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Review

In lumpfish We Trust? The Efficacy of Lumpfish *Cyclopterus lumpus* to Control *Lepeophtheirus salmonis* Infestations on Farmed Atlantic Salmon: A Review

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Abstract: In this review, we have systematized current knowledge about the effect of stocking lumpfish (*Cyclopterus lumpus*) as cleaner fish to control *Lepeophtheirus salmonis* infestations on farmed Atlantic salmon (*Salmo salar* L.). The review was prompted by recent reports in which the usefulness of lumpfish has been doubted, and the urgent need to investigate whether common lumpfish can be used to reduce *L. salmonis* numbers on farmed Atlantic salmon by active grazing on this species. Available published data clearly indicate that lumpfish graze on *L. salmonis*, and can significantly lower the lice burden in Atlantic salmon farming. It is possible to enhance the lice grazing behavior of lumpfish with the assistance of live feed conditioning prior to sea pen transfer, and with selective breeding. Data indicate that lice grazing of lumpfish is size dependent, and grazing effect is low for lumpfish larger than 200–250 g. Observations from large-scale rearing of Atlantic salmon in open sea cages in Norway, Iceland, the Faroe Islands, and Scotland also indicate that lumpfish can be effective in lowering infestations of *L. salmonis* on salmon. Overall, this present review reveals that lumpfish can actively contribute to lower numbers of *L. salmonis* on farmed Atlantic salmon.

Keywords: sea lice; cleaner fish; lumpfish; salmon farming; welfare; sustainable aquaculture

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1. Introduction

The sea louse *Lepeophtheirus salmonis* and various *Caligus* (Copepoda: Caligidae) species are ectoparasites of marine finfish. They have a major impact on salmonid aquaculture worldwide [1,2], causing losses of over ISK 440 million in Norway annually [3]. The problems of adverse welfare outcomes associated with infestations and increased infestation pressure have escalated with the commercial production of Atlantic salmon (*Salmo salar* L) and rainbow trout (*Oncorhynchus mykiss* Walbaum) in sea cages [1,2,4]. Biological control using cleaner fish that pick the sea lice from salmonids [5–7] has been effective in reducing lice numbers, and is being adopted widely by the salmon farming industry [5,6,8,9,10–12].

The parasitic copepod family Caligidae comprises more than 30 genera [13] and more than 450 species [14]. Two genera within this family, *Lepeophtheirus* and *Caligus*, have achieved notoriety by having the greatest economic impact of any group of parasites in salmonid fish mariculture [15,16], and have become collectively known as "sea lice". A major difference between *L. salmonis* and *Caligus* spp. lies in their host specificities; *L. salmonis* is essentially a parasite of salmonid fish [17,18], whereas many *Caligus* spp. tend to be much less host-specific [18,19], and have been found on > 80 fish species [17].

Lumpfish, *Cyclopterus lumpus* (Linnaeus, 1758) is a non-shoaling, coldwater marine fish in the family Cyclopteridae (lumpsuckers), and it is the only member of the genus

Cyclopterus, living mainly in high latitudes. It is widely distributed across the North Atlantic from Cape Cod (USA) to Canada on the western side, to Greenland and Iceland, and all the way to Spitsbergen on the eastern side, as well as in the North Sea, the Baltic Sea, the Barents Sea, and the White Sea [20]. Lumpfish feed on a variety of organisms, mainly large planktonic organisms living in the surface/mid-waters such as gelatinous zooplankton, fish eggs, and small crustaceans. They will also occasionally browse upon benthic organisms [21,22].

Lumpfish are now extensively used as cleaner fish in Norway [6,8,9,23], Ireland [24], Scotland [25], Iceland [26], and the Faroe Islands [27]; however, there is a need to systematize knowledge and produce guidelines on the effect of lumpfish on *L. salmonis*. Earlier research has indicated that lumpfish prefer adult female *L. salmonis* [6,9, 28,29], but lumpfish in sea pens can be classified as strongly opportunistic [9,10,27], and the fish do not restrict themselves or rely on a single food source if others are present [10]. Lumpfish seem to switch their preference towards whichever food item is most readily available to them within their sea cage environment. This is important to bear in mind when looking for methods to optimize and increase the efficacy of lumpfish in sea pens.

A recent study on cleaner fish in Norway, based on national data from Barentswatch (https://www.barentswatch.no/en), reported small and varying effects of cleaner fish against lice [30]. They pointed out that few studies have demonstrated high efficacy of cleaner fish in sea cages with proper controls and replication, although it can be achieved (e.g., large cages [20], small cages [5,6,8,9]). Knowledge of cleaner fish use has increased considerably in recent years through research and industry trial-and-error, and efficacy may be improving [7,31]. Evaluation of the effect of the use of cleaner fish is complicated, and there is no good explanation for the divergent results cited above. It is unknown how large the cleaner fish density is at all times, and it is more challenging to uncover a small but even effect, rather than a greater and immediate effect, such as in medical treatments [32]. Furthermore, there may be regional differences in efficiency when using various cleaner fish species because of sea temperature, different modes of operation, and other factors. Overall, there is a need for more knowledge about the effect of cleaner fish on sea lice occurrence on Atlantic salmon in aquaculture.

Much of the production biology and health management issues of cleaner fish have been extensively addressed in two previous reviews [7,28]. Overton at al. [33] reviewed the evidence base of cleaner fish use in salmon aquaculture and assessed the current evidence base for cleaner fish efficacy. Overall, they concluded that there is a mismatch between the current evidence base for the efficacy of cleaner fish and the extent of their use by the industry. The authors recommended the use of replicated studies with a focus at the full commercial scale, and concluded that more targeted, evidence-based use of cleaner fish should increase their efficacy and help to alleviate economic, environmental, and ethical concerns. In this mini-review, we aim to summarize findings from replicated small- and large-scale trials with lumpfish, where grazing on *L. salmonis* has been reported, to provide recommendations on the possible use of lumpfish to combat *L. salmonis* on Atlantic salmon in sea pens, and to answer some of the concerns raised in a recent review study [30]. We have tried to summarize the industrial findings in the countries where lumpfish are currently used as a biological delouser on an industrial scale.

2. Materials and Methods

To discover all available literature surrounding the efficacy of lumpfish to control *Lepeophtheirus salmonis* infestations on farmed Atlantic salmon, we searched the Web of Science database in March 2022 using the following search terms: (lumpfish* and aquaculture*) and (lumpfish* and sea lice*). Results were manually screened by title and abstract to identify articles or reports that were relevant to lumpfish use in salmon aquaculture. For inclusion, studies needed to have addressed use of lumpfish for removal of sea lice in salmon aquaculture. We then discovered additional studies by reading the reference lists of studies returned by the initial search. Within these search results, we conducted systematic reviews of (1) studies that assessed the delousing efficacy of lumpfish in tanks or sea cages; and (2) behavioral studies looking at the overlap and interaction between lumpfish and salmon when stocked together in sea cages.

- *Lumpfish Efficacy*

To be included in the systematic review of efficacy, studies must have measured lice removal by lumpfish using either a before–after or control–treatment experimental design. We reviewed all published studies found in the criteria given above. Studies were divided into small-scale studies (small experimental units) and large-scale (production-size sea pens) studies. For the small-scale studies, we reviewed effects of:

a) Different density of lumpfish used in studies with salmon.
b) Habituation of lumpfish prior to transfer from net to pen.
c) Possible genetic effect on sea lice grazing in lumpfish.
d) Effect of lumpfish size on sea lice grazing.

For the large-scale studies, we reviewed the effect of lumpfish on sea lice numbers found in:

a) Different seasons.
b) Under different environmental conditions.
c) In different countries where lumpfish are currently used for the delousing of salmon.

We summarized the current literature (peer-reviewed journal articles and scientific reports) and observations (including pers. comms.) on experiments with lumpfish and its effect on *L. salmonis* infestations on farmed Atlantic salmon. Data included: experimental period and temperature, experimental unit, experimental site/country, stocking density of lumpfish, effect investigated, and whether an effect induced by the numbers of *L. salmonis* was found.

3. Results: Small-scale Studies

3.1. Different Density of Lumpfish: Effect on Occurrence of L. salmonis on Atlantic Salmon

In the first published trial on lumpfish efficacy, Imsland et al. [6] investigated the efficacy of lumpfish grazing on attached *L. salmonis* on Atlantic salmon at two different lumpfish densities (10 and 15% of the salmon density in the sea cage). The results show that from day 25 onwards, significantly lower average numbers of adult male and female lice were found in groups with different densities of lumpfish compared to the control. At termination (day 54), there were 58% and 55% fewer adult male sea lice per Atlantic salmon in the 10% and 15% lumpfish groups, respectively, compared to the control (Figure 1A). For adult female lice the trend was even clearer, as the 10% and 15% lumpfish treatments had 93% and 97% fewer female lice, respectively, compared to the control group at termination of the trial (Figure 1B).

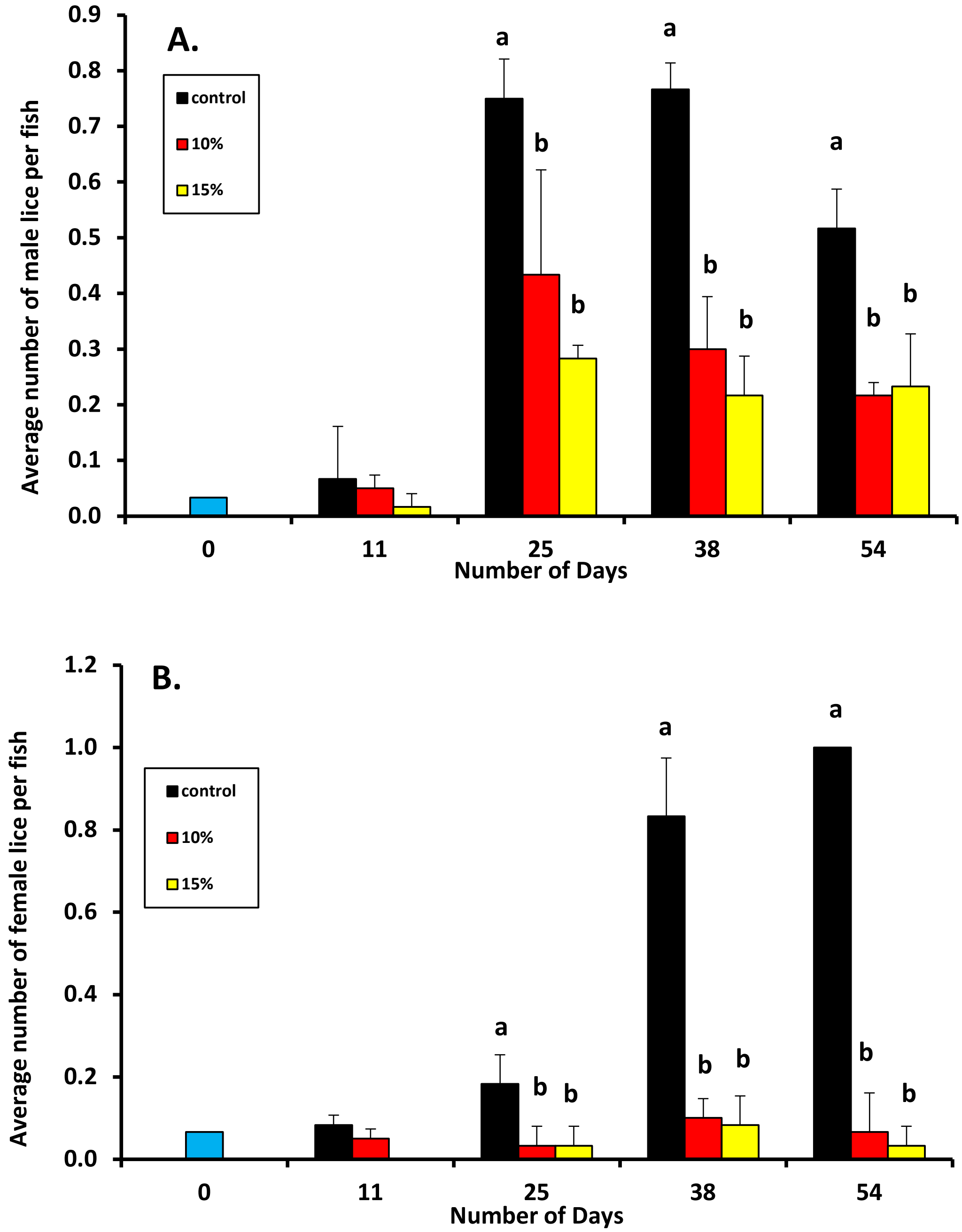

Figure 1. Total average number of adult male (**A**) and adult female (**B**) *L. salmonis* on Atlantic salmon reared with two different densities of lumpfish. Control group was not reared with lumpfish. Values are presented as means ± S.D. Mean values that do not share a letter are significantly different according to ANOVA and Tukey`s multiple range test ($P < 0.05$). Figure modified from [6].

3.2. Habituation of Lumpfish Prior to Transfer from Net to Pens: Effect on Occurrence of L. salmonis

Imsland et al. [34] established two groups of individually tagged lumpfish in land-based tanks. One group received marine pelleted feed (MF group) whilst the other received a mix of pelleted feed, live adult *Artemia*, and frozen sea lice (LF group). These two groups were subsequently transferred to small-scale sea pens with Atlantic salmon, and the occurrence of *L. salmonis* on the salmon was investigated. Overall, there was significantly less *L. salmonis* in both the LF and MF groups compared to the control (Figure 2).

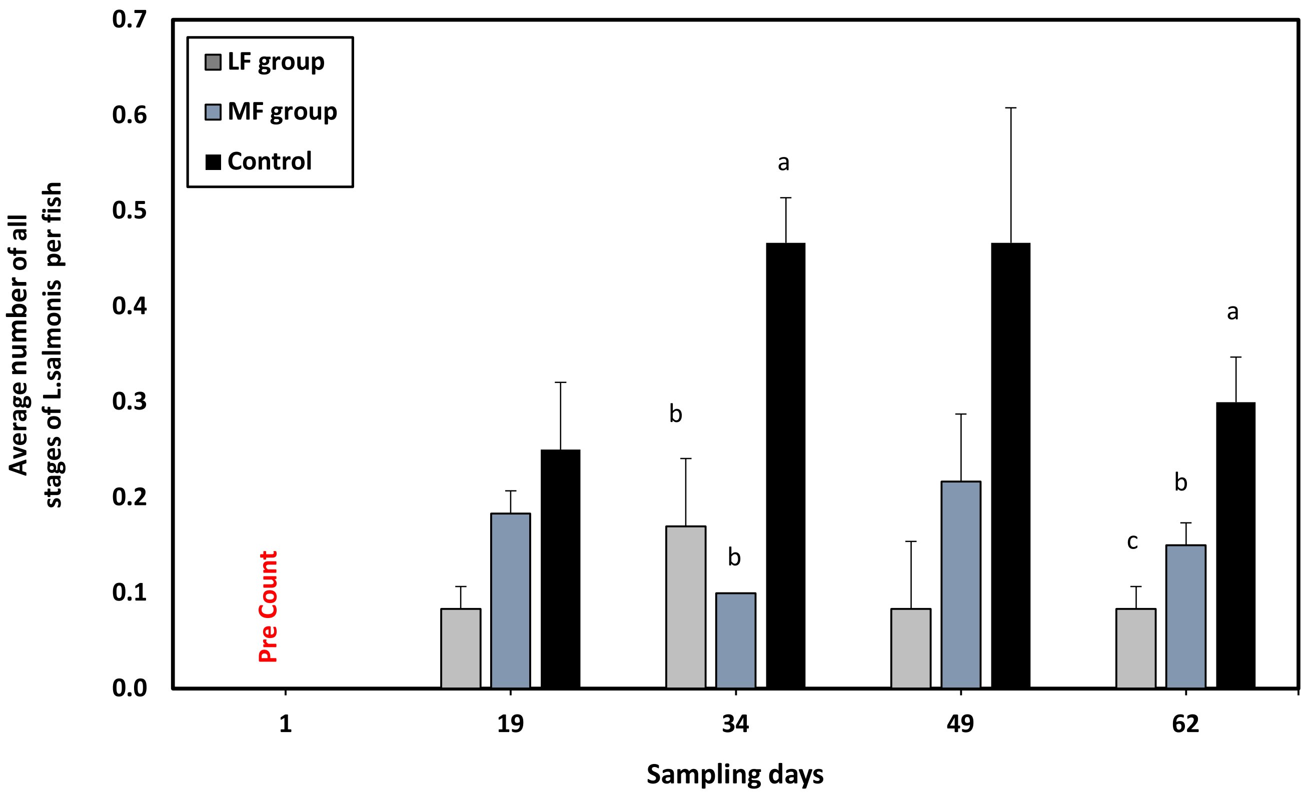

Figure 2. Average of all stages (chalimus, pre-adult, adult male and female) of *L. salmonis* per fish recorded for Atlantic salmon in sea pens with lumpfish start-fed with either marine dry feed (MF) or combination of dry and live feed (LF). The control group contained salmon without lumpfish present. Values are presented as means ± S.D. Mean values that do not share a letter are significantly different according to ANOVA and SNK post hoc test. Figure modified from [34].

3.3. Lumpfish Grazing on L. salmonis: Possible Parental Control

Imsland et al. [28,35] investigated possible parental control in the grazing of *L. salmonis* in different families (half- and full-sibs) of lumpfish stocked together with Atlantic salmon. Although the *L. salmonis* infestation rate was very low in the study of Imsland et al. [28], the percentage of lumpfish found to have consumed *L. salmonis* varied significantly between the families (Figure 3A). In a follow-up study by Imsland et al. [35], the consumption of *L. salmonis* once again varied (Figure 3B) between different lumpfish families. Recently, Whittaker et al. [36] investigated whether there were differences in the behavioral profiles of lumpfish that were more predisposed to inspect salmon. They found that personality profiling can be used to predict how lumpfish will interact with salmon and, possibly, whether they will make effective cleaner fish. Their results indicate that neophilic (non-aggressive) lumpfish were more likely to inspect salmon, while the most active and social individuals were more likely to cause salmon to flee. They further found that these behaviors were repeatable, and, therefore, likely heritable [36], suggesting that artificial selection could be used to select better cleaner fish through domestication. This is consistent with results that show that delousing behavior is parentally controlled [28,35], and thus likely inherited.

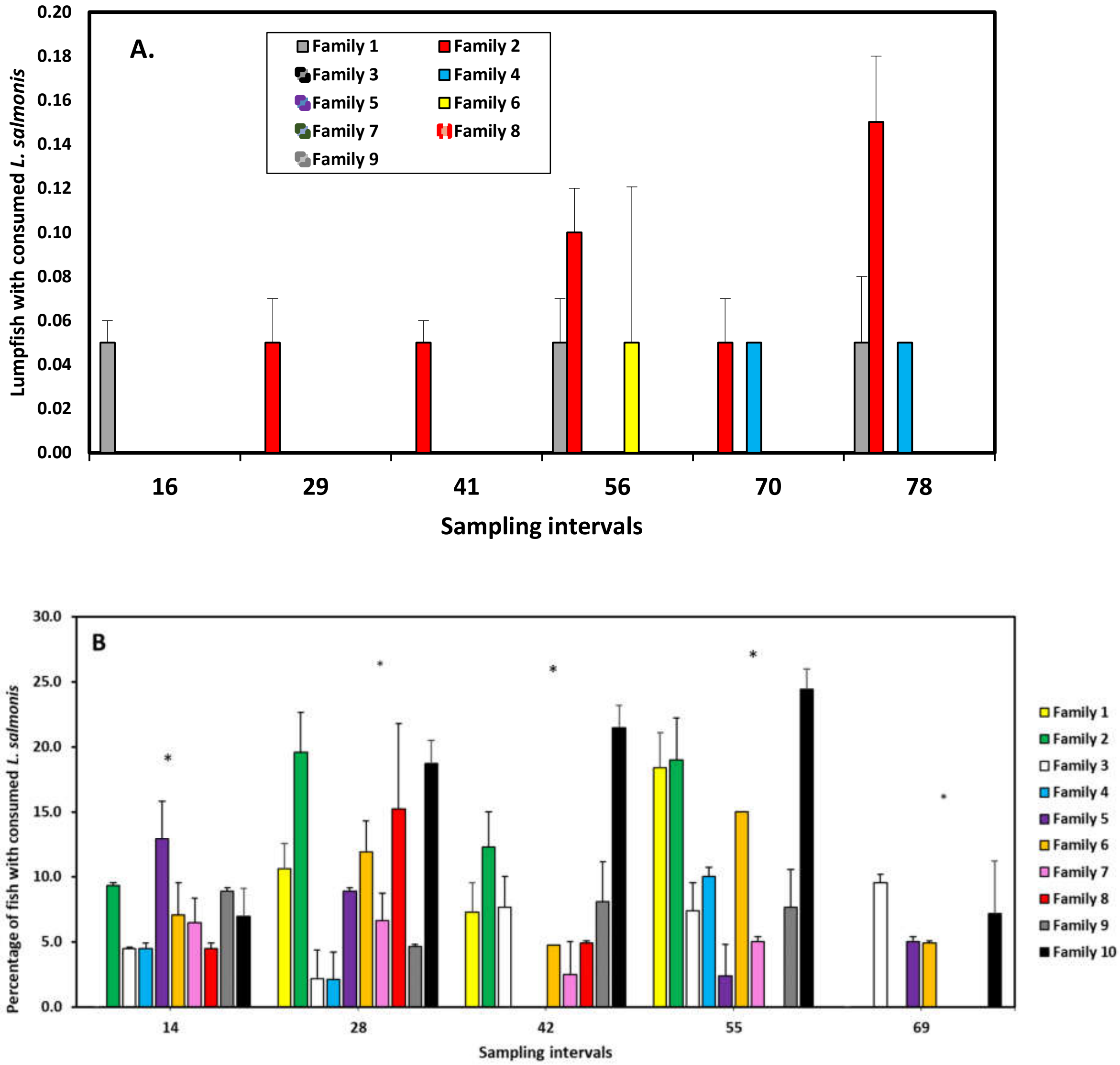

Figure 3. (**A**,**B**). Mean percentage values *L. salmonis* found in the stomach of different lumpfish families reared together with Atlantic salmon in small sea cages. Values are presented as means ± S.E. The figure is modified from [24], Figure 3A and [31], Figure 3B. * indicates significant differences between families.

3.4. Effects of Lumpfish Size on Sea Lice Grazing

Imsland et al. [29] investigated the possible size effect of sea lice grazing efficiency in lumpfish. The results indicate that small lumpfish (initial size approx. 20 g) have a higher overall preference for natural food items compared to larger conspecifics. Imsland et al. [8] found that significantly lower sea lice infection levels were observed on Atlantic salmon when reared together with small lumpfish (initial weight 54 g) compared to the control group without lumpfish, whereas this trend was not as clear when salmon were reared with larger lumpfish (initial weight 360 g), although indications of sea lice grazing were reported.

In the study of Imsland et al. [29], there was a general trend for sea lice grazing to decrease as the lumpfish grew, but this trend varied between the families, possibly indicating parental control over this effect. In some families, very few or no lumpfish over

120 g grazed on sea lice, whereas a more equal size class distribution of sea lice grazing was seen in the other families.

Overall, published studies strongly indicate a size-related effect on sea lice grazing among lumpfish weighing approx. 20 g to 360 g, but that this may vary based on the genetic composition of the lumpfish population.

4. Results: Large-scale Observations

4.1. Large-scale Trial: Autumn and Winter

Imsland et al. [19] performed a large-scale trial with lumpfish at a commercial Atlantic salmon sea farm from October to May of the following year. Numbers of pre-adult *L. salmonis* were low (≤ 0.25 per fish) in all lumpfish groups throughout the experimental period (Figure 4A). Significantly, lower levels of mature female *L. salmonis* were seen in the lumpfish groups from January to April (Figure 4B). Moreover, there was a relationship between lumpfish density and levels of adult female lice, as progressively fewer adult female lice were seen in the 4% to 8% density groups. Between weeks 4–11, 60–100% fewer adult female lice were seen in the lumpfish groups compared with the control group.

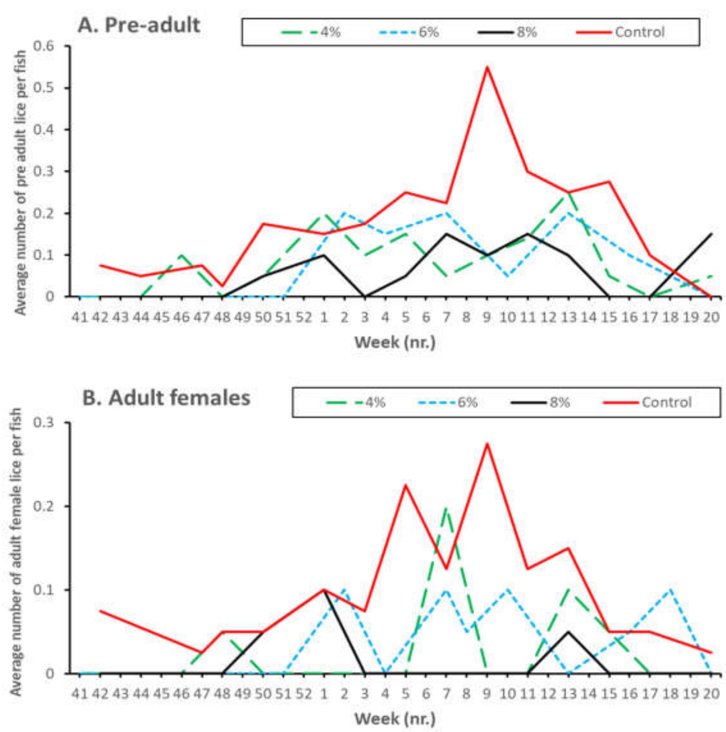

Figure 4. Occurrence of pre-adult (**A**) and adult female (**B**) *L. salmonis* on Atlantic salmon in large-scale sea cages at Lerøy Aurora, northern Norway, with 0 (control), 4, 6, and 8% density of lumpfish recorded for duplicate treatments during biweekly sampling. Figure modified from [23].

4.2. Large-scale Observations: Year Round

Boissonnot et al. [12] sampled a total of 2104 lumpfish from eight Norwegian salmon farms over 2 years. Weight and sex was determined for each individual. Stomach content was visually identified and categorized as sea lice, lumpfish feed, salmon feed, biofouling organisms, and zooplankton. Proportions of lumpfish with sea lice in their stomachs varied from 0 to 47% (average of 8.7% for the whole study), and the number of ingested sea lice varied from 0 to 120 (average of 0.6) between Atlantic salmon farms and sampling dates. The authors found that individuals with the highest cleaning efficacies were small

(< 100 g) and fed on additional prey items, mainly biofouling organisms. Lumpfish sex did not influence cleaning efficacy.

4.3. Large-scale Observation: Summer to Winter

Imsland et al. [37] performed a large-scale trial at a commercial Atlantic salmon sea farm from July 2017 to February 2018. Two nearby locations, Finnkjerka (with lumpfish) and Mollgavlen (without lumpfish), in the same seawater basin (10 km between them) were monitored. Overall, fewer *L. salmonis* were found on the salmon when lumpfish were present (Finnkjerka location) compared with the location with no lumpfish (Figure 5). Overall, there were more sea lice challenges at the Mollgavlen location, and this resulted in an approximately 600 g lower final slaughtering weight of the salmon at this production site despite a similar smolt weight at the onset of the rearing period.

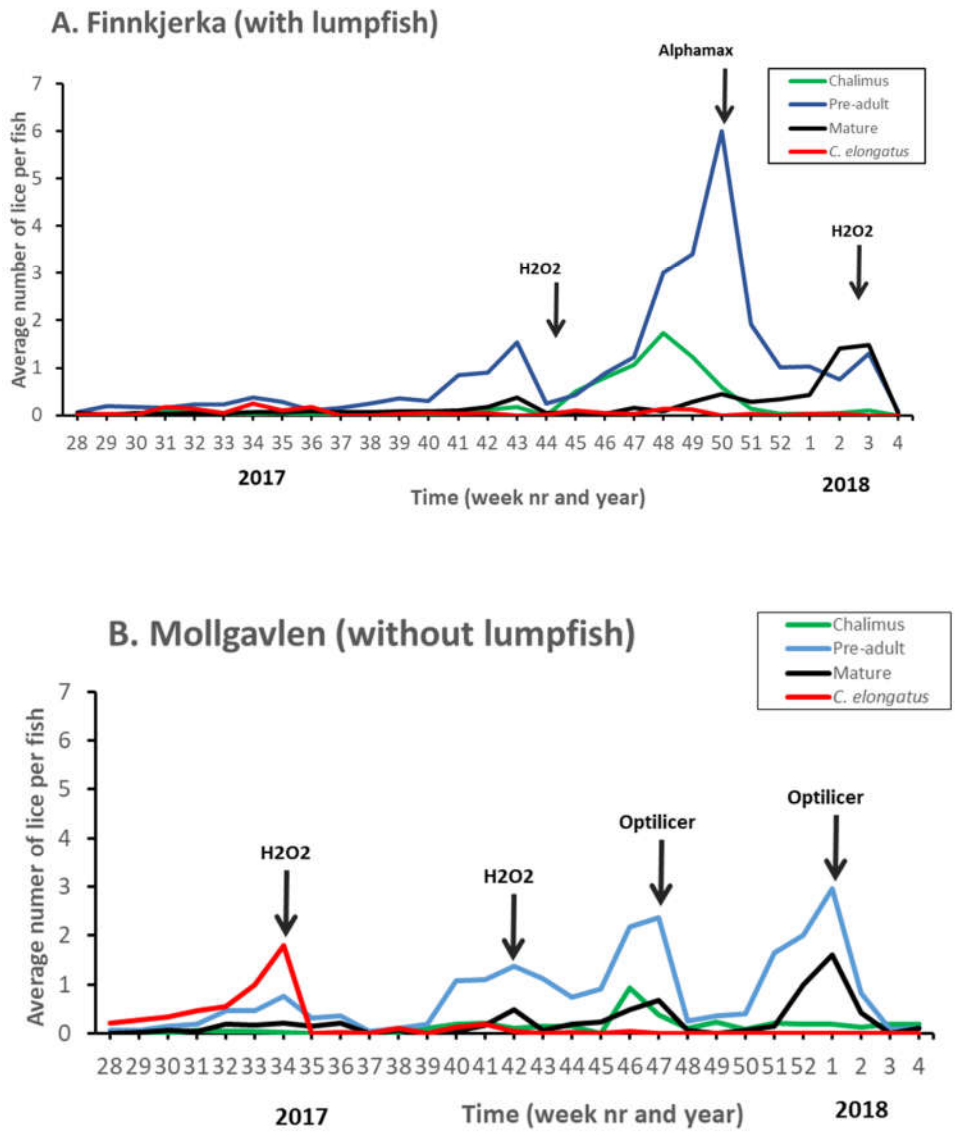

Figure 5. Sea lice development at two production sites of Nordlaks in northern Norway 2017–18 with lumpfish (**A**) and without lumpfish (**B**) in sea pens with Atlantic salmon. Arrows indicate mechanical (Optilicer®) and chemotherapeutical (H_2O_2 (hydrogen peroxide), AlphaMax™) delousing operations during the observation period. Previously unpublished data.

4.4. Large-scale Observation: Combination of Lumpfish and Tarpaulin Net (Lice Skirt)

A large-scale observation was performed at a commercial Atlantic salmon sea farm at Røssøy, Nordland county, Norway (67.90 °N, 14.93 °E), from 10 September 2018 to 12 December 2018. The observation was conducted in four large sea cages (90 m circumference) holding an average of 150,0000+ Atlantic salmon smolts in each cage. The mean weight (± SEM) of the Atlantic salmon was 505 ± 85 g at the start of the study period. The sea cages in the study were fitted with a surrounding tarpaulin net (lice skirt), to a depth of 7.5 m, and a closed fish cage system (CFC) with in situ impellers that was activated to lift seawater from depth to provide suitable continual oxygenation. In two of the cages, 1,4250 juvenile lumpfish (9.5% density) with a mean weight of 71 ± 6 g, were reared together with the salmon. The lumpfish were fed with feed blocks (World Feeds UK [38,39]).

Thirty salmon from each sea pen were sedated every second week during the observation period, individually weighed, and any lice present were recorded. After counting was complete, any lice remaining in the container were also recorded. Lice were registered in three categories: 1) *Lepeophtheirus salmonis*, adult female; 2) *L. salmonis*, pre-adult; 3) *L. salmonis*, chalimus.

Infestation levels of chalimus stages of *L. salmonis* were higher during weeks 1, 2, and 4 (between 33% and 67%) in the cages with stocked lumpfish compared to cages with no lumpfish (Figure 6A). There were lower infestation levels of pre-adult *L. salmonis* recorded for the cages stocked with lumpfish compared to the sea cages with no lumpfish in weeks 2, 9, and 12 (Figure 6B). The numbers of mature female stages of *L. salmonis* fluctuated but remained low throughout the study period in both treatments. Cages stocked with lumpfish had lower infestation levels on three occasions (Figure 6C), with no mature female lice recorded during weeks 3, 9, and 11.

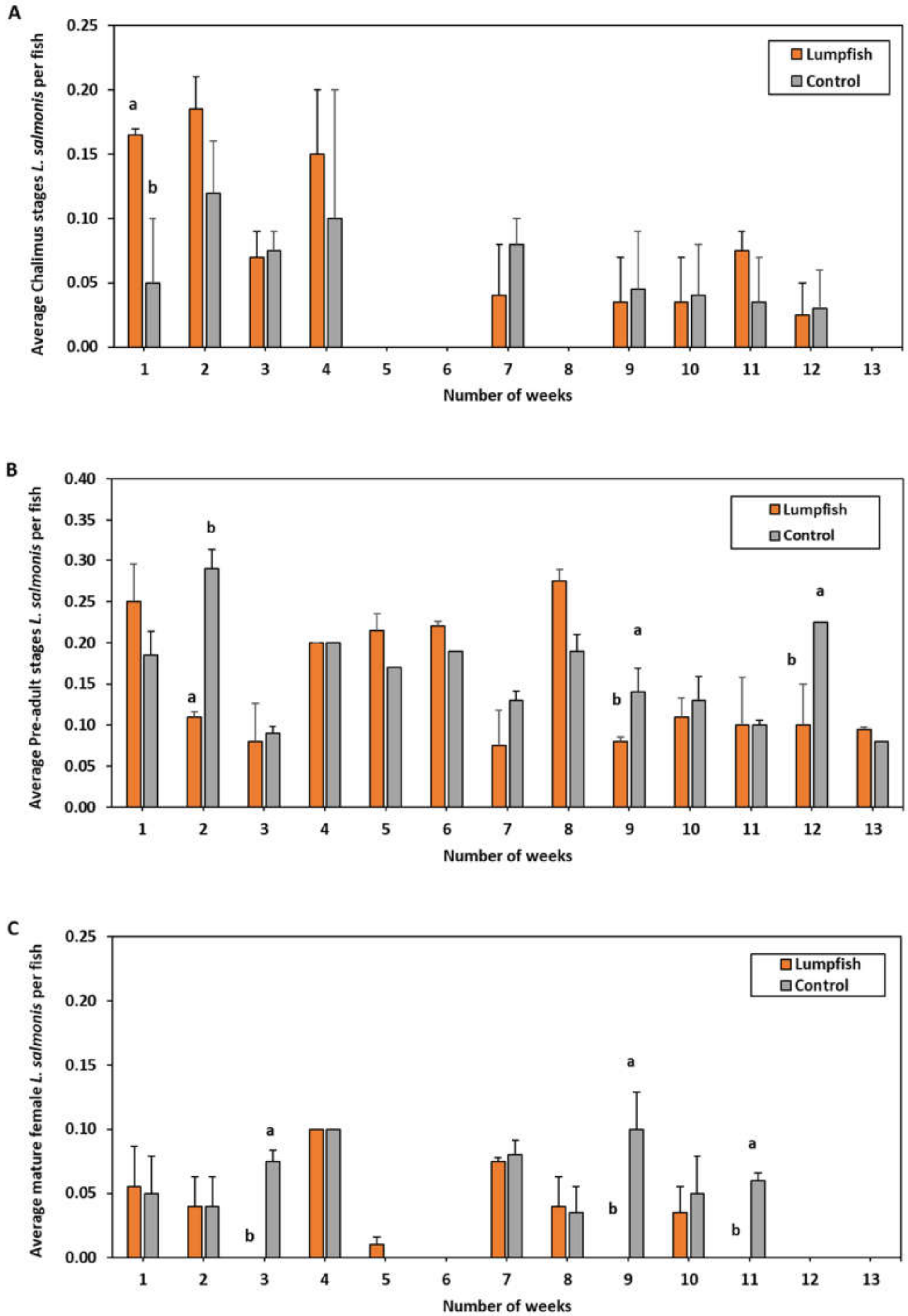

Figure 6. Mean occurrence of the chalimus (**A**), pre-adult (**B**), adult female (**C**) stages of *L. salmonis* per salmon (N = 60) in sea cages with lumpfish present and without lumpfish (Control) at the Røssøy facility. Values are presented as means ± SE. Different letters indicate significant differences (SNK post hoc test) between cages with and without lumpfish present. Previously unpublished data.

4.5. Large-scale Studies: the Faroe Islands

Eliasen et al. [27] investigated the cleaning efficacy of lumpfish in Faroese salmon farming pens in relation to lumpfish size and seasonality. The background to their study was that, although about half of the Faroese salmon farming sites use lumpfish as cleaner fish, large variations in their cleaning efficacy are frequently observed, especially seasonally. The authors examined 5511 lumpfish stomachs over a period of 2 years, and found a significantly lower prevalence of sea lice in the lumpfish stomachs during the summer months, while the prevalence of zooplankton in the lumpfish stomachs was highest during summer (Figure 7). Surprisingly, a positive association between the prevalence of organisms associated with biofouling and sea lice was found, indicating, that the occurrence of alternative food opportunities, in the form of biofouling organisms, had a positive influence on the cleaning efficacy of lumpfish. It was speculated that biofouling and the associated organisms stimulate a more active foraging behavior, which is supported by the data from [34] showing that live feed habituation stimulates sea lice grazing rate and efficacy of lumpfish. Data from Norway [10] indicate that lumpfish favor zooplankton as prey when it is available, reducing the sea lice grazing efficacy in periods with a large natural occurrence of zooplankton in sea pens, i.e., during summer.

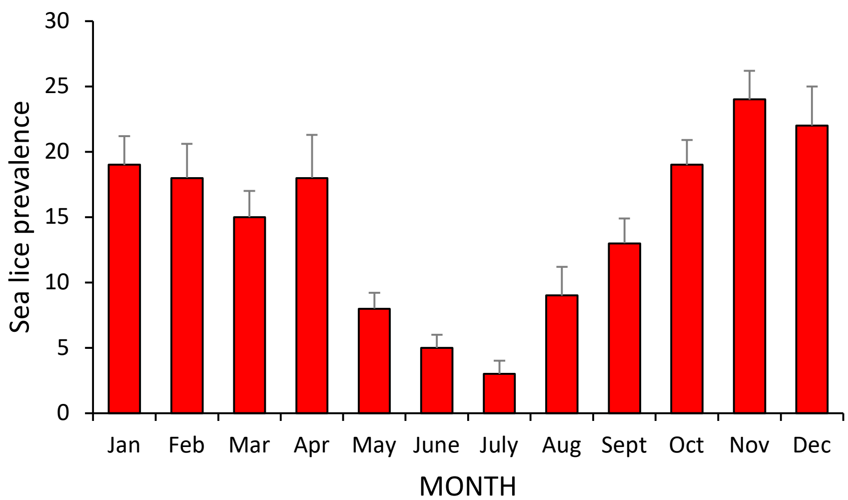

Figure 7. Average monthly prevalence of sea lice in lumpfish stomachs in Faroese salmon farms. Vertical bars indicate standard error (SE). Data modified from [27].

Overall, the data from the Faroe Islands [27] show that, depending on season, around 5–23% of the lumpfish population in the sea pens had eaten sea lice prior to being sampled, thereby significantly lowering the sea lice burden in the sea pens.

5. Discussion

5.1. Small-scale Studies

Data from several small-scale sea cage studies with lumpfish indicate a clear grazing effect of *L. salmonis* on Atlantic salmon, and that this may lower the lice burden on salmon by between 40% [29] and 97% [6]. In the study of [6], there was found to be a relatively large increase in numbers of lumpfish with ingested sea lice in their stomachs, suggesting that the level of grazing intensified throughout the study period. This may be indicative of some form of learning or habituation event (see below) among lumpfish, or an underlying genetic component (see below).

Habituation treatment influenced the ability of lumpfish to effectively forage on *L. salmonis*, as lumpfish conditioned prior to sea pen rearing were nearly 40% more efficient at grazing *L. salmonis* compared to controls. These results suggest that lumpfish fed live feed (here *Artemia* and frozen sea lice) prior to transfer to sea pens consumed more sea lice compared to the marine feed group. Imsland et al. [34] observed the behavior of the lumpfish at regular intervals during the study. Significant differences were detected between lumpfish fed only on marine dry feed during the juvenile stage (MF) versus lumpfish fed with a combination of dry and live feed (LF). The consistency of the differences in the behavior shown may indicate that the dietary treatment during the juvenile phase resulted in a persistently altered behavior. A positive effect of feeding habituation has also been seen in other cleaner fish species, e.g., Ballan wrasse, *Labrus bergylta* [40].

Another way of encouraging habituation is to expose the lumpfish to salmon prior to transfer to sea pens. Indeed, Staven et al. [41] have shown that previous exposure to salmon may reduce stress and improve cohabitation. They tested the effect of habituation by comparing naïve lumpfish (fish not previously reared with Atlantic salmon) with experienced lumpfish (fish from sea pens with Atlantic salmon). The found that naïve lumpfish exposed to Atlantic salmon for the first time showed increased swimming activity, increased interspecies distances, and elevated plasma cortisol concentrations. In comparison, experienced lumpfish showed no change in swimming activity when reintroduced to Atlantic salmon, shorter interspecies distances, and additional desensitized physiological stress responses depicted as significantly lower plasma cortisol levels. They concluded that the length of the habituation period should be taken into account when lumpfish are introduced for commercial use to improve the welfare of the species concerned.

Another possible way of increasing the understanding of underlying causes of variation in the efficacy of lumpfish is to use biological modeling techniques to explore the interactive effect of lumpfish grazing and mate limitation on sea louse population dynamics under different environmental scenarios. McEwan et al. [42] used an agent-based model (ABM) to simulate cleaner fish on a salmon farm to explore interactions between sea louse mating behavior, cleaner fish feeding rate, temperature, and external sea louse pressure. They found that sea louse mating has a substantial effect on sea louse infestations under a variety of environmental conditions. Their results suggest that lumpfish can control sea louse infestations most effectively by maintaining the population below critical density thresholds (0.5 adult female lice per salmon). Furthermore, their data confirmed the effectiveness of lumpfish at controlling sea lice, particularly when lumpfish stocking is combined with low-density thresholds for chemical treatments, which can leverage sea lice mate limitation as an additional mechanism for control.

5.2. Is Lumpfish Consumption of *L. salmonis* a Heritable Trait?

Given the differences recorded for the consumption of *L. salmonis* in published family trials [28,35], it has been suggested that this behavior may have a genetic basis. It is well known that behavioral traits respond to both natural [43,44] and sexual selection [45,46]. Recent studies have indicated both maternal [47] and paternal [48] effects on offspring behavior via epigenetic alterations to the genome. Results from both published family trials [28,35] on lumpfish indicate that consumption of *L. salmonis* can vary between families, and could be enhanced through selection and targeted breeding programs. In Norway there are now two ongoing breeding programs for lumpfish, with a focus on increasing the sea lice grazing efficacy and robustness of lumpfish (Kyst.no. Available online: https://www.kyst.no/aquagen-namdal-rensefisk-rogn/starter-avlsprogram-pa-rognkjeks/669709 (accessed on 1 June 2021)) [35]. The findings from [36] on personality profiling of lumpfish indicate that selecting the most active and boldest lumpfish for breeding could increase the time lumpfish spend inspecting and pursuing salmon 1.4–3.5-fold within a generation. Currently, many lumpfish do not engage in cleaning behavior [6,8,9,27], and selecting for behaviors that make good cleaners [37], combined with the use of targeted breeding [28,35], could drastically reduce the number of lumpfish required on farms, thus reducing costs and improving welfare [34,49].

5.3. Size-related Sea Lice Grazing of Lumpfish

Smaller lumpfish (initial size approx. 20–60 g) have a higher overall preference for natural food items, including sea lice, compared to larger conspecifics [8,12,29]; more recent results seem to confirm this [35]. At the end of the study of Imsland et al. [35], the lumpfish from 10 different half- and full-sib families were arranged into size classes, and the sea lice grazing potential of each was recorded. Generally, it was found that it was the smallest size classes that exhibited higher sea lice grazing potential compared to the larger size classes. Lumpfish between 40 and 140 g had the greatest grazing effect overall, similar to that seen in the studies of [8] and [29]. Furthermore, Imsland et al. [35] reported that the frequency of repeated lice grazers (investigated by gastric lavage) differed between sibling families. Considering that sea lice grazing efficacy is a trait that is strongly desirable in future breeding programs, then the frequency of lice grazing by individuals within families should also be used as a selection criterion for such programs.

5.4. Large-scale Studies

All reviewed large-scale studies reveal active sea lice grazing by lumpfish. Moreover, all the reviewed large-scale studies in the present review are based on replicated studies. Concern with the lack of replication in small- and large-scale studies with cleaner fish has appropriately been raised in a previous review [33]. In all large-scale trials reviewed here, with lumpfish present and absent (control groups), the mean numbers of *L. salmonis* were significantly lower in groups with lumpfish present. Available data indicate that lumpfish are effective at lowering sea lice numbers on Atlantic salmon all year round [12,20,27], but that this effectiveness may be reduced in periods with a high abundance of natural live feed in the sea pens [27]. Lumpfish seem to tolerate low sea temperatures well, with grazing activity seen to occur at temperatures as low as 2–3°C in Iceland (H. Methúsalemsson, Arnarlax Ltd., Iceland, pers. comm.). It is necessary to offer the lumpfish reared together with Atlantic salmon in large-scale sea pens additional feed, as this has been found to reduce mortality and improve the welfare of the fish [38]. Indeed, continued use of lumpfish must be accompanied with an increased focus on fish welfare in the sea pens [33]. The use of feed blocks seems to be a good option for lumpfish, with studies reporting lower mortalities and lower operational welfare indicators (OWIs) when feed blocks were used in large-scale rearing with Atlantic salmon [39].

Sea lice skirts on pens act as a barrier to salmon lice. Lice skirts are widely used in Norway, with > 900 lice skirts sold by a single company in 2017 [50], and with two to three skirts used depending on cage size. Previous research has shown that lice skirts can reduce infestation levels by 30% (with a 5-m skirt [51]) to 80% (10-m skirt [52]). However, lice skirts can reduce dissolved oxygen concentrations in cages [52,53], which can lead to poor welfare and reduced growth of salmon [54]. The combined use of lice skirts and lumpfish was tested in a large-scale trial reviewed here (i.e., Røssøy, Norway). The combined reductions observed in this large-scale study show that lumpfish and lice skirt systems can reduce sea lice infestation levels when used in tandem. However, the study period was relatively short, and thus further longer-term studies are required to fully elucidate this potential using combined treatment methods.

6. Summary of Effects Found Using Lumpfish

To summarize the relationship between the use of lumpfish and the occurrence of *L. salmonis* on Atlantic salmon (Table 1), we have compiled the current knowledge from the published literature, reports, and from interviewing fish health personnel and biological controllers working in the salmon farming industry in Norway (N = 18), the Faroe Islands (N = 5), Scotland (N = 4), and Iceland (N = 2) [37]. All available data clearly indicate that lumpfish graze on *L. salmonis*, and that it is possible to enhance this grazing with the assistance of live feed conditioning prior to sea pen transfer, and with selective breeding. Grazing has been observed in various size classes (25 g to 360 g, Table 1), at temperatures ranging between 2 to 13°C, and in all seasons (Table 1). The majority of published data are from northern Norway, but there are also published data from the Faroe Islands, and observations from Scotland and Iceland, that clearly indicate that lumpfish graze on *L. salmonis*. In the Faroe Islands, an investigation into the contents of 5511 lumpfish stomachs [27] reported that *L. salmonis* was found in 13.5% of these stomachs, and of the 13.5%, around 80% also had *C. elongatus* in their stomach (K. Eliasen, Fiskaaling, Faroe Islands, pers. comm.). The consensus in the salmon farming industry in the Faroe Islands is that lumpfish are effective at reducing the numbers of *L. salmonis*, but the data of Eliasen et al. [27] show that lumpfish seem to favor zooplankton as prey when it is available. In the Faroe Islands, this has a large influence on the cleaning efficacy of lumpfish, reducing the average effect by a factor of approximately five. Eliasen et al. [27] concluded that this knowledge should be implemented in the sea lice strategies of farming sites using lumpfish as cleaner fish and where secondary production, i.e., naturally occurring food, can negatively affect the cleaning efficacy.

In Scotland, both lumpfish and wrasse are presently being used as cleaner fish. Lumpfish are used as a routine practice, especially during the winter months when the wrasse are less active, and because lumpfish are more active than wrasse at these colder temperatures (L. Bennett, Cleaner fish Manager, Loch Duart, pers. comm.). No experimental trials with lumpfish are being carried out in Scotland at the moment (J. Treasurer, FAI Aquaculture, Scotland, pers. comm.). The efficacy of lumpfish is judged by investigation into gut content (Figure 8), and farming data indicate effective lice grazing of lumpfish when stocked (L. Bennett, Cleaner fish Manager, Loch Duart).

Table 1. A summary of the current literature (peer-reviewed journal articles and scientific reports) and observations (including pers. comm.) on experiments with lumpfish and their effect on *L. salmonis* infestations on farmed Atlantic salmon. Data include: experimental period and temperature, experimental unit, experimental site/country, stocking density of lumpfish, effect investigated, and whether an effect was found.

Citation	Experimental period and temperature	Experimental unit (number and size)	Experimental site/country	Size and density of lumpfish (numbers in relation to salmon)	Effect investigated	Effect on *L. salmonis* found?
			Small-scale studies			
Imsland et al. (2014a) [6]	June–August, 123Ema9.0–12.1°C	4 small sea cages 5 × 5 × 5 m (125 m^3)	Nordland county, Norway	53–182 g123Ema10% and 15%	Different density of lumpfish	Yes, increased effect at 15% density
Imsland et al. (2016a) [28]	May–August, 123Ema7.1–13.2°C	9 small sea cages, 5 × 5 × 5 m (125 m^3)	Nordland county, Norway	169–549 g123Ema10%	Different families, parental effect	Yes, and varied between families
Imsland et al. (2019a) [34]	May–July, 123Ema7.2–13.3°C	4 small sea cages 5 × 5 × 5 m (125 m^3)	Nordland county, Norway	114–180 g123Ema10%	Habituation of lumpfish	Yes, and habituation of lumpfish increased the effect
Imsland et al. (2021) [35]	September–December,123Ema10.5–6.8°C	10 small sea cages, 5 × 5 × 5 m (125 m^3)	Nordland county, Norway	30–123 g,123Ema12%	Different families	Yes, and varied between families
			Large-scale studies			
Imsland et al. (unpublished data)	September–December,123Ema12.1–8.5°C	4 large sea cages (90 m circumference)	Røssøy, Nordland county, Norway	71–125 g,123Ema9.5%	Large-scale evaluation of sea lice grazing in lumpfish	Yes. Increasing effect of lumpfish seen during the trial

Imsland et al. (unpublished data)	July–January,123Ema12.2-5.5°C	12 large sea cages (160 m circumference, 58,900 m^3 volume)	Nordlaks AS, Nordland county, Norway	32–157 g,123Ema6%	Large-scale evaluation of sea lice grazing in lumpfish	Yes. Less mechanical treatment, 600 g larger salmon at slaughter with lumpfish present
Imsland et al. (2018a) [23]	October–May,123Ema8.3°C in October 3.6°C in March 6.8°C in May	8 large sea cages (130 m circumference, 37,688 m^3 volume)	Lerøy Aurora AS, Troms county, Norway	25–115 g,123Ema4, 6, and 8%	Different densities of lumpfish in large-scale sea cages	Yes, similar effect seen at all densities
Boissonnot et al. [12],	Year round123Ema4–15°C	Large sea cages from 8 farming sites	Norway, northern Trøndelag county	10 and 1050 g123Ema(average of 129.5 ± 131.1 g), density not given	Cleaning efficacy of lumpfish in relation to size, season, diet and sex	Yes, Proportions of lumpfish with sea lice in their stomachs varied from 0 to 47% (average of 8.7% for the whole study). Sea lice grazing most efficient in August–October
Eliasen et al. (2018) [27], Kirsten Eliasen, Fiskaaling, Faroe Islands, pers. comm.)	Year round,123Ema6–11°C	Large sea cages from 9 farming sites	Faroe Islands	13–545 g,123EmaDensity not given	Cleaning efficacy of lumpfish in relation to size and season	Yes, but seasonal effect seen. Sea lice grazing most efficient during October–April
Eva Dögg Jóhannesdóttir, Arctic Fish Ltd. (pers. comm.)	June–December,123Ema10.1–3.2°C	7 sea pens (160 m circumference)	Iceland, Dýrafjörður	20–255 g,123Ema8–10%	Comparison of sea lice at sites with and without lumpfish	Yes, significantly lower *L. salmonis* with lumpfish present

Hjörtur Methúsalemsson, Arnarlax Ltd. (pers. comm.)	September–September (one year)123Ema1.9°C (February)123Ema11.1°C (early September).	12 sea pens (160 m circumference)	Iceland, Arnarfjörður	32–340 g123Ema8–10%	Comparison of sea lice at sites with and without lumpfish	Yes, significantly lower *L. salmonis* with lumpfish present

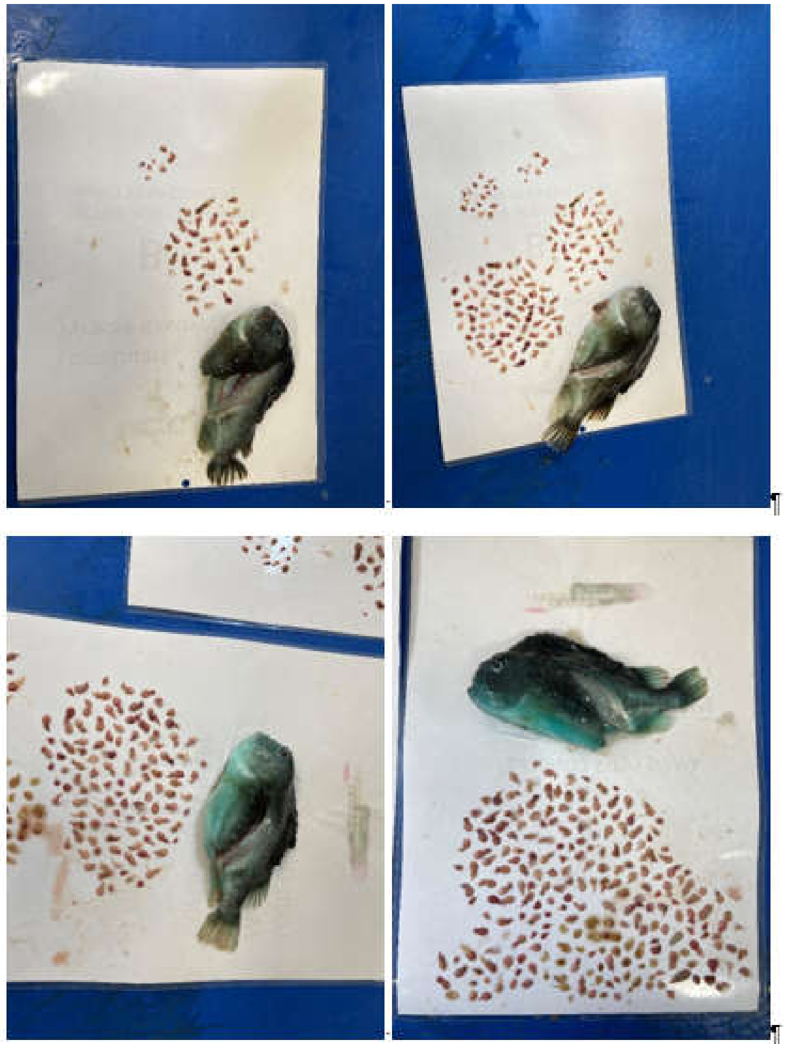

Figure 8. Gut content of stocked lumpfish from Scotland. Samples were taken during a harvest operation, on 16 July 2021. Fish samples were varied, but all fish were above 100 g and in good health. They were transferred into sea cages on 9 February 2021 at an average weight of 30 g and at a rate of 9–11% stocking density. All lice seen in the picture are *L. salmonis.* Photos: L. Bennett, Cleaner fish Manager, Loch Duart.

In the Westfjords area of Iceland, *C. elongatus* infestations are presently considered a more severe problem than those of *L. salmonis*, and the numbers of *C. elongatus* on each salmon can be high (> 10) in late autumn (October–November) (Eva D. Jóhannesdóttir, Arctic Sea Farm Ltd., pers. comm., Hjörtur Methúsalemsson, Arnarlax Ltd., pers. comm.). In this area, large-scale trials have shown that lumpfish are very effective at lowering numbers of *L. salmonis* (Eva D. Jóhannesdóttir, Arctic Sea Farm Ltd., pers. comm., Hjörtur Methúsalemsson, Arnarlax Ltd., pers. comm.).

7. Conclusion and Best Practice to Increase Lumpfish Efficacy

We have reviewed all available large-scale studies from Norway, Iceland, the Faroe Islands, and Scotland, covering sea temperatures from 2 to 15°C, a size range between 13 and 1050 g, and year-round use. The data reveal that lumpfish can actively contribute to lower numbers of *L. salmonis* on farmed Atlantic salmon under both experimental-size sea pens as well as in industrial-scale rearing in open sea pens. Data show that it is possible to enhance the lice grazing efficacy of lumpfish with the assistance of live feed conditioning prior to sea pen transfer, along with selective breeding and with targeted use of small juvenile lumpfish.

Based on the findings reviewed in this study, and findings reported in a recent Norwegian Seafood Research Fund project (FHF.no. Available online: https://www.fhf.no/prosjekter/prosjektbasen/901652/(accessed on 15 March 2022)), the following best practice conditions can be provided for lumpfish rearing in sea pens together with Atlantic salmon.

It is recommended to put lumpfish out in sea cages in the autumn [12] and to combine this with a reduced period in the sea (up to 6–7 months, [12]). This will allow the fish farmer to keep lice numbers low during this period. Furthermore, this combination will mean that the lumpfish are not in the sea cages during the delousing season, or during the period when the sea temperature is highest. Both delousing [12,55] and high temperatures (> 16°C, [56]) have a strong negative effect on the welfare status of lumpfish, and these measures will thus improve this status among lumpfish in sea cages.

Considering the present knowledge and recent data showing that the welfare of lumpfish can be compromised if mechanical delousing operations are conducted once they are in sea pens with salmon, we recommend to avoid any mechanical delousing operations when lumpfish are in sea cages with salmon.

Reducing the period in the sea should be combined with initial stocking of small individuals (< 40 g). This will help to develop a large proportion of small individuals in the population (< 300 g). Since small lumpfish have the highest appetite for lice, this will most likely increase lice grazing efficiency [12,27,29,35].

If possible, habituation towards salmon [41,57] and live feed types [34] should be applied to increase efficiency in the first phase after stocking in the sea cages. In addition, adaptation to salmon reduces stress at sea cage stocking, which helps to improve the welfare of lumpfish [38,57].

It is important to feed the lumpfish separately from the salmon, preferably using special feed designed for this species [38,39].

Exposed sites may have sea currents that are too strong for lumpfish that have limited swimming ability [56,58]. It is therefore highly likely that the use of lumpfish should be limited to less-exposed locations. Several salmon farmers in Norway, with particularly exposed sites, have, after several trials with compromised or poor lumpfish welfare and little effect on sea lice grazing, decided not to use lumpfish [12].

Good routine follow-ups of the welfare of lumpfish should be implemented. These should be carried out by trained personnel in order to identify reduced welfare and possible outbreaks of the disease early, and thus implement preventive measures [12,35,49]. In this way, one can also identify which procedures and operations affect the health and welfare of lumpfish, in order to further adapt and optimize them. Standards for routine follow-ups will be achieved by setting the correct and sufficient resources for the commercial use of lumpfish [12,35,49,59].

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