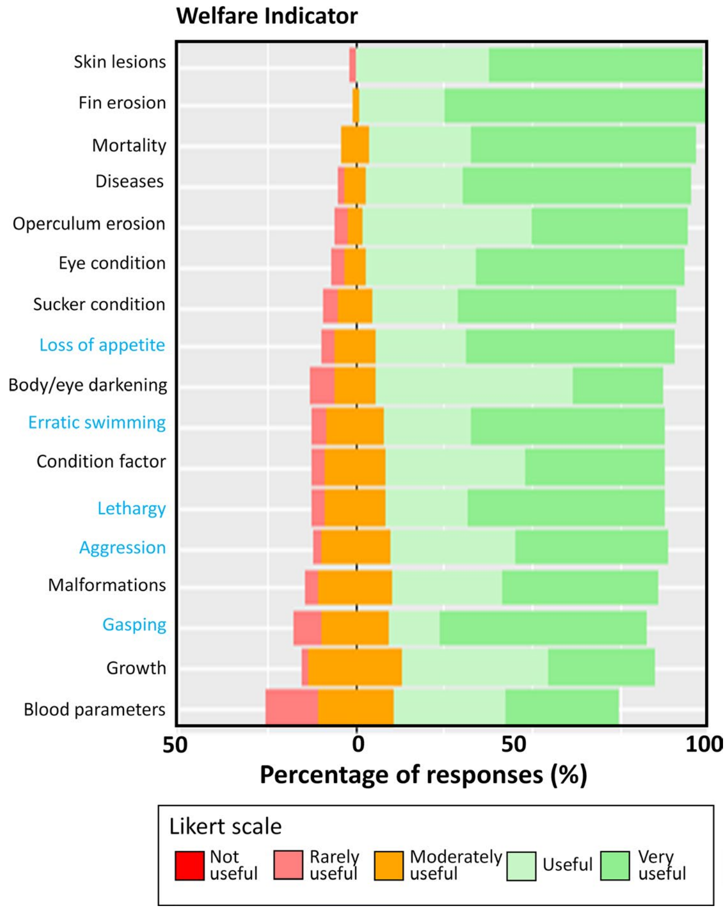

FIGURE 2 Perceived utility on a 4-point Likert scale of 5 behavioural indicators (in blue) and 12 physical indicators (in black) for lumpfish. Shown are the responses of 53 participants in the first workshop on the *Welfare of Lumpfish*

Other challenges highlighted by the focus group included lack of standard operating procedures (SOPs) and guidance for collecting data, particularly in sea cages (including data on mortalities and delousing efficacy), the need for staff training and guidance on monitoring and assessing body condition and optimal weight as condition factor is unreliable for this species owing to its round shape.[51] Lumpfish are often injured or stressed unnecessarily when salmon are treated and harvested at sea,[7,29] and these, along with their humane slaughter, are the aspects that would also benefit from having clear SOPs.

The impacts of noise pollution, potential water quality issues due to high microbial loads[76,77] and the risk posed by escapees through genetic introgression[88] were flagged as environmental issues, along with biosecurity risks derived from using wild broodstock and the impacts that this may have on wild populations.[43,71] Poor communication between hatchery plants and sea farms and the high costs of producing and caring for lumpfish were also highlighted as minor challenges in relation to economics. Accurate figures on the cost of cleaner fish in relation to salmon production costs are not readily available, but a recent study of 11 sea-lice control measures[40] estimated that cleaner fish had an efficacy of 0.72 (range 0.60–0.90) and were the third most cost-effective control measure (£0.14 per fish per unit of effectiveness), after in-feed medication and use of skirts as physical barriers (£0.10 cost-effectiveness).

6.2 | Solutions

The focus group identified 40 potential solutions to the challenges highlighted above (Table 1). Most of the solutions proposed by the expert group referred to husbandry and logistics, training and staffing, knowledge exchange and communication, and research and development. Other, less popular, solutions addressed challenges in relation to monitoring and screening, nutrition and economics.

The main solutions in relation to husbandry and logistics include acclimatising lumpfish to live in net-pens before cage deployment (including feeding on sea lice[89]), closing the breeding cycle of the species in captivity,[13] using tanks and facilities specifically suited for the needs of this species, using clinging devices to retrieve lumpfish from cages without damaging them, using surviving lumpfish as broodstock, setting a sperm bank and collecting sperm from live males non-destructively,[90,91] lowering rearing densities, selectively breeding fish for high delousing efficacy and robustness[26,49,92] and growing fish to a larger size before deployment to reduce escapes[88] and increase salmon-cleaner fish interactions.[93] Other solutions included using tank enrichment and freshwater baths for specific diseases,[94] using sterile fish to reduce the impact of escapees,[13] deploying lumpfish with other cleaner fish,[65] determining habitat

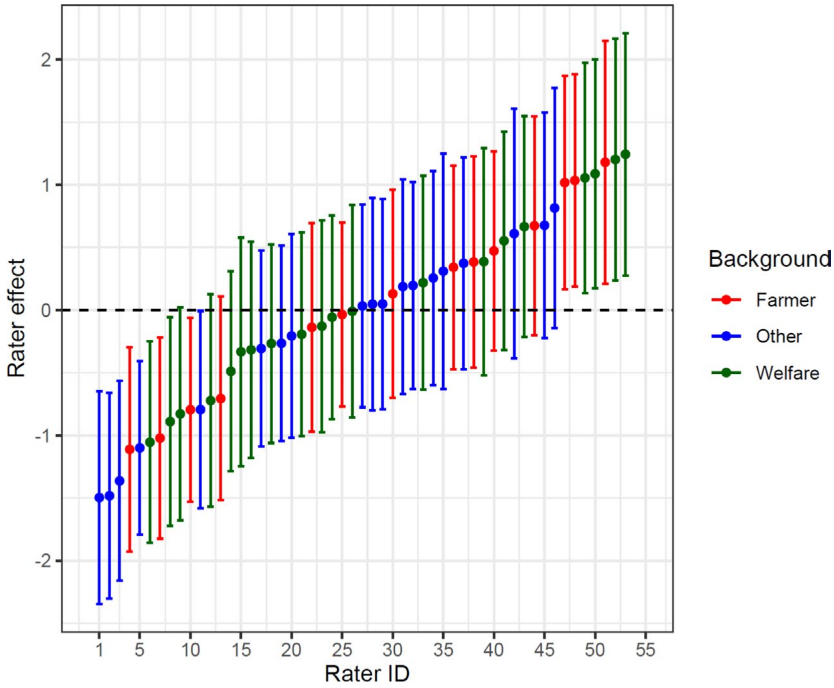

FIGURE 3 Variation among 53 participants in the *Welfare of Lumpfish* Workshop on the utility of 17 welfare indicators (5 behavioural + 12 physiological) for farmed lumpfish. Shown are estimated 95% confidence deviations from the average rater (dotted line) based on the conditional variance, classified by rater background. Consensus among raters was 89% for behavioural indicators, 87% for physical indicators and 68% overall

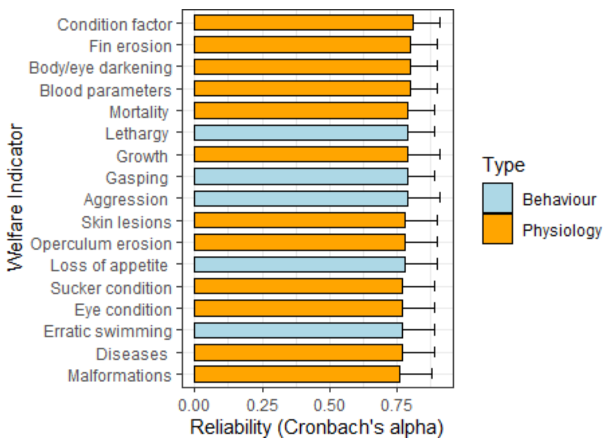

FIGURE 4 Reliability (Cronbach's alpha ± 95CI) of 5 behavioural indicators (in blue) and 12 physical indicators (in orange) for lumpfish

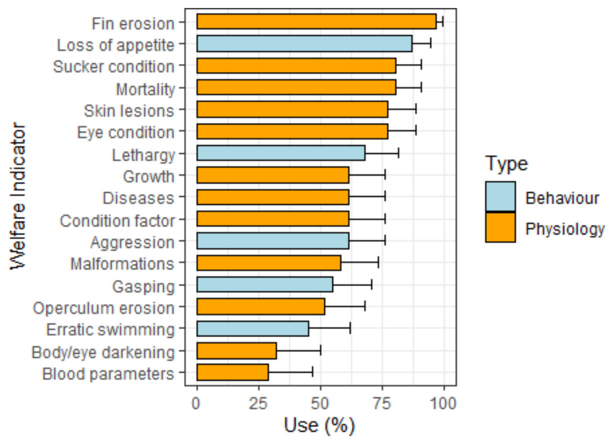

FIGURE 5 Welfare indicators used by lumpfish farmers (n = 31). Shown are the proportion of fish farmers (% ± binomial 95CI) who reported using each of the 17 welfare indicators considered

preferences from choice tests, and developing disease challenges to advance the production of vaccines.

In terms of training, experts highlighted the benefits (and need for) specific guidelines and welfare indicators for lumpfish, particularly in relation to cage deployment and transport.[95] Greater effort in marketing, in raising public awareness, extending knowledge and forging new collaborations, as well as better internal communication between hatcheries and sea farms, were noted under knowledge exchange and communication. The main areas of research and development that the group recommended should be targeted included the consequence of variation in morphology, vaccine development, nutrition, impacts on wild stocks, sucker deformities and reuse of farmed lumpfish at the end of the salmon production cycle. Better and more frequent monitoring was seen as beneficial for improving welfare, particularly in relation to disease, broodstock management and delousing efficacy. To address nutritional deficits, improvement in feeding management and use of feed blocks[67,96,97] were recommended. Perhaps surprisingly, economics was not ranked high, and more funding came last in the list of potential solutions.

TABLE 2 Habitat and niche preferences of lumpfish.

Trait	Optimal or Reference value	Reference
Water quality		
Dissolved oxygen (%)	>80% (>7.3 mg/L @ 10°C) 110% at high temp or density 110 = 115% up to 150 dph 100% (9.2 mg/L @ 10°C)	84,85,106,115
Hypoxia tolerance	27% saturation @ 9°C (same as A. salmon)	115
Water temperature (°C)	7–16; 2–17 for egg development	63,68,69,103,104
Critical thermal max (°C)	22	116
Onset of mortality (°C)	18	70
pH	7.3 – 8.5	34,63
Free Ammonia (NH3, mg/L)	<0.005 (<0.5 TAN @ pH7.8,10°C, 35ppt) <0.015 (<1.6 TAN @ pH7.8, 10°C, 30ppt) <0.005 (<0.5 TAN @ pH7.9, 9°C, 35ppt)	34,106,117
Nitrite (NO_2, mg/L)	<0.2; <0.125; <1.00	34,106,118
Nitrate (NO_3, mg/L)	<50; <100	34,106,118
Salinity (ppt)	30–35	63,104
Osmolality (mOsm/kg)	350–360	83
Magnesium (mmol/L)	<1.5	83
Chloride (mmol/L)	<150	83
Habitat preferences		
Substrate	Adults: Benthopelagic, rocky bottoms Juveniles: Floating seaweed	118-120
Water depth	50–150 m Shallows for spawning	102,121
Flow (L/min)	20	70,102-104
Water velocity (cm/s)	80 Flow through 100–400%/h not exceeding 150% when <3 g	
Light intensity	Low intensity; 420 nm (blue) (eggs/juveniles)	27,74
Husbandry		
Photoperiod (hrs. L:D)	24:0, 18:6, 12:12	104,105
Fish density (kg/m^3)	<40, <60	27,106
Feeding ration (% BW)	5% larvae, 3–4% @ 10 g, 1.5–2% @ 50 g; 10% @ <0.5 g, 3–4% @ 0.5–10 g	104,106
SGR (%/day)	1.5–3.5	103
Tank cover	Not needed; Light shut out during egg incubation	104,106
Nutritional requirements	Larvae: 56.3–58.3% protein 12.9–15.9% fat, 1.6–2.6 fibre Ongrowing: 50–54.3% protein 15.1–20.1% fat, 6–9% starch Vit. C 372–1000 mg/kg, astaxanthin 2 mg/kg	13,73,80,122-124
Shelter type	Smooth, flat surfaces to attach Kelp like structures	24,106,125
Grading	Yes, with several benefits: (1) Reduces fin damage (2) Disrupts hierarchies (3) Maximises growth	104,106,126
Weaning	From week 3 (28 dph) to week 8 Artemia from week 1 Fine dry feed from week 4 0–30 dph enriched Artemia 7–14 dph marine microdiets	13,24,106
Tank colour	Dark; Aversion to white or bright colours	104,106

Abbreviation: dph, days post-hatch.

TABLE 3 Main differentiating traits of lumpfish, welfare implications and potential consequences for commercial production

Trait/characteristic	Welfare implications	Potential consequences for production
Production derived from wild caught broodstock	Wild fish are more prone to stress in captivity	Higher risk of stress-related conditions
Used as cleaner fish to graze on sea lice	Cannot rely on sea lice alone as source of food Grazing on sea lice is energy expensive	Supplemental feeding in salmon net-pens is required High risk of starvation
Nutritional requirements poorly known	Risk of malnutrition or lack of essential dietary nutrients	Specialised diets needed
Lack swim bladder	May have difficulty maintaining buoyancy and adjusting position in water column	Stratification may confine fish to some parts of the net-pens
Sit and wait visual feeders	Require eyes in good condition for feeding Food particle density must be high and pass close by	May not be able to feed at low light levels Need to adjust feeding ration frequently
Testicles deep inside body cavity	Difficult to strip males non-destructively	Risk of wastage of males, males only used once in captive breeding
Lacks scales	Skin is particularly sensitive to infection	Careful handling required
Weak swimmers	Prone to suffer from exhaustion	Need shelters and protection from strong currents
Pronounced round shape	Limited swimming ability	More difficult to grade Need to develop suitable body condition indices
Clumping behaviour	High level of intra-specific contacts Aggression can develop	Difficult to count and establish suitable densities Tanks need to provide substrates to cling
Low cortisol response	Reduced ability to deal with acute stress	Difficult to establish stress levels
High fecundity	Deformities common in captivity, high larval mortality	Need to screen out maladapted phenotypes
Lack Mauther neurons	Low stress response Long startle response latency	Difficult to establish stress levels Need to provide shelters
Suction disk	Deformities common and may affect ability to cling and rest	Rearing tanks need structures to cling
Prefer cold temperatures	Risk of thermal stress during the summer	Chillers needed during hatchery production Net-pens need to avoid hotspots
Aggressive behaviour	May increase stress levels, fin nipping and eye damage	Tank enrichment needed to provide shelters and increase visual isolation
Cannibalism common in juveniles (1–5 g)	May increase stress levels	Frequent grading necessary

6.3 | Opportunities

Participants identified 43 opportunities to improve the welfare of lumpfish and to make their use as cleaner fish more sustainable, mostly through research and development and through technological improvements (Table 1). The main opportunities lay in reusing lumpfish at the end of the salmon cycle, although this may be limited by size constraints and concerns about transmitting diseases from one salmon cycle to the next,[32,54,98] closing the breeding cycle of the species in captivity and optimising rearing conditions. Other opportunities lay in increasing survival, welfare and delousing efficacy through selective breeding,[49,72] the development of improved diets [79,81] and food delivery systems,[67,96] as well as better disease management strategies.[13] In this sense, recent advances in non-destructive tissue sampling through laparoscopy and real-time PCR assays for rapid disease screening[86] should improve disease management.

Opportunities were also identified to improve knowledge exchange and communication (e.g. enhancing networking between industry and academia, developing welfare certification schemes and improving marketing and openness), in husbandry and logistics (e.g. improving adaptation to cages), in nutrition (e.g. better diets and food delivery systems), as well as in monitoring and screening (e.g. particularly of mortalities in sea cages), training (e.g. improved recruitment) and economics (e.g. funding for innovative applied research).

A flow analysis (Figure 1) identified that the most useful solutions to address the top knowledge gaps and challenges identified by the group were selective breeding and investment in R&D, better monitoring and specialised training, collaborations to improve the skill sets of fish farmers, developing specific welfare guidelines and acclimatising lumpfish before deployment in the sea.

TABLE 4 Differences between lumpfish and Atlantic salmon traits

Trait	Lumpfish	Atlantic salmon	References
Resting plasma cortisol (ng/ml)	<10	>20 (saltwater) 4 (parr) 11 (smolt)	84,127,128
Body shape	Anterior and posterior compression	Streamlined fusiform	63,129
Social behaviour	Solitary, aggregating during breeding season Males territorial	Juv. Territorial Adult. shoaling	102,130,131
Swimming ability	Low 1.3–1.7BLs^{-1}	High >4 m/s^{-1} burst Sust. 1–1.2 m/s^{-1}	70,132-134
Metabolic rate (MMR; mg/O_2/kg/h)	Low 148–300	High ~400 and above	132,135
Escape reaction	Proactive/reactive Swimming/freezing	Proactive/Flee	27,124,136
Temperature range (°C)	0–20	2–9 0–22 to 28	69,102,103,137
Level of domestication	2	5	1
Life strategy	mostly *r*-strategist	mostly *K*-strategist	34,63,69,138
Absolute fecundity (No)	50–200k 49–60 egg/g	8k–26k	34,63,69,102,138,139
Longevity max (years)	♀12–14 ♂ 8	1–10	63,140-142
Scales	No	Yes	62
Swim bladder	No	Yes	62
Habitat	Epibenthic-Pelagic	Benthopelagic	62
Preferred depth (m)	100	16.5	62
Latitudinal range (°)	48	35	62
Egg development CTU	221.5	500	102,143
Trophic level	3.9	4.5	62
Generation time (years)	4.2	2.9	62
Age at 1st maturity (years)	2.7	1.4	62
Food consumption (Q/B)	1.10	7.14	62

7 | UTILITY AND USE OF WELFARE INDICATORS FOR FARMED LUMPFISH

Participants ranked the utility of the 5 behavioural and 12 physical welfare indicators for lumpfish differently (Figure 2; Likelihood-Ratio Test (LRT) = 81.97, df = 16, $p < 0.001$). Skin damage and fin erosion were considered to be the most useful, while blood parameters and behavioural indicators were considered to be the least useful, perhaps because these are more time consuming and cannot be easily scored on site, although new developments in sensor and tag technology may make it easier to monitor behaviour under farm conditions.[99,100] The perceived utility was independent of participant background (LRT = 2.88, df = 2, $p = 0.236$), and consensus among participants was high, consensus being 89% for behavioural indicators, 87% for physical indicators and 68% overall (Figure 3). This was corroborated by a reliability analysis, which yielded Cronbach's alpha estimates >0.75 for all welfare indicators (Figure 4), and an overall Cronbach's alpha of 0.79 (95 CI = 0.69–0.92) indicating good reliability.

Not all welfare indicators were used to the same extent by fish farmers (Figure 5; $\chi^2 = 72.74$, df = 16, $p < 0.001$). Fin erosion, loss of appetite, deformities of the suction cup, increases in mortality and lesions in the skin and eyes were used frequently (>75%), while erratic swimming, body and eye darkening and blood parameters were not commonly used (<50%).

8 | SPECIES PROFILING: HOW UNIQUE ARE LUMPFISH?

A search of the literature was undertaken to bridge some of the knowledge gaps highlighted by the focus group (Table 2) and to explore the potential welfare implications and consequences for production (Table 3). This revealed that while some traits, like water quality requirements, are generally well known and do not appear to be markedly different from those of many other farmed marine fish, others are very uncertain. For example, adult lumpfish are naturally found in deeper waters than most farmed fish but the implications of this for farming are largely unknown.

The species has a relatively low swimming ability [70,101] and has difficulty withstanding fast currents,[102-104] and it is, therefore, likely to struggle to both swim and cling to surfaces in salmon net-pens which are often situated in areas with strong currents.[35] Lumpfish

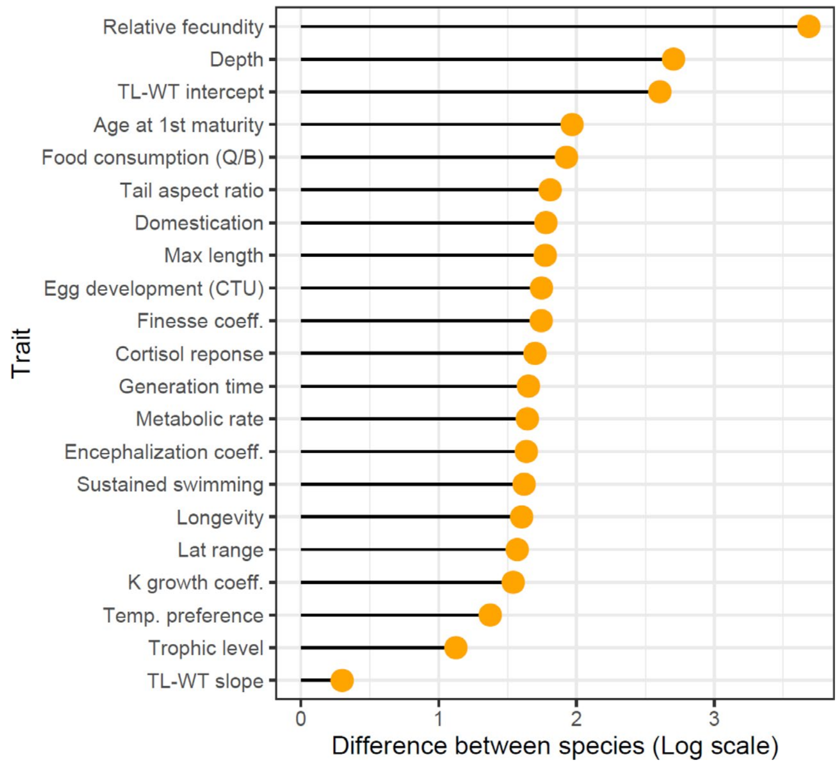

FIGURE 6 Species differences in habitat preferences and selected life-history traits between lumpfish and Atlantic salmon (% difference in $\log_{10}$ scale)

prefer low-intensity blue lighting [27,74] and cling to dark structures,[104] but there is very little practical guidance that can be used to inform best practices. For example, while some producers cover eggs during incubation, most leave the rearing tanks open during the rest of the cycle. Likewise, some farmers use a 12:12 photoperiod regime, while others use continuous lighting.[104,105]

Gaps in knowledge relevant to welfare are also evident with regards to optimal densities, tank flows, nutritional requirements and recommended feeding rations. Some studies suggest that densities of <60 kg/m^3 or even <40 kg/m^3 should be maintained,[27,106] but other studies indicate that juveniles can survive well at densities of up to 85 kg/m^3 in small (150 L) experimental tanks.[107] However, as lumpfish prefer to cling during parts of their life cycle, biomass per surface area is perhaps a more informative metric for this species than biomass per unit volume. Guidance on timing and frequency of grading is conspicuously absent, despite the fact that cannibalism appears widespread during the larval stages.[106]

Similarly, there is uncertainty about optimal feeding rations. Larvae (<0.5 g) are being fed at 5–10% body weight, 10 g juveniles at 3–4% and juveniles just before deployment at 1.5–2%.[13,104] This level of feeding should result in specific growth rates of 1.5–3.5% per day in hatcheries.[103] However, traditional ways to detect underweight fish in fish farming, like the use of Fulton's condition, do not work well in lumpfish owing to their round shape and different growth stanzas, and there is little information on feed conversion ratios. It is suspected that current feeding rations may be too high and lead to wastage. Overfeeding has been associated with a higher incidence of cataracts in lumpfish,[13,108] so more precise information on appropriate feeding levels is obviously needed. Feeding in lumpfish depends on prey density and metabolic rate[109], but how this translates into guidance on feeding management merits further investigation.

Ensuring lumpfish are fed adequately is particularly important in sea cages, as the species is at risk of malnutrition[51,110] and cannot survive grazing solely on sea lice. The lack of agreed standards for feeding lumpfish in sea cages was highlighted as one of the main knowledge gaps and is made worse by the difficulty of obtaining accurate data on the number of lumpfish actually present in sea cages. In this sense, advances in tracking methods and in fish image recognition may help to obtain more accurate estimates of fish biomass, both in hatchery tanks and in sea cages.[100,111]

9 | DIFFERENCES BETWEEN ATLANTIC SALMON AND COHABITING LUMPFISH

One of the problems highlighted by the focus group was the tendency by farmers to prioritise the welfare needs of Atlantic salmon over those of lumpfish. We, therefore, asked whether conditions that favour salmon might also benefit lumpfish. Although uncertainties exist, our comparative analysis reveals profound differences between the two species that will likely have welfare implications (Table 4). Compared with salmon, lumpfish have a lower cortisol response and metabolic rate, are solitary, have a weaker swimming ability and a reactive response to threat; they also prefer colder and deeper waters, are much less domesticated, live longer, feed lower in the food web, grow more slowly, and are generally closer to the *r* end of the r-K life-history continuum (sensu Pianka[112]) than salmon, that is they have a life strategy characterised by high fecundity, rapid development, broad niche and density-independent mortality, better suited to living in highly variable and unpredictable habitats. Some of these differences vary by over three orders of magnitude (Figure 6). This means that a common 'one-size-fits-all' approach to ensuring high welfare in salmon net-pens will not work for lumpfish, particularly in relation to habitat preferences (water current, depth), feeding and the response to stress. Yet, we trust that the approach shown in our study can be used to prioritise the welfare needs of other cleaner fish species and identify workable solutions.

10 | 16 PRACTICAL WAYS TO IMPROVE THE WELFARE OF LUMPFISH

Based on the advice of the expert group, and our comparative analysis, we suggest the following practical ways of improving the welfare of lumpfish used as cleaner fish to control sea lice in salmon farming:

1. Adopt welfare guidelines specifically developed for this species [49,51,67,113]
2. Train staff in their use and implementation
3. Monitor fish often and look for early signs of poor welfare
4. Watch for underweight fish and adjust feeding rations, feed frequency and feed delivery accordingly
5. Monitor mortality rates regularly and investigate whether mortality exceeds the norm (defined by the median and the 10th-90th percentile historical benchmark [114]
6. Keep densities within optimal values for the species, typically <60 kg/m^3
7. Screen-out lumpfish with deformed suckers at the earliest opportunity
8. Reduce potential disturbance and handling as much as possible
9. Provide shelters and cover in tanks
10. Check water quality regularly
11. Grade frequently, as adequate for the size and condition of the fish
12. Vaccinate against infectious diseases
13. Avoid areas with strong currents or outside the optimal thermal niche
14. Avoid prolonged transport whenever possible and check water quality during transport
15. Be prepared to cull fish with suboptimal welfare under veterinary advice
16. Slaughter lumpfish humanely

Many of the recommendations listed above will also apply to cleaner wrasse used to control sea lice in salmon farming, but it must be remembered that cleaner fish differ in their behaviour and habitat requirements,[65] and likely also in their welfare needs. The approach shown in our study can be used to prioritise such needs and propose workable solutions.

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ORCID

Carlos Garcia de Leaniz https://orcid.org/0000-0003-1650-2729
Carolina Gutierrez Rabadan https://orcid.org/0000-0002-5517-9808
Sara I. Barrento https://orcid.org/0000-0003-2986-5422
Rebecca Stringwell https://orcid.org/0000-0002-3663-6487
Ben A. Whittaker https://orcid.org/0000-0001-9316-6285
Jessica F. Minett https://orcid.org/0000-0001-6449-0801
Sofia Consuegra https://orcid.org/0000-0003-4403-2509
Sonia Rey Planellas https://orcid.org/0000-0002-3406-3291
Amanda Deakin https://orcid.org/0000-0001-7934-6984
Guillermo Bardera https://orcid.org/0000-0003-3559-4075
Maria F. Castanheira https://orcid.org/0000-0001-5901-4077
Maria Scolamacchia https://orcid.org/0000-0002-2117-9535
Nancy Clarke https://orcid.org/0000-0002-6259-011X
Michalis Pavlidis https://orcid.org/0000-0001-9135-2340

REFERENCES

1. Teletchea F, Fontaine P. Levels of domestication in fish: implications for the sustainable future of aquaculture. *Fish Fish*. 2014;15(2):181-195. https://doi.org/10.1111/faf.12006.
2. FAO. *The State of World Fisheries and Aquaculture*, vol. 2020:224. Rome, Italy: FAO; 2020.
3. Branson EJ, ed. Fish Welfare. Blackwell Publishing Ltd; 2008.
4. Kristiansen TS, Fernö A, Pavlidis MA, Van de Vis H, eds. *The Welfare of Fish*. Springer; 2020.
5. Kiessling A, van de Vis H, Flik G, Mackenzie S. Welfare of farmed fish in present and future production systems. *Fish Physiol Biochem*. 2012;38(1):1-3.
6. Noble C, Gismervik K, Iversen MH, et al, Welfare Indicators for farmed Atlantic salmon: tools for assessing fish welfare. Nofima; 2018. FHF project 901157 «FISHWELL: Kunnskapssammenstilling om fiskevelferd for laks og regnbueørret i oppdrett»
7. RSPCA. RSPCA Standards for Farmed Atlantic Salmon. 2018:89. February 2018.
8. Pettersen JM, Bracke MBM, Midtlyng PJ, et al. Salmon welfare index model 2.0: an extended model for overall welfare assessment of caged Atlantic salmon, based on a review of selected welfare indicators and intended for fish health professionals. *Reviews in Aquaculture*. 2014;6(3):162-179. https://doi.org/10.1111/raq.12039.
9. Noble C, Gismervik K, Iversen MH, et al, Welfare Indicators for farmed rainbow trout: tools for assessing fish welfare. Nofima; 2020. FHF project 901157 «FISHWELL: Kunnskapssammenstilling om fiskevelferd for laks og regnbueørret i oppdrett»
10. RSPCA. RSPCA Standards for Farmed Rainbow Trout; 2020:51p, Horsham, UK. https://science.rspca.org.uk/documents/14949

35/9042554/RSPCA+Trout+Welfare+Standards+2020.pdf/3f74881f-577b-d4bb-22f0-a9792a298db6?t=1618819287216. Accessed 4 June, 2021.
11. Cooke M. Animal Welfare in Farmed Fish. Business Benchmark on Farm Animal Welfare (BBFAW) Investor Briefing No. 23; 2016:16p, London. https://www.bbfaw.com/media/1432/investor-briefing-no-23-animal-welfare-in-farmed-fish.pdf. Accessed 4 June, 2021.
12. World Organisation for Animal Health. OIE Aquatic Animal Health Code; 2019. https://www.oie.int/standard-setting/aquatic-code/. Accessed 6 July, 2020.
13. Powell A, Treasurer JW, Pooley CL, et al. Use of lumpfish for sea-lice control in salmon farming: challenges and opportunities. *Rev Aquacult*. 2018;10(3):683-702.
14. Haugland GT, Imsland AKD, Reynolds P, Treasurer J. Application of biological control: use of cleaner fish. *Aquacult Health Manag*. 2020;319-369.
15. Treasurer J. An introduction to sea lice and the rise of cleaner fish. In: Treasurer J ed. *Cleaner Fish Biology and Aquaculture Applications*. 5M Publishing; 2018.
16. Torrissen O, Jones S, Asche F, et al. Salmon lice - impact on wild salmonids and salmon aquaculture. *J Fish Dis*. 2013;36:171-194. https://doi.org/10.1111/jfd.12061.
17. Costello MJ. The global economic cost of sea lice to the salmonid farming industry. *J Fish Dis*. 2009;32:115-118. https://doi.org/10.1111/j.1365-2761.2008.01011.x.
18. Costello MJ. Ecology of sea lice parasitic on farmed and wild fish. *Trends Parasitol*. 2006;22(10):475-483. https://doi.org/10.1016/j.pt.2006.08.006.
19. Costello MJ. How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proc R Soc B Biol Sci*. 2009;276(1672):3385-3394.
20. Hersoug B. The greening of Norwegian salmon production. *Marit Stud*. 2015;14(1):16.
21. Jackson D, Moberg O, Stenevik Djupevåg E, Kane F, Hareide H. The drivers of sea lice management policies and how best to integrate them into a risk management strategy: An ecosystem approach to sea lice management. *J Fish Dis*. 2018;41(6):927-933.
22. Aaen SM, Helgesen KO, Bakke MJ, Kaur K, Horsberg TE. Drug resistance in sea lice: a threat to salmonid aquaculture. *Trends Parasitol*. 2015;31:72-81.
23. Treasurer J, Feledi T. The physical condition and welfare of five species of wild-caught wrasse stocked under aquaculture conditions and when stocked in Atlantic salmon, *Salmo salar*, production cages. *J World Aquacult Soc*. 2014;45(2):213-219. https://doi.org/10.1111/jwas.12099.
24. Brooker AJ, Papadopoulou A, Gutierrez C, Rey S, Davie A, Migaud H. Sustainable production and use of cleaner fish for the biological control of sea lice: recent advances and current challenges. *Vet Rec*. 2018;183(12):383. https://doi.org/10.1136/vr.104966
25. Kvd B, Schrijver R, Bergevoet R, et al. Welfare of farmed fish. Common practices during transport and at slaughter. 2017:12.
26. Imsland AK, Reynolds P, Eliassen G, et al. Is cleaning behaviour in lumpfish (*Cyclopterus lumpus*) parentally controlled? *Aquaculture*. 2016;459:156-165. https://doi.org/10.1016/j.aquaculture.2016.03.047.
27. Noble C, Iversen MH, Lein I, et al. Rensvel OWI Fact Sheet Series: An introduction to Operational and Laboratory-based Welfare indicators for lumpfish (*Cyclopterus lumpus* L.). 2019. 9788282965910.
28. European Union Reference Laboratory for Fish Diseases. *Cleaner fish in aquaculture: Health management and legislative issues*; 2016:35.
29. OneKind. Cleaner Fish Welfare on Scotland's Salmon Farms. 2018:24. https://www.scot/wp-content/uploads/cleaner-fish-report-final-low-res.pdf. Accessed 6 July, 2020.
30. Geitung L, Wright DW, Oppedal F, Stien LH, Vågseth T, Madaro A. Cleaner fish growth, welfare and survival in Atlantic salmon sea cages during an autumn-winter production. *Aquaculture*. 2020;528:735623. https://doi.org/10.1016/j.aquaculture.2020.735623.
31. Stien LH, Størkersen KV, Gåsnes SK. Analysis of mortality data from a survey on welfare in cleaner fish. Report from the Institute of Marine Research, Norway [in Norwegian]. 2020:33. https://imr.brage.unit.no/imr-xmlui/bitstream/handle/11250/2685911/RH+2020-06.pdf?sequence=1. Accessed 4 June, 2021.
32. Erkinharju T, Dalmo RA, Hansen M, Seternes T. Cleaner fish in aquaculture: review on diseases and vaccination. *Rev Aquacult*. 2021;13(1):189-237.
33. Hjeltnes B, Bang-Jensen B, Bornø G, Haukaas A, Walde CS, eds. *The Health Situation in Norwegian Aquaculture 2017*. Norwegian Veterinary Institute; 2018.
34. Treasurer J, Noble C, Puvanendran V, Rey Planellas S, Iversen MH. Cleaner fish welfare. In: Treasurer J, ed. *Cleaner Fish Biology and Aquaculture Applications*. 5M Publishing Ltd; 2018:287-318: chap 15.
35. Jónsdóttir KE, Hvas M, Alfredsen JA, et al. Fish welfare based classification method of ocean current speeds at aquaculture sites. *Aquacult Environ Interact*. 2019;11:249-261. https://doi.org/10.3354/aei00310.
36. Barrett LT, Overton K, Stien LH, Oppedal F, Dempster T. Effect of cleaner fish on sea lice in Norwegian salmon aquaculture: a national scale data analysis. *Int J Parasitol*. 2020;50(10–11):787-796. https://doi.org/10.1016/j.ijpara.2019.12.005.
37. Overton K, Barrett LT, Oppedal F, Kristiansen TS, Dempster T. Sea lice removal by cleaner fish in salmon aquaculture: a review of the evidence base. *Aquacult Environ Interact*. 2020;12:31-44. https://doi.org/10.3354/aei00345.
38. Imsland AKD, Hanssen A, Nytrø AV, et al. It works! Lumpfish can significantly lower sea lice infestation in large-scale salmon farming. *Biol Open*. 2018;7(9). https://doi.org/10.1242/bio.036301.
39. Barrett LT, Oppedal F, Robinson N, Dempster T. Prevention not cure: a review of methods to avoid sea lice infestations in salmon aquaculture. *Rev Aquacult*. 2020;12(4):2527-2543. https://doi.org/10.1111/raq.12456.
40. Toma L, Shrestha S, Leinonen I, et al. *Understanding the Relative Cost-Effectiveness of Sea Lice Management Measures for Farmed Salmon Production in Scotland*; 2020:68.
41. Eurogroup for Animals. *Looking Beneath the Surface: Fish Welfare in European Aquaculture*; 2018:44.
42. Grimsrud KM, Nielsen HM, Navrud S, Olesen I. Households' willingness-to-pay for improved fish welfare in breeding programs for farmed Atlantic salmon. *Aquaculture*. 2013;372–375:19-27. https://doi.org/10.1016/j.aquaculture.2012.10.009.
43. Just Economics. Dead Loss: The High Cost of Poor Farming Practices and Mortalities on Salmon Farms; 2021:64. https://www.justeconomics.co.uk/health-and-well-being/dead-loss
44. Merakerås GK. Cleaner fish being sacrificed in the fight against salmon lice. Norwegian SciTech News. 2020. https://norwegianscitechnews.com/2020/04/cleaner-fish-being-sacrificed-in-the-fight-against-salmon-lice/#:~:text=Research%20shows%20that%20even%20fish,the%20use%20of%20certain%20species. Accessed 4 June, 2021.
45. van de Vis JW, Poelman M, Lambooij E, Begout ML, Pilarczyk M. Fish welfare assurance system: initial steps to set up an effective tool to safeguard and monitor farmed fish welfare at a company level. *Fish Physiol Biochem*. 2012;38(1):243-257. https://doi.org/10.1007/s10695-011-9596-7.
46. North BP, Ellis T, Knowles T, Bron J, Turnbull JF. *The Use of Stakeholder Focus Groups to Identify Indicators for the On-Farm Assessment of Trout Welfare*. Oxford: Fish welfare Blackwell; 2008:243-267.

47. Folkedal O, Pettersen JM, Bracke MBM, et al. On-farm evaluation of the Salmon Welfare Index Model (SWIM 1.0): theoretical and practical considerations. *Anim Welf*. 2016;25(1):135-149. https://doi.org/10.7120/09627286.25.1.135.
48. Noble C, Iversen MH, Lein I, et al. An introduction to Operational and Laboratory based Welfare Indicators for ballan wrasse (*Labrus bergylta*); 2019:43. RENSVEL OWI FACT SHEET SERIES.
49. Imsland AKD, Reynolds P, Hangstad TA, et al. Quantification of grazing efficacy, growth and health score of different lumpfish (*Cyclopterus lumpus* L.) families: Possible size and gender effects. *Aquaculture*. 2021;530. https://doi.org/10.1016/j.aquaculture.2020.735925.
50. Eliasen K, Patursson EJ, McAdam BJ, et al. Liver colour scoring index, carotenoids and lipid content assessment as a proxy for lumpfish (*Cyclopterus lumpus* L.) health and welfare condition. *Sci Rep*. 2020;10(1):1-12.
51. Gutierrez Rabadan C, Spreadbury C, Consuegra S, Garcia de Leaniz C. Development, validation and testing of an Operational Welfare Score Index for farmed lumpfish *Cyclopterus lumpus* L. *Aquaculture*. 2021;531:735777. https://doi.org/10.1016/j.aquaculture.2020.735777.
52. Hustad A. *Effects of crude oil contaminated sediment on the early life stages of lumpsucker (*Cyclopterus lumpus *L.)*. University of Tromsø; 2008.
53. Fjelldal PG, Madaro A, Hvas M, Stien LH, Oppedal F, Fraser TW. Skeletal deformities in wild and farmed cleaner fish species used in Atlantic salmon *Salmo salar* aquaculture. *J Fish Biol*. 2021;98(4):1049-1058. https://doi.org/10.1111/jfb.14337.
54. Murray AG. A model of the process of spillover and adaption leading to potential emergence of disease in salmon held with cleaner fish used to control lice. *Aquaculture*. 2017;473:283-290. https://doi.org/10.1016/j.aquaculture.2017.02.028.
55. Jones AC, Mead A, Kaiser MJ, et al. Prioritization of knowledge needs for sustainable aquaculture: a national and global perspective. *Fish Fish*. 2015;16(4):668-683. https://doi.org/10.1111/faf.12086.
56. Rioja-Lang F, Bacon H, Connor M, Dwyer CM. Prioritisation of animal welfare issues in the UK using expert consensus. *Vet Rec*. 2020;187(12):490-490. https://doi.org/10.1136/vr.105964.
57. Rioja-Lang F, Bacon H, Connor M, Dwyer CM. Rabbit welfare: determining priority welfare issues for pet rabbits using a modified Delphi method. *Vet Rec Open*. 2019;6(1):e000363.
58. Rioja-Lang FC, Connor M, Bacon HJ, Lawrence AB, Dwyer CM. Prioritization of farm animal welfare issues using expert consensus. *Front Vet Sci*. 2020;6:495.
59. Gu Z, Gu L, Eils R, Schlesner M, Brors B. circlize implements and enhances circular visualization in R. *Bioinformatics*. 2014;30(19):2811-2812.
60. "ordinal—Regression Models for Ordinal Data." R package Version 2019.12-10. 2019. https://CRAN.R-project.org/package=ordinal
61. Office for Research Development and Education. Cronbach Alpha - Free Statistics Software (Calculator) Version 1.2.1. Free Statistics Software; 2021. https://www.wessa.net/
62. Froese R, Pauly D. FishBase World Wide Web electronic publication; 2019 www.fishbase.org
63. Davenport J. Synopsis of biological data on the lumpsucker. *Cyclopterus lumpus* (Linnaeus, 1758). Food & Agriculture Org; 1985.
64. Leclercq E, Zerafa B, Brooker AJ, Davie A, Migaud H. Application of passive-acoustic telemetry to explore the behaviour of ballan wrasse (*Labrus bergylta*) and lumpfish (*Cyclopterus lumpus*) in commercial Scottish salmon sea-pens. *Aquaculture*. 2018;495:1-12. https://doi.org/10.1016/j.aquaculture.2018.05.024.
65. Imsland AK, Reynolds P, Eliassen G, et al. Investigation of behavioural interactions between lumpfish (*Cyclopterus lumpus*) and goldsinny wrasse (*Ctenolabrus rupestris*) under controlled conditions. *Aquac Int*. 2016;24(5):1509-1521. https://doi.org/10.1007/s10499-016-0008-y.
66. Imsland AK, Reynolds P, Eliassen G, et al. Notes on the behaviour of lumpfish in sea pens with and without Atlantic salmon present. *J Ethol*. 2014;32(2):117-122. https://doi.org/10.1007/s10164-014-0397-1.
67. Imsland AKD, Reynolds P, Lorentzen M, Eilertsen RA, Micallef G, Tvenning R. Improving survival and health of lumpfish (*Cyclopterus lumpus* L.) by the use of feed blocks and operational welfare indicators (OWIs) in commercial Atlantic salmon cages. *Aquaculture*. 2020;527. https://doi.org/10.1016/j.aquaculture.2020.735476.
68. Pountney SM, Lein I, Migaud H, Davie A. High temperature is detrimental to captive lumpfish (*Cyclopterus lumpus*, L) reproductive performance. *Aquaculture*. 2020;522: 735121.
69. Mortensen A, Johansen RB, Hansen ØJ, Puvanendran V. Temperature preference of juvenile lumpfish (*Cyclopterus lumpus*) originating from the southern and northern parts of Norway. *J Therm Biol*. 2020;89: 102562.
70. Hvas M, Folkedal O, Imsland A, Oppedal F. Metabolic rates, swimming capabilities, thermal niche and stress response of the lumpfish, *Cyclopterus lumpus*. *Biol Open*. 2018;7(9). https://doi.org/10.1242/bio.036079
71. Whittaker BA, Consuegra S, Garcia de Leaniz C. Genetic and phenotypic differentiation of lumpfish (*Cyclopterus lumpus*) across the North Atlantic: implications for conservation and aquaculture. *PeerJ*. 2018;6:e5974. https://doi.org/10.7717/peerj.5974.
72. Maduna SN, Vivian-Smith A, Jonsdottir ODB, et al. Genome- and transcriptome-derived microsatellite loci in lumpfish *Cyclopterus lumpus*: molecular tools for aquaculture, conservation and fisheries management. *Sci Rep*. 2020;10(1):559. https://doi.org/10.1038/s41598-019-57071-w
73. Johannesen A, Joensen NE, Magnussen E. Shelters can negatively affect growth and welfare in lumpfish if feed is delivered continuously. *PeerJ*. 2018;6:e4837. https://doi.org/10.7717/peerj.4837.
74. Skiftesvik AB, Bjelland RM, Durif C, et al. Program rensefisk: Kunstig lys og rensefisk. Rapport fra havforskningen. Vol. 16/2017; 2017:43.
75. Jacobsen JV, Steen K, Nilssen KJ. Anaesthetic efficacy of Aqui-S, Benzoak, and MS-222 on lumpfish (*Cyclopterus lumpus*) fries. Impact from temperature, salinity, and fasting. *PLoS One*. 2019;14(1):e0211080.
76. Dahle SW, Bakke I, Birkeland M, Nordøy K, Dalum AS, Attramadal KJK. Production of lumpfish (*Cyclopterus lumpus* L.) in RAS with distinct water treatments: Effects on fish survival, growth, gill health and microbial communities in rearing water and biofilm. *Aquaculture*. 2020;522. https://doi.org/10.1016/j.aquaculture.2020.735097.
77. Roalkvam I, Dronen K, Dahle H, Wergeland HI. Microbial communities in a flow-through fish farm for lumpfish (*Cyclopterus lumpus* L.) during healthy raring conditions. *Front Microbiol*. 2019;10:1594. https://doi.org/10.3389/fmicb.2019.01594.
78. Rian ST. *Start-feeding of lumpfish (*Cyclopterus lumpus *L.) larvae with Artemia and copepods, focusing on growth effects, survival, live prey selection and larval robustness*. Norwegian University of Science and Technology; 2019.
79. Willora FP, Nadanasabesan N, Knutsen HR, Liu C, Sørensen M, Hagen Ø. Growth performance, fast muscle development and chemical composition of juvenile lumpfish (*Cyclopterus lumpus)* fed diets incorporating soy and pea protein concentrates. *Aquaculture Reports*. 2020;17. https://doi.org/10.1016/j.aqrep.2020.100352.
80. Imsland AKD, Reynolds P, Jonassen TM, et al. Effects of three commercial diets on growth, cataract development and histopathology of lumpfish (*Cyclopterus lumpus* L.). *Aquac Res*. 2018;49(9):3131-3141. https://doi.org/10.1111/are.13776.

81. Klakegg Ø, Myhren S, Juell RA, Aase M, Salonius K, Sørum H. Improved health and better survival of farmed lumpfish (*Cyclopterus lumpus*) after a probiotic bath with two probiotic strains of Aliivibrio. *Aquaculture*. 2020;518:734810. https://doi.org/10.1016/j.aquaculture.2019.734810.
82. Erkinharju T, Lundberg MR, Isdal E, Hordvik I, Dalmo RA, Seternes T. Studies on the antibody response and side effects after intramuscular and intraperitoneal injection of Atlantic lumpfish (*Cyclopterus lumpus* L.) with different oil-based vaccines. *J Fish Dis*. 2017;40(12):1805-1813. https://doi.org/10.1111/jfd.12649
83. Sällebrant JB. *Chronic allostatic overload on the hypothalamic-pituitary-interrenal axis of lumpfish (*Cyclopterus lumpus*). Effect of size*. Nord University; 2018.
84. Jørgensen EH, Haatuft A, Puvanendran V, Mortensen A. Effects of reduced water exchange rate and oxygen saturation on growth and stress indicators of juvenile lumpfish (*Cyclopterus lumpus* L.) in aquaculture. *Aquaculture*. 2017;474:26-33. https://doi.org/10.1016/j.aquaculture.2017.03.019.
85. Haatuft AC. *Effects of reduced water oxygen saturation on growth and plasma cortisol levels in juvenile lumpfish (*Cyclopterus lumpus *L.). in aquaculture*. UiT The Arctic University of Norway; 2015.
86. Naung M, Uren Webster TM, Lloyd R, Garcia de Leaniz C, Consuegra S. A novel qPCR assay for the rapid detection and quantification of the lumpfish (*Cyclopterus lumpus*) microsporidian parasite *Nucleospora cyclopteri*. *Aquaculture*. 2021;531:735779. https://doi.org/10.1016/j.aquaculture.2020.735779.
87. Lloyd R, Garcia de Leaniz C. The use of laparoscopy for non-destructive disease screening of broodstock Atlantic lumpfish, *Cyclopterus lumpus* Linnaeus. *J Fish Dis*. 2020;43(9):1107-1110. https://doi.org/10.1111/jfd.13218
88. Herrmann B, Sistiaga M, Jorgensen T. Size-dependent escape risk of lumpfish (*Cyclopterus lumpus*) from salmonid farm nets. *Mar Pollut Bull*. 2021;162:111904. https://doi.org/10.1016/j.marpolbul.2020.111904
89. Imsland AKD, Frogg N, Stefansson SO, Reynolds P. Improving sea lice grazing of lumpfish (*Cyclopterus lumpus* L.) by feeding live feeds prior to transfer to Atlantic salmon (*Salmo salar* L.) net-pens. *Aquaculture*. 2019;511:734224. https://doi.org/10.1016/j.aquaculture.2019.734224.
90. Opeifa BT. *Large volume cryopreservation of lumpfish (*Cyclopterus lumpus *L.) sperm for commercial hatchery production*. UiT The Arctic University of Norway; 2019.
91. Norðberg G, Johannesen A, Arge R. Cryopreservation of lumpfish *Cyclopterus lumpus* (Linnaeus, 1758) milt. *PeerJ*. 2015;3:e1003.
92. Whittaker BA, Consuegra S, Garcia de Leaniz C. Personality profiling may help select better cleaner fish for sea-lice control in salmon farming. *bioRxiv*; 2021. https://doi.org/10.1101/2021.05.21.444956.
93. Whittaker BA, Maeda S, Boulding EG. Strike a pose: Does communication by a facultative cleaner fish, the cunner wrasse (*Tautogolabrus adspersus*), facilitate interaction with Atlantic salmon (*Salmo salar*)? *Appl Anim Behav Sci*. 2021;236: 105275.
94. Treasurer J, Turnbull T. Tolerance of lumpfish, *Cyclopterus lumpus*, to freshwater bath treatment for amoebic gill disease, *Neoparamoeba perurans*, infection and efficacy of different treatment regimens. *J World Aquaculture Soc*. 2019;50(1):42-53.
95. Jonassen T, Remen M, Lekva A, Steinarsson A, Árnason T. Transport of lumpfish and wrasse. In: Treasurer J ed. *Cleaner Fish Biology and Aquaculture Applications*. 5M Publishing; 2018:319-335.
96. Imsland AKD, Reynolds P, Jonassen TM, et al. Comparison of diet composition, feeding, growth and health of lumpfish (*Cyclopterus lumpus* L.) fed either feed blocks or pelleted commercial feed. *Aquac Res*. 2019;50(7):1952-1963. https://doi.org/10.1111/are.14083.
97. Imsland AK, Reynolds P, Hangstad TA, et al. Feeding behaviour and growth of lumpfish (*Cyclopterus lumpus* L.) fed with feed blocks. *Aquac Res*. 2018;49(5):2006-2012. https://doi.org/10.1111/are.13657.
98. Murray AG, Peeler EJ. A framework for understanding the potential for emerging diseases in aquaculture. *Prev Vet Med*. 2005;67(2–3):223-235. https://doi.org/10.1016/j.prevetmed.2004.10.012.
99. Martins CI, Galhardo L, Noble C, et al. Behavioural indicators of welfare in farmed fish. *Fish Physiol Biochem*. 2012;38(1):17-41. https://doi.org/10.1007/s10695-011-9518-8.
100. Macaulay G, Warren-Myers F, Barrett LT, Oppedal F, Føre M, Dempster T. Tag use to monitor fish behaviour in aquaculture: a review of benefits, problems and solutions. *Reviews in Aquaculture*. 2021;13(3):1565-1582. https://doi.org/10.1111/raq.12534
101. Hvas M, Folkedal O, Oppedal F. Fish welfare in offshore salmon aquaculture. *Rev Aquacult*. 2021;13:836–852. https://doi.org/10.1111/raq.12501.
102. Powell A, Pooley C, Scolamacchia M, Garcia de Leaniz C. Review of lumpfish biology. In: Treasurer JW ed. *Cleaner Fish Biology and Aquaculture Applications*. 5M Publishing Ltd; 2018:98-121:chap 6.
103. Nytrø AV, Vikingstad E, Foss A, et al. The effect of temperature and fish size on growth of juvenile lumpfish (*Cyclopterus lumpus* L.). *Aquaculture*. 2014;434:296-302. https://doi.org/10.1016/j.aquaculture.2014.07.028.
104. Jonassen TM, Lein I, Nytrø AV. Hatchery management of lumpfish. In: Treasurer JW ed. *Cleaner Fish Biology and Aquaculture Applications*. 5M Publishing Ltd.; 2018:114-136:chap 7.
105. Mortensen, A., et al., Photoperiod and temperature change on the gonadal development and maturation of lumpfish Cyclopterus lumpus L. Bull. Aquacul. Assoc. Canada 2016. 2016-2: p. 59-64.
106. CSAR. *Personal Observation*. Centre for Sustainable Aquatic Research (CSAR); 2020.
107. Hosteland LTS. Lumpfish Happy in a Crowd, Study Reveals. FishFarmingExpertcom2017.
108. Imsland AK, Reynolds P, Jonassen TM, et al. Effects of different feeding frequencies on growth, cataract development and histopathology of lumpfish (*Cyclopterus lumpus* L.). *Aquaculture*. 2019;501:161-168.
109. Killen SS, Brown JA, Gamperl AK. The effect of prey density on foraging mode selection in juvenile lumpfish: balancing food intake with the metabolic cost of foraging. *J Anim Ecol*. 2007;76(4):814-825. https://doi.org/10.1111/j.1365-2656.2007.01237.x.
110. Eliasen K, Danielsen E, Johannesen Á, Joensen LL, Patursson EJ. The cleaning efficacy of lumpfish (*Cyclopterus lumpus* L.) in Faroese salmon (*Salmo salar* L.) farming pens in relation to lumpfish size and seasonality. *Aquaculture*. 2018;488:61-65. https://doi.org/10.1016/j.aquaculture.2018.01.026.
111. Li D, Wang Z, Wu S, Miao Z, Du L, Duan Y. Automatic recognition methods of fish feeding behavior in aquaculture: a review. *Aquaculture*. 2020;528:735508.
112. Pianka ER. On r-and K-selection. *Am Nat*. 1970;104(940):592-597.
113. Eliasen K, Patursson EJ, McAdam BJ, et al. Liver colour scoring index, carotenoids and lipid content assessment as a proxy for lumpfish (*Cyclopterus lumpus* L.) health and welfare condition. *Sci Rep*. 2020;10(1):8927. https://doi.org/10.1038/s41598-020-65535-7
114. Soares S, Green DM, Turnbull JF, Crumlish M, Murray AG. A baseline method for benchmarking mortality losses in Atlantic salmon (*Salmo salar*) production. *Aquaculture*. 2011;314(1):7-12. https://doi.org/10.1016/j.aquaculture.2011.01.029.
115. Hvas M, Oppedal F. Physiological responses of farmed Atlantic salmon and two cohabitant species of cleaner fish to progressive hypoxia. *Aquaculture*. 2019;512:734353. https://doi.org/10.1016/j.aquaculture.2019.734353
116. Ern R, Norin T, Gamperl AK, Esbaugh AJ. Oxygen dependence of upper thermal limits in fishes. *J Exp Biol*. 2016;219(21):3376-3383. https://doi.org/10.1242/jeb.143495.

117. Prickett P. *Personal Observation*. Dorset Cleanerfish Ltd; 2020.
118. Christensen JM. *Die Fische der Nordsee*. Kosmos, Franckh'sche Verlagshandlung; 1977:128.
119. Daborn GR, Gregory RS. Occurrence, distribution, and feeding habits of juvenile lumpfish, *Cyclopterus lumpus* L. in the Bay of Fundy. *Can J Zool*. 1983;61:797-801.
120. Ingólfsson A, Kristjánsson BK. Diet of juvenile lumpsucker *Cyclopterus lumpus* (Cyclopteridae) in floating seaweed: effects of ontogeny and prey availability. *Copeia*. 2002;2002(2):472-476.
121. Stein DL. Cyclopteridae. In: Whitehead PJP, Bauchot M-L, Hureau J-C, Nielsen J, Tortonese E, eds. *Fishes of the North-eastern Atlantic and the Mediterranean*. UNESCO; 1986:1269-1274.
122. PTAqua. 2021. Pacific Trading Aquaculture Ltd. Dublin, Ireland. https://ptaqua.eu/feeds/. Accessed 4 June, 2021.
123. Jonassen T, Hamadi M, Remø SC, Waagbø R. An epidemiological study of cataracts in wild and farmed lumpfish (*Cyclopterus lumpus* L.) and the relation to nutrition. *J Fish Dis*. 2017;40:1903-1914. https://doi.org/10.1111/jfd.12664.
124. Johannesen Á, Arge R, Rearing EK. Rearing, farm application and behaviour of lumpfish (*Cyclopterus lumpus*) in the Faroes. In: Treasurer JW, ed. *Cleaner Fish Biology and Aquaculture Applications*. 5M Publishing Ltd; 2018:429-443:Chap 22.
125. Imsland AK, Reynolds P, Eliassen G, et al. Assessment of suitable substrates for lumpfish in sea pens. *Aquac Int*. 2015;23:639-645. https://doi.org/10.1007/s10499-014-9840-0.
126. Pattillo C. Project report: The effects of fin damage on the condition of juvenile lumpfish (*Cyclopterus lumpus*). *Hatcheries and Sea Cages*. 2017:5.
127. Carey JB, McCormick SD. Atlantic salmon smolts are more responsive to an acute handling and confinement stress than parr. *Aquaculture*. 1998;168(1–4):237-253.
128. Einarsdóttir IE, Nilssen KJ. Stress responses of Atlantic salmon (*Salmo salar* L.) elicited by water level reduction in rearing tanks. *Fish Physiol Biochem*. 1996;15(5):395-400.
129. Keith P, Allardi J. *Atlas des poissons d'eau douce de France. Patrimoines Naturels*. Paris: Muséum National d'Histoire Naturelle; 2001:387.
130. Keenleyside MH, Yamamoto FT. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). *Behaviour*. 1962;19(1–2):139-168.
131. Blanchet S, Bernatchez L, Dodson JJ. Behavioural and growth responses of a territorial fish (Atlantic salmon, *Salmo salar*, L.) to multiple predatory cues. *Ethology*. 2007;113(11):1061-1072.
132. Bowden AJ, Andrewartha SJ, Elliott NG, Frappell PB, Clark TD. Negligible differences in metabolism and thermal tolerance between diploid and triploid Atlantic salmon (*Salmo salar*). *J Exp Biol*. 2018;221(5):1–10. https://doi.org/10.1242/jeb.166975.
133. Colavecchia M, Katopodis C, Goosney R, Scruton D, McKinley R. Measurement of burst swimming performance in wild Atlantic salmon (*Salmo salar* L.) using digital telemetry. *Regul Rivers*. 1998;14(1):41-51.
134. Peake S, McKinley R, Scruton D. Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. *J Fish Biol*. 1997;51(4):710-723.
135. Hvas M, Folkedal O, Imsland A, Oppedal F. The effect of thermal acclimation on aerobic scope and critical swimming speed in Atlantic salmon, *Salmo salar*. *J Exp Biol*. 2017;220(15):2757-2764. https://doi.org/10.1242/jeb.154021.
136. Bui S, Oppedal F, Korsøen ØJ, Sonny D, Dempster T. Group behavioural responses of Atlantic salmon (*Salmo salar* L.) to light, infrasound and sound stimuli. *PLoS One*. 2013;8(5):e63696.
137. Elliott JM, Elliott JA. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *J Fish Biol*. 2010;77(8):1793-1817.
138. Hedeholm RB, Post S, Grønkjær P. Life history trait variation of Greenland lumpfish (*Cyclopterus lumpus*) along a 1600 km latitudinal gradient. *Polar Biol*. 2017;40(12):2489-2498. https://doi.org/10.1007/s00300-017-2160-x.
139. Mills D. *Ecology and Management of Atlantic salmon*. Springer Science & Business Media; 1989.
140. Hedeholm R, Blicher ME, Grønkjær P. First estimates of age and production of lumpsucker (*Cyclopterus lumpus*) in Greenland. *Fish Res*. 2014;149:1-4. https://doi.org/10.1016/j.fishres.2013.08.016.
141. Thorsteinsson V. The ageing validation of the lumpsucker (Cyclopterus lumpus) and the age composition of the lumpsucker in Icelandic lumpsucker fisheries. ICES CM. 1981;1981/G58 Demersal Fish Committee:26.
142. Hutchings JA, Jones ME. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Can J Fish Aquat Sci*. 1998;55(S1):22-47.
143. Benchmark Genetics. Atlantic salmon hatchery manual. Benchmark Holdings plc. Egg to first feeding. v1; 2019:9. https://www.benchmarkplc.com/wp-content/uploads/2019/08/Atlantic-Salmon-Hatchery-Manual_A5_EN.pdf. Accessed 4 June, 2021.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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