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Use of lumpfish for sea-lice control in salmon farming: challenges and opportunities

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Abstract

Efficient sea-lice control remains one of the most important challenges for the salmon farming industry. The use of wrasse (*Labridae*) as cleaner fish offers an alternative to medicines for sea-lice control, but wrasse tend to become inactive in winter. Lumpfish (*Cyclopterus lumpus*) continue to feed on sea-lice at low temperatures, and commercial production has escalated from thousands of fish in 2010 to well over 30 million juveniles deployed in 2016. However, production still relies on the capture of wild broodstock, which may not be sustainable. To meet global industry needs, lumpfish production needs to increase to reach c. 50 million fish annually and this can only come from aquaculture. We review current production methods and the use of lumpfish in sea cages and identify some of the main challenges and bottlenecks facing lumpfish intensification. Our gap analysis indicates that the areas in most need of research include better control of maturation for year-round production; formulation of appropriate diets; artificial selection of elite lines with desirable traits; and development of vaccines for certified, disease-free juvenile production. The welfare of farmed lumpfish also needs to be better quantified, and more information is needed on optimal densities and tank design. Finally, the risk of farmed lumpfish escaping from net pens needs to be critically assessed, and we argue that it might be beneficial to recover cleaner fish from salmon cages after the production cycle, perhaps using them as broodstock, for export to the Asian food markets or for the production of animal feeds.

Key words: biological pest control, cleaner fish, salmon farming, sea-lice, sustainable aquaculture.

Introduction: Lumpfish, a 'green' alternative for sea-lice control

Global production of Atlantic salmon, *Salmo salar*, reached 2.07 million tons in 2014 (worth over 9 billion Euros (Marine Harvest 2015)), but losses due to sea-lice are limiting industry growth and compromising its sustainability (McVicar 2004; Costello 2009; Jones *et al.* 2015). Sea-lice control has cost salmon farmers more than €305 million year⁻¹ during the last decade (Costello 2009) and escalated to €430 million in Norway alone during 2015 (Iversen *et al.* 2015), not including loss of productivity. Costs are set to increase as there is no effective vaccine against sea-lice, only a small number of antiparasitic therapeutants are currently

licensed for treatment, and these are losing their efficacy due to evolved parasite resistance (Lees *et al.* 2008; Jones *et al.* 2013). The search for non-medicinal solutions for sea-lice control, including commercial production of cleaner fish, has been singled out as the area in most urgent need of research and is a major priority for industry (Marine Harvest 2015) and governments (NERC 2015; Norwegian Directorate of Fisheries 2015). The use of cleaner fish is particularly attractive as they can reduce the use of chemo therapeutants, may be more cost-effective than medicating (Pike & Wadsworth 1999; Liu & vanhauwaer Bjelland 2014) and is potentially less stressful to farmed fish (Treasurer 2002, 2013). For these reasons, the number of cleaner fish used by the salmon farming industry has increased exponentially since 2008, and

almost 26 million were used by Norway alone during 2015 (Fig. 1). It is estimated that 50 million cleaner fish will be required by 2020 (10 million in the UK alone), most of which will be lumpfish. Such large numbers can only be achieved through commercial production.

Labrid fish (mostly ballan wrasse, *Labrus bergylta*, and goldsinny wrasse, *Ctenolabrus rupestris*) have been used to delouse farmed Atlantic salmon in floating net pens for almost 30 years (Bjordal 1991), and these can significantly reduce sea-lice prevalence (Treasurer 2013). Commercial production of wrasse, particularly of ballan wrasse, has since developed (Skiftesvik *et al.* 2013), and improvements have been made with regard to delousing efficiency, sustainability, disease management and welfare (Helland *et al.* 2014; Skiftesvik *et al.* 2014). However, wrasse exhibit winter dormancy and do not feed below 6°C (Kelly *et al.* 2014), which limits their use as cleaner fish over winter (Treasurer 2002, 2013). This has prompted interest in alternative cleaner fish that may remain active during winter and spring, and the lumpfish or lumpsucker is the species that offers the greatest potential (Imstrand *et al.* 2014a,b,c, 2015a,b, 2016a) and the species that is now most commonly used (Fig. 1). Lumpfish continue feeding at temperatures as low as 4°C (Nytrø *et al.* 2014) and can be ready for deployment in salmon farms in as little as 4 months, much sooner than ballan wrasse which typically require 1.5 years (Helland *et al.* 2014).

Unlike production of wrasse, which has increased only modestly, commercial production of lumpfish has grown

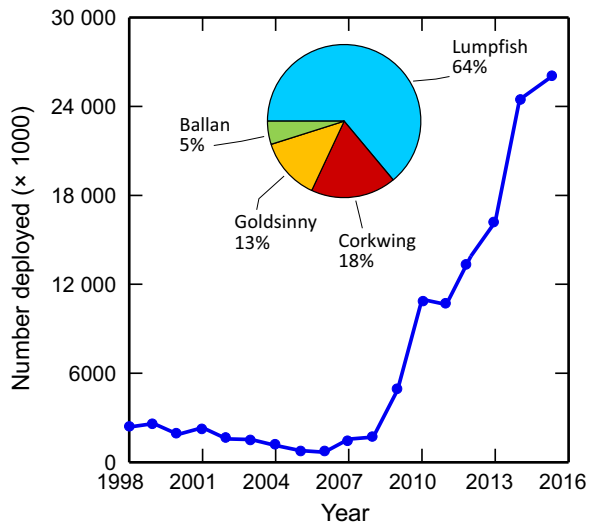


Figure 1 Number of cleaner fish (x1000) deployed in Atlantic salmon and rainbow trout sea cages in Norway during 1998–2015, including both wild-caught and farmed fish. Inset shows species breakdown (% numbers) during 2015. Data source: Norwegian Directorate of Fisheries (2015). <http://www.fiskeridir.no/English/Aquaculture/Statistics/Cleanerfish-Lumpfish-and-Wrasse>.

exponentially in the last few years (Fig. 2). It reached 11.8 million juveniles in Norway during 2015 (Norwegian Directorate of Fisheries 2015) and 0.8 million in the UK (R. Prickett, pers. comm., 2016) and is expected to exceed 30 million juveniles by 2016, 20 million in Norway alone (Nodland 2016). The average price paid per cleaner has continued to increase and is currently c. 18 NOK/fish for lumpfish (€1.98) and c. 23 NOK/fish (€2.53) for wrasse of deployment size, suggesting the market is still expanding, as demand exceeds supply (Fig. 2).

Currently, nearly all lumpfish used as cleaner fish by the salmon farming industry are derived from wild parents, which may pose a strain on natural populations. The species has moderate to high vulnerability (Froese & Pauly 2014) and has been classified as near threatened (NT) in the IUCN Red List (Lorance *et al.* 2015). A significant decrease in Canadian and Icelandic spawning stocks has been recorded in recent decades, suggesting that some stocks may already be overexploited (Pampoulie *et al.* 2014). Across the FAO assessment zone, the abundance of

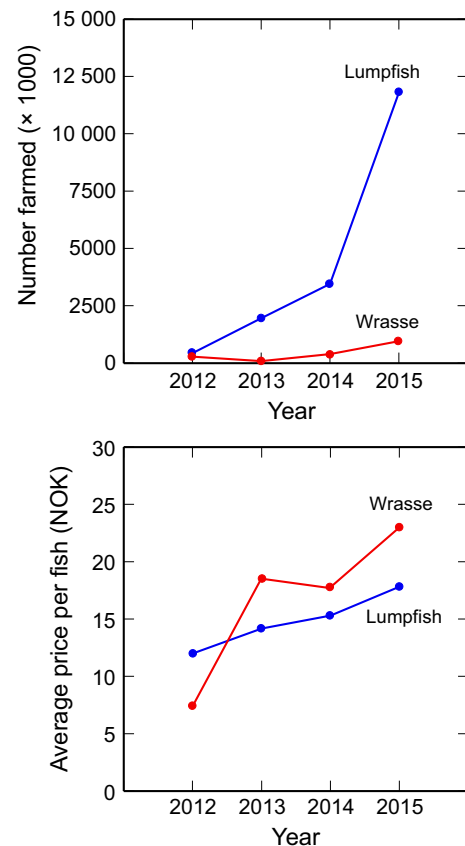


Figure 2 Sale of farmed cleaner fish to Atlantic salmon and rainbow trout producers in Norway. Numbers are expressed in 1000 individuals, and average price paid per deployed fish in 1000 NOK (1 NOK = €0.11). Data source: Norwegian Directorate of Fisheries (2015).

lumpfish has also declined by 25–35% over the last 20 years (Lorance *et al.* 2015).

Previously, lumpfish had received little attention, other than as a source of roe which is processed and sold as a substitute for caviar, and there are several dedicated lumpfish fisheries across the North Atlantic (Davenport 1985). Lumpfish had little economic value up until the early 20th century. Small fisheries existed in both sides of the North Atlantic for local consumption, but fish caught as bycatch were often used as animal feed or bait (Stevenson & Baird 1988). The use of lumpfish roe as a caviar substitute expanded the industry in the late 20th century. Ripe females yield between 15% and 36% of roe by weight (Davenport 1985; Stevenson & Baird 1988; Mitamura *et al.* 2007; Hedeholm *et al.* 2014) and can be quickly targeted by the fishery. World lumpfish roe production has averaged c. 3400 tonnes since 1992, but production has declined in more recent years, possibly due to overexploitation (Johannesson 2006). Other pressures that may have affected lumpfish populations include invasive species that feed on lumpfish eggs (Mikkelsen & Pedersen 2012), climate change (Perry *et al.* 2005), emerging diseases (Freeman & Kristmundsson 2013) and antifoulants (Bellas *et al.* 2005). In Iceland, the lumpfish fishery is closely regulated and both a licence and a catch report are required, having recently been granted the world's first MSC certification for the species (Anon 2013a), 2 years ahead of the lumpfish fishery in Greenland (Lassen *et al.* 2015). However, most lumpfish fisheries elsewhere are largely unregulated. Whilst the number of adult lumpfish taken by the incipient cleaner fish industry (c. 300 in the UK in 2014) is currently only a fraction of the numbers taken for roe and human consumption by the commercial fishery (14 367 in Greenland and 6225 in Iceland; Marine Stewardship Council 2014), there is concern about the sustainability of unregulated fisheries (Anon 2013b). A recent demographic study indicates that lumpfish achieve maximum production when they reach 20 cm in the case of males and 32 cm in the case of females (Hedeholm *et al.* 2014), suggesting that removing broodstock older than 2–3 years of age may have a disproportionately high impact on wild populations. Thus, our aim here is to summarize current knowledge on the artificial production of lumpfish for sea-lice control and address the challenges faced by lumpfish intensification, one that should not impact on wild stocks, or pose a disease risk to farmed salmon.

Gaps in knowledge and research priorities

The first pilot trials for the commercial production of lumpfish started in 2011 (Chilvers 2013; Imsland *et al.* 2014a), and consequently research and development are still at a very early stage, with production still relying on

the capture of wild broodstock, which has been argued by some as unsustainable (Farm Animal Welfare Committee 2014). To supply the salmon farming industry with the number of lumpfish required for sea-lice control, the species needs to be reared entirely in captivity. Aspects of the lumpfish fishery are relatively well known (Davenport 1985; Stevenson & Baird 1988), but knowledge of the biology of the species in captivity and its aquaculture potential is still very limited or not readily accessible, as much of it is anecdotal or lies in the grey literature.

Knowledge of the use of cleaner fish to delouse farmed salmon has increased much in recent years (Google Scholar cites 1080 papers during 1980–2015), but 87% of studies refer to the use of wrasse and only 13% refer to lumpfish. As with other novel species in aquaculture, there are critical gaps in knowledge that need to be overcome to make commercial lumpfish production sustainable (Table 1); these are examined next.

Genetic variation and population differentiation in lumpfish

Lumpfish are distributed across a large area on both sides of the North Atlantic Ocean: from Nunavut, Hudson Bay and Labrador to New Jersey and Bermuda in the Western Atlantic, to the Barents Sea, Iceland and Greenland and the Iberian Peninsula in the Eastern side (Vasconcelos *et al.* 2004; Bañón *et al.* 2008; Froese & Pauly 2014). More recent records have also extended the species' distribution to the Mediterranean Sea, although the significance of this is still uncertain (Dulčić & Golani 2006). Little is known about the extent of population differentiation of lumpfish from different origins, and this is an area where studies are much needed in support of the development of hatchery stocks with desirable traits. Twenty-two novel microsatellite DNA loci have been characterized for the species (Skirnisdottir *et al.* 2013), and its use in genetic stock identification has so far revealed three distinct genetic groups in the North Atlantic: Maine–Canada–Greenland; Iceland–Norway, and the Baltic Sea (Pampoulie *et al.* 2014) with little evidence of gene flow amongst these. However, no information is available for most other Atlantic areas, and new genetic data from the English channel suggest that lumpfish there have low to moderate levels of genetic diversity ($H_e = 0.53–0.61$) and low genetic differentiation (Consuegra *et al.* 2015; Pooley *et al.* 2015). Tagging studies indicate that lumpfish carry out extensive movements (up to 49 km day⁻¹, Kennedy *et al.* 2014) and display homing behaviour, returning to breed in the same areas more than once (Davenport 1985; Stevenson & Baird 1988; Kennedy *et al.* 2014). In a recent tracking study, females remained in a fjord for up to a week and then disappeared, either to move offshore or to spawn in other fjords (Mitamura *et al.*

Table 1 Gap analysis on commercial production of lumpfish

Stage/phase	Current state	Desired state	Proposals & actions
Source of broodstock	100% Wild caught	100% Farmed	<ol style="list-style-type: none"> 1 Need to close breeding cycle in captivity 2 Information is needed on genetic stock structure
Collection of gametes (sperm)	Males are routinely culled to extract their sperm	Sperm collected non-destructively; males used more than once	<ol style="list-style-type: none"> 1 Better control over maturation 2 Short-term storage of sperm 3 Long-term sperm bank though cryopreservation
Egg development	Eggs naturally stick together, decreasing oxygenation	Free eggs	<ol style="list-style-type: none"> 1 Research on egg degumming 2 Better incubators
Juvenile survival to deployment	High weaning mortality	Survival from egg to deployment +50%	<ol style="list-style-type: none"> 1 Optimize rearing protocols 2 Develop specific diets for different stages of lumpfish development
Health status	Risk of infection to salmon and other fish	Disease-free, fully certified fish become available	<ol style="list-style-type: none"> 1 Develop vaccines 2 Develop methods of rapid disease screening
Selective breeding	No selective programme in place (new species in aquaculture)	Develop elite lines with desirable traits	<ol style="list-style-type: none"> 1 Estimate heritability of commercial traits 2 Develop molecular markers for parentage assignment and marker assisted selection (MAS)
Reconditioning of post-spawning adults (kelts)	Fish only spawn once in captivity	Multiple spawnings over consecutive years	<ol style="list-style-type: none"> 1 Research on health and stress management 2 Develop adult diets 3 Better control over maturation
Deployment in salmon cages	Number remaining in cages is not known. Some fish escape. Variable sea lice grazing Upper temperature tolerance unknown	Attrition rates and lumpfish biomass are accurately known. Sea-lice grazing is maximized through selection and weaning	<ol style="list-style-type: none"> 1 Monitor and prevent lumpfish escapes 2 Develop accurate ways of live monitoring of lumpfish biomass in cages 3 Investigate QTL markers for sea-lice grazing 4 Develop family-based breeding programme to enhance sea-lice grazing 5 Determine effects of temperature on cage survival and sea-lice grazing
Delousing rates	Delousing performance is difficult to assess in salmon cages	Seasonal and cage to cage variation in delousing performance is known and can be related to the number of salmon and lumpfish	<ol style="list-style-type: none"> 1 Develop methods of monitoring changes in delousing activity under commercial conditions
Post-deployment	Lumpfish are culled after every salmon production cycle	Reduce wastage. Lumpfish are reused as cleaner fish and/or put to alternative uses	<ol style="list-style-type: none"> 1 Carry out feasibility study & market research to assess potential for source of caviar and fish feed 2 Consider use as broodstock for captive breeding

2012), unlike males which are known to remain in the same location for several weeks to tend the eggs (Davenport 1983). These results indicate that lumpfish likely display population structuring, as well as sex-biased dispersal, which will affect their patterns of gene flow and extent of population differentiation, as seen in other species (e.g. Consuegra & García de Leániz 2007).

Reproduction of lumpfish in captivity

To provide the numbers of lumpfish required by the salmon farming industry, research is needed on reproduction and control of maturation for year-round production, possibly using photoperiod and hormone control. In Britain, adults breed in shallow waters over rocky substrates during

the winter (Blacker 1983; Davenport 1985) and typically mature at 3–5 years of age (Anon 2003; Hedeholm *et al.* 2014), although some populations may mature after only 2 years (Albert *et al.* 2002). Males are typically smaller than females, develop a larger suction cup and mature earlier (Davenport & Lonning 1983; Hedeholm *et al.* 2014). Post-spawning survival is typically low, sometimes as little as 10% (Stevenson & Baird 1988; Kasper *et al.* 2014), which suggests that fish may only spawn once. A semelparous life strategy (i.e. only one spawning) is also suggested by the unusually high female reproductive investment (GSI in excess of 30%, Hedeholm *et al.* 2014).

For use as broodstock, wild adults are typically captured during the spawning season using gill nets deployed in shallow waters (up to ~30 m deep) close to shore. A mesh size

of 267 mm is used in Iceland (Kennedy *et al.* 2014), and whilst it is possible to use other means of capture that are potentially less damaging (e.g. SCUBA, Killen *et al.* 2007a), these tend to be less efficient. Lumpfish lack a swim bladder but adults hauled quickly to the surface may experience barotrauma. This can be reduced by returning animals to depth in a cage, followed by gradual decompression.

In captivity, fertilization can be carried out using the 'dry method', that is mixing the sperm with eggs and adding seawater to activate the sperm (Fig. 3). However, wild-caught males can be difficult to strip and sperm may need to be collected following dissection of the testes, which are then macerated and passed through a sieve to obtain the sperm. It is possible to obtain viable sperm from the testes

several days after removal from the fish (Davenport 1983), and lumpfish sperm can also be cryopreserved (Norðberg *et al.* 2015). However, culling males to obtain sperm is not a viable long-term approach (Kyûshin 1975; Davenport 1983) and greatly limits the development of an efficient captive breeding programme for the species. This is an area where improvements are required.

Wild females readily spawn in small tanks and without the need of substrate, but such eggs tend to yield lower survival as they are difficult to incubate optimally once they have hardened; for this reason, artificial fertilization of lumpfish is recommended (Kyûshin 1975; Brown *et al.* 1992; Nytrø *et al.* 2014) as it allows manipulation of the egg mass before it hardens. When artificial fertilization is

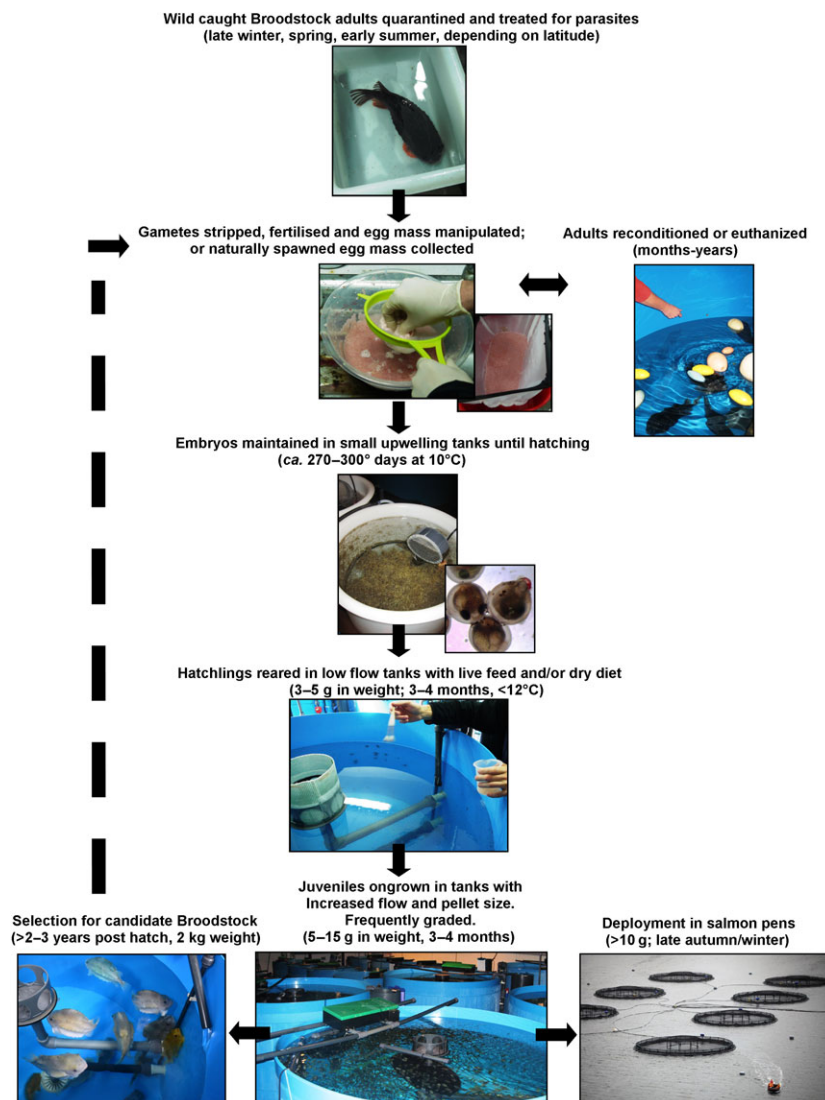


Figure 3 Overview of the commercial rearing of lumpfish, showing approximate size and duration of each production stage. A full cycle typically requires 6.5–7 months from egg to deployment at c. 10 g.

not possible, egg clumps from natural spawned females can be broken into smaller units to assist water flow over the eggs (Benfey & Methven 1986). This tends to result in more uniform embryo development and higher survival, as embryos deep in natural clumps tend to receive less oxygen and develop more slowly (Davenport 1985).

Egg incubation

Lumpfish eggs are naturally sticky and are found in large clumps in the wild, which are tended by the male through fanning and puffing water to maintain proper aeration; males also make funnel-like depressions in the egg mass which likely assist aeration (Goulet *et al.* 1986). In the wild, hatching is typically synchronous and most embryos hatch within 1 or 2 weeks (Brown 1986; Nytrø *et al.* 2014). Parental care by the male is thought to reduce egg loss from predators, removes waste products and in the later stages of development assists gas transfer via increased ventilation behaviour (Davenport 1983; Goulet *et al.* 1986; Mikkelsen & Pedersen 2012). Lumpfish eggs have been successfully reared in UV-treated upwelling incubators consisting of 70 L hoppers loaded with 0.5–1.0 kg of eggs, equivalent to c. 50 000–100 000 eggs per hopper (Fig. 3). Trials with vertical incubators and horizontal hatching boxes used in salmon rearing did not produce such good results. Flow rate is maintained at 20 L min⁻¹ during incubation, but this needs to be reduced to 10 L min⁻¹ at hatching to avoid the larvae being damaged. Hardening of the egg mass occurs a few minutes after fertilization and contact with seawater (Davenport & Lonning 1983), and during this period eggs can be shaped gently into a flat mat to increase oxygenation, as without the attention of the male they would starve of oxygen under artificial incubation conditions. Research on egg degumming, as performed with other species, may improve embryo survival and hatching rates and may also reduce the risk of pseudo-vertically transmitted pathogens. Preliminary trials on degumming agents such as milk, trypsin and alcalase tested previously on other species (Grant *et al.* 2016) have produced mixed results in lumpfish. Thus, alcalase in liquid form appears efficient at concentrations above 0.5% for 10 min at 8°C, but embryo development was poor and degumming could not be trialled under large-scale commercial conditions (Powell *et al.* 2015a). More research on egg degumming is clearly needed. Hatching typically requires 198–245 degree days, but does not occur at temperatures below 4°C (Collins 1976). Lumpfish eggs take c. 250 degree days to hatch at 10°C, fertilization success being typically above 90% (mean = 93.6%, SE = 0.853; M. Scolamacchia, unpubl. data 2015). As with other marine fish species, eggs are regularly treated with 50% bronopol (2-bromo-2-nitro-1,3 propanediol), a broad spectrum bactericide that is the active ingredient of *Pyceze*

(Birkbeck *et al.* 2006). *Buffodine*, an iodine-based product with neutral pH used to treat salmonid eggs, has also been used with lumpfish (Brown *et al.* 1992; Nytrø *et al.* 2014).

Larviculture

Lumpfish larviculture is still in its infancy, and this is also an area where research is much needed. Lumpfish are a highly fecund species and may be expected to experience a type III mortality (Deevey 1947), whereby the lowest age-specific survival is observed early in life, coinciding with the onset of external feeding, as is typical of many other fish species. This stage has been termed the critical time for survival (Elliott 1989) and is the stage where the greatest gain in survival can be achieved through larviculture. In culture, the critical period for survival (t_c) in lumpfish can be identified at around 25–30 days post-hatch (dph) at 10°C, which is consistent with weaning stress (Fig. 4), average survival at 30 dph being c. 78% although this can vary considerably among families. In the wild, recently hatched larvae are found in the top few centimetres of rockpools and on floating seaweed (Daborn & Gregory 1983; Moring 2001; Ingólfsson & Kristjánsson 2002), and, like many other species, begin feeding before they have completely reabsorbed their yolk sac, primarily on small prey such as crustacean larvae and halacarid mites (Ingólfsson & Kristjánsson 2002).

The first attempts at rearing lumpfish larvae under controlled conditions probably took place in the mid-1980s (Benfey & Methven 1986; Brown 1986), building on detailed information on the developmental of a closely related species, the smooth lumpsucker *Aptocyclus ventricosus* (Kyūshin 1975). In a pioneering study, Benfey and

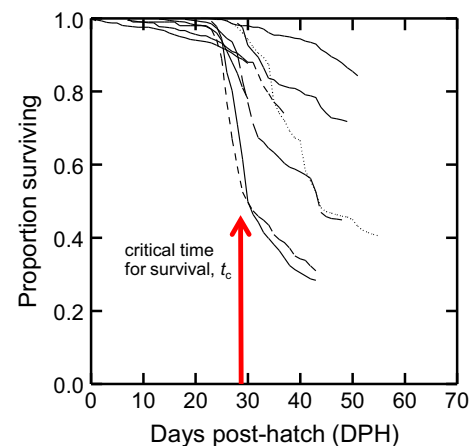


Figure 4 Variation in survival (proportion of fish remaining) of juvenile lumpfish from different families scaled to a common stage of development (days post-hatch) at the Centre for Sustainable Aquatic Research, Swansea University.

Methven (1986) transferred batches of c. 100 newly hatched larvae into submerged 'baskets' suspended in a trough at 9–15°C. A dry feed (trout starter diet) was offered and larvae began feeding at 7 dph, 3–4 days before full yolk resorption was completed at 10–11 dph. In a contemporary study, Brown (1986) reared larvae at 9.5–14°C and at a density of 1 larvae L⁻¹, and compared the growth of larvae fed on dry feed with those fed on live *Artemia salina*. After 1 month, average juvenile size was 7 and 12 mm for dry and live fed larvae, respectively, highlighting the benefits of using live *Artemia* shortly after hatching, a point which is supported by more recent studies (Nytrø 2013; Nytrø *et al.* 2014; Belova 2015). Large-scale larviculture trials began in the early 1990s, by which time larvae derived from artificially spawned broodstock were weaned on day-old *Artemia* nauplii four to 6 days after hatching (Brown *et al.* 1992). At the Centre for Sustainable Aquatic Research (CSAR; Swansea, UK), recently hatched lumpfish larvae are initially fed enriched *Artemia* nauplii and after two to 3 weeks are weaned on 250 µm Otohime (≥50% crude protein and ≥10% lipid by dry weight; Reed Mariculture, Campbell, CA, USA). Feed size is then gradually increased to 360–650, 580–840 µm and finally 800–1200 µm over a further 2–3 weeks (Fig. 3). One month later, pellet size is increased to 1.5 mm and eventually, when lumpfish reach 10 g a pellet size of 1.8 mm is used.

In lumpfish, the regression of oxygen consumption on dry weight has a slope of 0.82 (Killen *et al.* 2007b) which is larger than the mean of 0.80 for teleost fish (Clarke & Johnston 1999) and serves to highlight their more limited aerobic scope. Lumpfish larvae feed differently to most other cultured fish due to the ventral suction cup, which influences their behaviour. This likely reduces energy expenditure and may enable larvae to feed passively, although they become more active a few weeks post-hatch (Brown 1986). In experimental conditions where food density was maintained constant at 1000 *Artemia* L⁻¹, lumpfish larvae grew faster when food was administered in short pulses than when it was administered continuously (Brown *et al.* 1997). However, foraging mode appears to depend on prey abundance. Thus, when prey is abundant (750 *Artemia* L⁻¹), lumpfish adopt a 'passive cling' foraging mode, but when prey is scarce (75 *Artemia* L⁻¹), they resort to the more costly 'active swim' mode (Killen *et al.* 2007a). The 'cling' foraging mode observed at high prey density is likely to be beneficial for lumpfish as it allows individuals to conserve their limited aerobic scope for other physiologically demanding processes such as growth and digestion (Killen *et al.* 2007a). A better understanding of the energy requirements of larvae, optimal densities and feed rations, and more efficient ways of weaning from live to dry feeds are areas where advances in lumpfish larviculture will need to be made. Making *Artemia* and other

live feed biosecure might also be desirable to avoid these posing an infection risk to lumpfish.

Ongrowing

In the wild, lumpfish leave surface waters and adopt a benthopelagic existence once they reach c. 50 mm in length (Daborn & Gregory 1983), at which time they may attach to floating seaweed. They tend to ignore sessile and slow-moving prey items such as worms and bivalves, and concentrate instead on larger planktonic organisms (harpacticoids, amphipods, isopods) and even conspecifics (Daborn & Gregory 1983; Ingólfsson & Kristjánsson 2002). Information on their length-weight indicates that growth is very rapid during the larval stages but little data are available past 45 mm (Daborn & Gregory 1983) and this an area where more information is also needed.

Some early attempts at rearing lumpfish commercially consisted of bringing wild-caught juveniles into salmon cages and feeding them on proprietary salmon and flatfish feeds. However, high mortality ensued, attributed to fat deposits in the liver and brain (Gibson *et al.* 2015), highlighting the need for the formulation of specific diets that take into account the needs of the species. Lumpfish accumulate high levels of EPA and DHA in the roe (Rincón-Cervera *et al.* 2009), and there also seem to be differences in fat content between the sexes, males having more lipid in the muscle than females (Davenport & Kjørsvik 1986), suggesting that the metabolism of lipid fractions may vary with gender. Studies also suggest that nutritional problems may ensue if lumpfish only feed on salmon pellets after deployment (Imsland *et al.* 2015b). Novel formulated feeds, based on body composition and having a lower oil composition, are being produced specifically for rearing lumpfish in cages and offered at rations of 4–6% BW day⁻¹ (Skretting 2016). Highest growth rates have been observed for automatic feeders compared to hand-fed fish, for fish reared at a low stocking density compared to high density and for fish fed under a more intensive feeding regime. Overall, it was thought economically viable to rear lumpfish in cages until sexual maturation (i.e. to a larger size than currently reared sea-lice control (Imsland *et al.* 2014a, 2015a).

Recent studies indicate that the optimal temperature for growth of cultured lumpfish decreases with body size. Thus, whilst a temperature of 15.7°C appears optimal for growth of juveniles 11–20 g in mass, it decreases to 8.9°C for 120–200 g fish (Nytrø *et al.* 2014). This suggests the need to adopt a rearing strategy of 'temperature steps' during ongrowing and grading, although eye cataracts were observed in some fish when temperature exceeded 13°C, which may also need to be taken into account when setting upper thermal limits. Although many data are anecdotal (e.g. from public aquaria), growth rate of lumpfish in

captivity appears to be rapid; juveniles may attain an specific growth rate (SGR) of 1.5–3.5% per day, or increase their mass to 20–260 g in about 3 months at 13°C with constant light (Nytrø 2013). It is thus possible to produce lumpfish ready for deployment at a size of c. 60 mm (10 g) in as little as 4 months, although there is much variation among families and some may take up to 7 months (Vestvik 2013). In captivity, lumpfish can become sexually mature in their second year, when they reach 1.5–2.0 kg (14 months post-hatch in Canada, D. Boyce, pers. comm. 2016), which should make it possible to develop elite lines although marker assisted selection in a few generations.

Disease management

As with any new species in aquaculture, the extent and incidence of infectious diseases such as the intranuclear microsporidian, *Nucleospora cyclopteri* (Mullins *et al.* 1994; Freeman *et al.* 2013), and the risks they may pose for Atlantic salmon, need to be addressed. It is not known to what extent lumpfish are susceptible to diseases listed in current aquatic animal health regulations, and this needs to be reviewed as a risk to the developing cleaner fish industry. For example, IPN and VHS have both been detected in farmed lumpfish (Anon 2015a; Towers 2015), and there have been recent instances of atypical Furunculosis, Pasteurellosis, Vibriosis and bacterial gill disease (Cockerill & Wallis 2015). Lumpfish have displayed specific antibodies upon immunization (Haugland *et al.* 2016a) and shown a significant role for phagocytic B cells in their innate immunity, suggesting that vaccination will likely confer protection against some infectious pathogens (Rønneseth *et al.* 2015). The development of vaccines for certified, disease-free production of juveniles is thus a research priority and some recent progress has been made with autologous vaccines (Cockerill & Wallis 2015; Rønneseth *et al.* 2016) although the highly variable nature of bacterial strains isolated from fish farms may complicate the development of full-scale vaccine trials (Gulla *et al.* 2015). Information on some common diseases of lumpfish is reviewed below.

Fungal infections

Fungal infection is a common disease of adult lumpfish in captivity and can be a major cause of mortality. For example, at a Scottish marine hatchery, fungal infection caused up to 45% losses in hatchery-reared broodstock over 2 years (J.W. Treasurer, pers. comm. 2016). Several species of fungi were probably involved, but those belonging to the genus *Exophiala* appear to be the most common. These cause systemic hyphal growth in the musculature, gills and internal organs, which are often manifested externally by the presence of large, dark lesions. *Exophiala* infection has

also been recorded among wild-caught lumpfish, which may need to be quarantined for several weeks. The source of infection, whether in the feed or in the environment, has not been identified. Treatment of *Exophiala* has been attempted via 200 ppm formalin and bronopol baths 25 ppm active for 30 min. However, treatment has not always been successful, and culling of heavily infected fish is recommended. Given the likely future restrictions on the use of formalin in fish farming (CEFAS 2016), control of fungal diseases is expected to become increasingly challenging until new treatments are developed.

Microsporidia

Microsporidia are unicellular animal parasites, once considered to be protists but now classified as fungi. In the early 1990s, juvenile lumpfish reared in RAS systems were observed to suffer chronic mortality that was attributed to the microsporidian fungus *N. cyclopteri* (Mullins *et al.* 1994). More recent studies have also detected the pathogen among wild lumpfish caught in Icelandic waters (Freeman & Kristmundsson 2013; Freeman *et al.* 2013) with approximately 25% of the fish sampled displaying clinical signs of infection. Clinical signs include exophthalmia; renomegaly; and branchial, hepatic and cardiac pallor. Moribund fish frequently show large amounts of clear to serosanguinous coelomic fluid. Intranuclear oval-shaped spores (ca. $1 \times 2\text{--}3 \mu\text{m}$) may be found in high numbers in this coelomic fluid as well as the kidney, gills, spleen, pancreas, pyloric caecae, ovary, skin and circulatory system. Mullins *et al.* (1994) originally suggested that the intranuclear microsporidian was similar to *Enterocytozoon* = *Nucleospora salmonis* found in pacific salmon *Oncorhynchus* sp., and a recent DNA sequence analysis has confirmed 96% similarity to isolates of *N. salmonis*, which has led authors to propose the name *N. cyclopteri* (Freeman *et al.* 2013). Like *N. salmonis*, *N. cyclopteri* seems to infect congeners via direct horizontal transmission, but other routes cannot be ruled out. For example, the close association of spores with eggs may also suggest vertical transmission. More speculatively, a more complicated transmission route has also been suggested involving *Caligus elongatus* as clinical signs can include skin lesions and microsporidian spores have also been found in histological examination of the most outer layers of the lumpfish skin around sites of lice attachment (Freeman *et al.* 2013).

Nucleospora cyclopteri is capable of causing mass mortalities under some conditions, and no effective treatment is available. For this reason, attempts to manage this microsporidian must include the adoption of stringent husbandry protocols designed to reduce the risk of infection and the impact of the disease (Mullins *et al.* 1994). With current broodstock originating from the wild, there is

clearly a need to carry out further research on the prevalence and pathology of the disease across different populations. Studies in Iceland indicated that diseased fish were found in 12 of the 43 sites sampled (28%), prevalence being more likely among females than males (Freeman *et al.* 2013). To reduce the risk of disease a possible strategy could involve rapid, non-lethal PCR screening of candidate broodstock, as has been achieved for *N. salmonis* using gill biopsies (Badil *et al.* 2011). However, such an assay would need to ensure high specificity, sensitivity and repeatability, to provide enough confidence on the interpretation of negative results. To assist hatchery and stock management, further investigations on microsporidians are required, in particular in relation to the extent of horizontal versus vertical transmission, and simple versus complex modes of infection. Such research might benefit from the use of molecular methods of detection on male and female gametes, as well as on resulting larvae. An orally administered Fumagillin analogue (TNP-70) has shown some efficacy at controlling mortalities in *N. salmonis*-infected chinook salmon, *Oncorhynchus tshawytscha* (Higgins *et al.* 1998), but whether this would produce similar results with *N. cyclopteri* is uncertain as results with Fumagillin DCH have been equivocal (Mullins *et al.* 1994). There are also concerns about the safety margin of this drug and associated toxic effects. Toltrazuril proved ineffective at slowing the disease during an outbreak of *N. cyclopteri* at CSAR, and an investigation on the efficacy of other chemotherapeutants would be of great benefit. The use of fish cell lines may facilitate the rapid testing of such treatments against microsporidia in the future (Saleh *et al.* 2014). However, until an effective treatment or vaccine is available, management via exclusion, containment and prevention offer the best approach.

Myxosporea

Myxosporea are aquatic parasitic animals with a two-host lifecycle, involving a fish and an annelid worm. During traditional drying and smoking of lumpfish for human consumption in Iceland, it has sometimes been noted that the muscle mass of some individuals almost completely disappears. Using histopathology and molecular techniques (Kristmundsson & Freeman 2014) described a new myxosporean species, *Kudoa islandica*, as the pathogen responsible for the extensive post-mortem myoliquefaction of the somatic muscle of lumpfish and wolfish, *Anarhichas* sp. These consist of microscopic spores which develop to larger, abundant plasmodia (up to 1×11 mm) which almost completely replace the muscle tissue of infected fish. Although the mode of transmission is not well understood, direct horizontal transmission appears unlikely, as it requires the passage of blood to a naïve host and infective stages could be removed by treatment of incoming water

(Moran *et al.* 1999a,b). Its life cycle involves an annelid worm vector, and the risk of infection can be minimized by appropriate treatment of wet feed or the development of specific pelleted feeds. It has been suggested that marine flukes such as *Gyrodactylus* sp. could also act as intermediate hosts for myxosporidians (Kristmundsson & Freeman 2014), and whilst these are easy to treat in a hatchery, they may be more difficult to control after deployment of lumpfish in sea cages. Given that *K. islandica* is not host-specific (i.e. it is found in several taxonomic orders), there is a chance that infected lumpfish may be able to transmit it to farmed salmon. Such a risk can be minimized by rearing lumpfish in well-managed recirculation system having optimal water quality and ensuring they are not exposed to intermediate hosts.

Another myxosporidian, *Myxobolus albi* (or potentially also *Myxobolus aeglefinus*), has been isolated from many tissues of lumpfish, including the skull cartilage, the branchial arches, the sclera, the vertebrae, the tongue, all fin insertions and the pectoral girdle (Cavin *et al.* 2012). There is uncertainty as to whether *M. albi* is different from *M. aeglefinus* found in many fish hosts (Picón-Camacho *et al.* 2009). External symptoms may include exophthalmia and erratic swimming behaviour, similar to those elicited by *Myxobolus cerebralis*, the causative agent of whirling disease in salmonids.

Ciliates

Heavy infections of the ectoparasitic ciliate *Trichodina* sp. have been associated with mortalities of juvenile lumpfish, most likely as consequence of gill damage and opportunistic secondary infection, possibly after periods of stress and aggression (Gibson *et al.* 2015). At CSAR, other ciliate species have also been observed in the sloughed skin of broodstock, as well as on dead and dying lumpfish eggs. Although these are primarily opportunistic, non-invasive pathogens, they can cause problems if left untreated in recirculation systems as their numbers increase. Treatment of affected lumpfish via formalin baths has been successful in this regard.

Amoebic gill disease

Amoebic gill disease (AGD) is attributed to amoebae of several species, but in salmon and lumpfish, *Paramoeba perurans* is the main species (Adams *et al.* 2012; Powell *et al.* 2015b). Amoebae feed on organic matter on the fish gills, and they can build up to such high numbers that can cause gill necrosis, fusion of lamellae, respiratory distress and eventually mortality through asphyxiation. AGD is common in farmed salmon in northern Europe and also affects ballan wrasse and lumpfish, having caused lumpfish

mortalities in the UK (Cockerill & Wallis 2015; Perry & Treasurer 2015) and Norway (Breck 2015). AGD can be controlled with hydrogen peroxide (Adams *et al.* 2012), but this can be very harsh on the fish. At Ardtoe, lumpfish appear tolerant of freshwater exposure, and the administration of freshwater baths for 3–5 h, or the continuous exposure to 15 ppt brackish water over 7–10 days have both been effective (Perry & Treasurer 2015).

Bacterial diseases

Since 2012, lumpfish across hatcheries and deployment sites in Norway have frequently shown signs of systemic bacterial infection, these being characterized by skin lesions, gill haemorrhages, and bacterial aggregations in the heart and spleen (Alarcón *et al.* 2016). The isolates were similar to *Pasteurella* sp. previously associated with systemic infection in farmed Atlantic salmon in Norway and Scotland, posing the possibility that the infection was transmitted from salmon to lumpfish. As the culture of lumpfish expands, other bacterial diseases present in Atlantic salmon and wrasse are also being detected in lumpfish. In addition to *Pasteurella* sp., there have been recent reports of *Vibrio anguillarum*, *Vibrio ordalii*, *Aeromonas salmonicida*, *Pseudomonas anguilliseptica*, *Moritella viscosa* and *Tenacibaculum maritimum* (Poppe *et al.* 2012, 2013; Johansen 2013; Marcos-López *et al.* 2013; Breiland *et al.* 2014; Hjeltnes 2014; Bornø & Lie 2015; Cockerill & Wallis 2015; Alarcón *et al.* 2016; Bornø *et al.* 2016; Gulla *et al.* 2016; Småge *et al.* 2016). The significance of other common bacterial pathogens such as *Aliivibrio lopei*, *Aliivibrio wodanis*, *Vibrio tapetis* and *Vibrio splendidus* is unclear (Gulla *et al.* 2015; Bornø *et al.* 2016). As the cleaner fish industry intensifies and the number of lumpfish in close contact with salmon increases, other bacterial pathogens will no doubt be detected.

Flukes

Monogenean flukes are commonly found on the gills and skin of many bony fish, and effects can range from minor irritation to heavy mortalities. The *Gyrodactylus* database (<http://www.gyrodactylus.net/>) lists *Gyrodactylus* sp. as a parasite of lumpfish (Scyborska 1948). Although direct horizontal transmission between all life stages is possible, with the capacity for prevalence to increase to problematic levels in recirculation systems, *Gyrodactylus* sp. have been easy to eliminate at CSAR using praziquantel administered via bath treatments on diagnosis (Powell *et al.* 2015a).

Sea-lice

Lumpfish appear to suffer from a high prevalence and severity of parasitization by sea-lice, particularly *C. elongatus*,

raising potential concerns about transmission to hatchery-reared juveniles, and to farmed salmon after deployment in sea cages. In the North Sea, prevalence of *C. elongatus* among lumpfish was 100% (Boxshall 1974) with a mean of 23 copepods/fish. However, this copepod is a generalist, recorded on 25 of 62 fish species investigated in that study. A more recent study in Norway found that lumpfish was the species most commonly infected with *C. elongatus* (prevalence = 61%, mean 4 copepods/ind.) out of 28 coastal fish species investigated (Heuch *et al.* 2007). Mature lumpfish, caught inshore, had higher levels of sea-lice infestation than immature fish and were infected with *C. elongatus* of exclusively 'type I' genotype (from mitochondrial cytochrome C oxidase DNA), in contrast to immature lumpfish, which were caught further offshore, and were also infected with ca. 10% of 'type II' genotype, which is the type associated with farmed salmon. Lumpfish are thought to act as important reservoirs for type I *C. elongatus*, potentially transmitting it to other species (Øines & Heuch 2005, 2007; Øines *et al.* 2007). However, although not proved conclusively, those studies suggest that deployed lumpfish are unlikely to be the main source of type II *C. elongatus* which precipitates late summer infestations in farmed salmon, although they may pose a transmission risk to farmed cod. Also, wild lumpfish do not appear to be attracted to salmon cages (Mitamura *et al.* 2007, 2012), suggesting there is reduced potential for wild fish to act as disease vectors via horizontal transmission. At CSAR, several steps are taken to minimize the potential risk of transferring *C. elongatus* from wild-caught lumpfish broodstock to hatchery-reared juveniles, including treating incoming broodstock with freshwater baths, quarantining, physical system separation of broodstock and larvae, and the use of targeted medications such as *emamectin*.

Caligus is typically the most common sea-lice present in lumpfish, but several other parasitic copepods may also be present at lower prevalence. For example, Boxshall (1974) found that 36% of lumpfish presented a low abundance (less than 1 parasite/ind.) of the generalist copepod *Bomolochus confusus*. Another sea louse, *Lernaeocera branchialis* ('cod louse'), was commonly observed on the gills of lumpfish, which acted as an intermediate host prior to its two final hosts, the Atlantic cod (*Gadus morhua*) and the Greenland cod (*Gadus ogac*) (Templeman *et al.* 1976). Ranched cod seem to have a high prevalence of *L. branchialis*, apparently resulting from transmission by lumpfish (Khan *et al.* 1990). To our knowledge, there are no records of the salmon louse, *Lepeophtheirus salmonis*, infecting lumpfish.

Parasitic worms

Parasitic worms have been recorded in over 60% of lumpfish in some Polish populations, including the cestode

Eubothrium crassum, the nematodes *Contracaecum osculatatum*, *Dichelyne minutus* and *Hysterothylacium aduncum*, and the acanthocephalans *Corynosoma strumosum*, *Echinorhynchus gadi* and *Pomphorhynchus laevis* (Rolbiecki & Rokicki 2008). Many other fish species are also hosts to these parasitic worms, including Atlantic cod but excluding salmonids, so the risk of transmission to farmed salmon must be considered low. In addition, fish raised on artificial diets are unlikely to be infected by parasitic worms, (e.g. Levsen & Maage 2016).

Eye cataracts

Eye cataracts are rare on lumpfish larvae and juveniles, but can be common among growers and broodstock. Cataracts do not appear to affect survival or growth, but they probably have welfare implications or may also impair delousing efficiency. The causes of eye cataracts are probably multiple and may be associated with several clinical conditions. For example lumpfish that suffer from Pasteurellosis often have cataracts (Dawit 2015). Cataracts may also be associated with rapid growth in hatcheries compared to the wild, and perhaps also to dietary deficiencies, as most lumpfish are still fed on standard marine diets as their specific nutritional requirements have only recently started to be addressed (Skretting 2016).

Welfare and deployment of lumpfish in sea cages

The welfare of lumpfish needs to be better quantified, and information is needed on preferred stocking densities during culture, optimal tank design and rearing conditions. Attention is being paid to substrate and colour preferences after deployment (Imsland *et al.* 2014c), but studies are also needed during on-growing. In the wild, lumpfish match the colour of seaweed, suggesting that light intensity, photoperiod and tank colour may also affect juvenile growth, as these factors have been observed to alter melanin concentrations under experimental conditions (Davenport & Bradshaw 1995). In hatcheries, lumpfish are typically reared in blue or light grey tanks (Fig. 3), but given a choice lumpfish have shown a preference for a black background, so black tanks may be preferred (Garcia de Leaniz *et al.* 2015). There is also potential to manipulate photoperiod and light intensity to alter growth rates, as already carried out during the commercial production of wrasse (Helmsland *et al.* 2014).

Efficacy of lumpfish grazing

Results of experimental trials provide some results on the efficacy of using lumpfish for the biological control of sea-

lice from infected Atlantic salmon. Imsland *et al.* (2014a) stocked six salmon sea cages (5 × 5 × 5 m) in Norway with 120 Atlantic salmon each (mean weight 619 g ± 49 SD). Two of the cages were stocked with juvenile lumpfish (mean weight 54.0 g ± 7.2 SD) at either 10% or 15% of the salmon density (12 or 18 lumpfish, respectively), whilst two cages were not stocked with lumpfish to serve as controls. Lumpfish grazing significantly reduced the mean number of pre-adult and mature *L. salmonis* per salmon attached to salmon, removing 93–97% of adult female sea-lice over a 54-day period (Fig. 5). Results from gastric lavaging revealed that 28% of lumpfish had ingested sea-lice on the last sampling day. Overall, the study indicates that lumpfish is a suitable cold-water option for the biological control of sea-lice parasitising Atlantic salmon. Based on these initial findings, interest in using lumpfish for delousing has rocketed, and commercial production has increased from thousands to millions of juvenile lumpfish in 5 years. Lumpfish are now being used for delousing by all major salmon farms in Norway, Scotland and elsewhere.

Behaviour in sea cages

The behaviour of lumpfish in cages has been studied via underwater cameras (Imsland *et al.* 2014c; Imsland *et al.* 2016a), and an ethogram has been constructed which identified 14 different behaviours, with and without

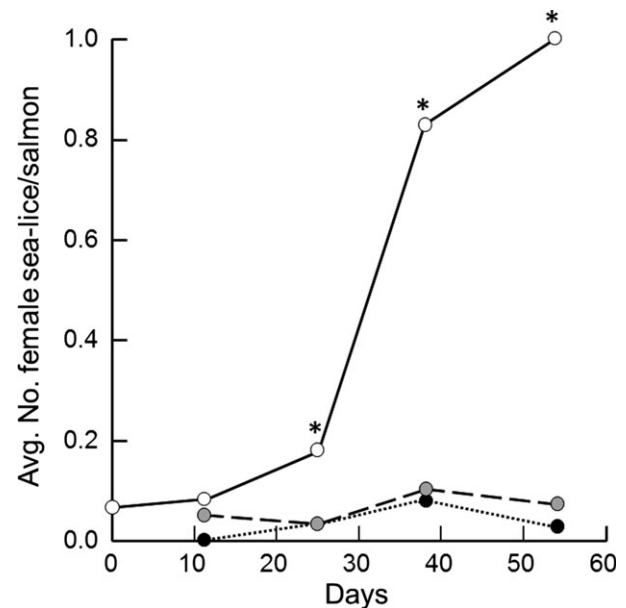


Figure 5 Mean number of adult female sea-lice (*Lepeophtheirus salmonis*) found on Atlantic salmon reared without lumpfish (control) or with 10% and 15% of lumpfish. Asterisks denote significant differences (modified from Imsland *et al.* 2014a). (—○—) Control; (---●---) 10% lumpfish and (····●····) 15% lumpfish.

Atlantic salmon present (Imsland *et al.* 2014c). Although lumpfish spend relatively little time removing lice, it is sufficient to reduce parasite loads significantly. During daylight hours, lumpfish spend the majority of time foraging for food, and when not foraging, they tend to be found resting on floating seaweed or remain stationary ('hovering') just under them (Imsland *et al.* 2014b). At night, they prefer to aggregate on smooth plastic and concrete substrates (thought to be similar to seaweed), rather than on stones or car tires (Imsland *et al.* 2015a). As with ballan wrasse (Helland *et al.* 2014), availability of suitable substrates is also thought to be important for health and welfare of lumpfish deployed in salmon cages. In the presence of salmon, lumpfish appear to be more active and spend less time resting. It is worth noting that no antagonistic behaviour between lumpfish and Atlantic salmon has been observed and that the two species seem to co-exist along each other in sea cages (Imsland *et al.* 2014b). Cleaning behaviour is considered to be a classical example of mutualism, but whether this also applies to delousing of salmon by lumpfish is unclear. Some information exists on the diet of lumpfish in the wild (Daborn & Gregory 1983; Davenport & Rees 1993; Ingólfsson & Kristjánsson 2002), and it seems that sea-lice and other copepods are regularly ingested by juvenile lumpfish (Ingólfsson & Kristjánsson 2002; Vandendriessche *et al.* 2007). Wild Atlantic salmon are frequently parasitized by sea-lice, particularly during the winter months (Jacobsen & Gaard 1997), and given the opportunity, lumpfish will readily graze on sea-lice attached to salmon in captivity (Imsland *et al.* 2014a,b). It may be speculated that such grazing behaviour may have developed in a manner similar to that seen in cleaner fish in the tropics (Grutter 1995; Clague *et al.* 2011), but whether lumpfish regularly delouse salmon in the wild is not known.

Feeding preferences

Recent data suggest that c. one-third of lumpfish may die of starvation in salmon cages within a few weeks after deployment (Breck 2015). Understanding their feeding preferences is, hence, essential. Increasing delousing efficiency without compromising welfare or growth is a major research priority (fewer sea-lice with fewer cleaner fish). In sea-cage trials, the proportion of lumpfish eating sea-lice increased from 13–17% at day 11 to 33–38% at day 77 (Imsland *et al.* 2015b), suggesting there may be a learning component. The actual proportion of lumpfish eating sea-lice may have been higher, as these values were derived from gastric lavaging, which would have missed fully digested sea-lice.

It has been estimated that if 30% or more lumpfish consumed sea-lice on a regular basis, then sea-lice infestation

levels would be greatly suppressed (Imsland *et al.* 2015b). However, lumpfish are opportunistic, omnivorous feeders and will not only feed on sea-lice, but also on salmon pellets and many organisms found in sea cages, which need to be kept clean to encourage delousing behaviour. Following deployment, the diet of lumpfish can vary temporally in sea cages, closely matching the seasonal changes in food availability (Imsland *et al.* 2015b). Such opportunistic feeding behaviour is not unique to cages and has also been reported in the wild (Ingólfsson 2000; Ingólfsson & Kristjánsson 2002; Vandendriessche *et al.* 2007). In experimental floating seaweeds, juvenile lumpfish appear to ignore small, as well as sessile and slow-moving organisms, such as ostracods, bivalves, gastropods, rotifers and worms (Ingólfsson & Kristjánsson 2002). They feed on most other organisms in approximately the same proportion as their availability, the dominant prey being crustaceans (harpacticoids, calanoids, cladoceroids), which make up to 91% of the diet, followed by molluscs and small fish, including conspecifics (Ingólfsson & Kristjánsson 2002; Imsland *et al.* 2015b, 2016a). It might be possible to increase delousing efficiency by selecting individuals that have a greater affinity for consuming sea-lice, and perhaps also by conditioning them prior to deployment.

Family variation and potential inheritance of delousing behaviour

Large differences in sea-lice grazing have been observed among individual lumpfish in a semi-commercial trial (Imsland *et al.* 2014a). It was also found that only 10% of lumpfish grazed on sea-lice at the beginning of the trial, increasing to 36% towards the end. In a follow-up study, Imsland *et al.* (2016b) found significant variation in sea-lice grazing among nine families deployed in sea cages, with cages housing the most efficient lumpfish showing a 70% reduction in sea-lice infestation. The existence of significant maternal and paternal effects suggests that cleaning behaviour in lumpfish may have a genetic component (Imsland *et al.* 2016a). Achieving efficient delousing is key for controlling sea-lice though the use of cleaner fish. Although behavioural traits tend to show low heritability in fish (Garcia de Leaniz *et al.* 2007), if the heritability of sea-lice grazing is high enough, this would open exciting possibilities for selecting lines with superior delousing performance, which would improve welfare and reduce the number of lumpfish required by industry.

Interactions between lumpfish and other cleaner fish

Up until recently, ballan wrasse and goldsinny wrasse were the most commonly used cleaner fish for controlling sea-lice in farmed salmon (Deady *et al.* 1995; Treasurer 2013).

Wrasse tend to eat more sea-lice than lumpfish but are not suitable for delousing below 6°C (Sayer & Davenport 1996; Sayer & Reader 1996). Lumpfish, on the other hand, can continue to feed at 4°C (Nytro *et al.* 2014) and have the potential to survive the winter even in the northernmost salmon farms, due to its broad geographical distribution (Blacker 1983). Thus, a two-species cleaner fish system involving wrasse and lumpfish might be an advantage, provided lumpfish can coexist with wrasse in sea cages. To determine whether goldsinny wrasse could coexist with juvenile lumpfish in sea cages, Imsland *et al.* (2016b) investigated the behavioural interactions between three size classes of lumpfish (110, 70 and 32 g), and one size class of goldsinny wrasse (30 g). The results (Fig. 6) indicated that there was size-dependent interspecific aggression by lumpfish. The largest lumpfish showed aggression towards goldsinny 13% of the time, whilst for the smaller lumpfish aggression was found in 6% of observations. Large lumpfish were observed chasing goldsinny and preventing them from having access to food and were in some instances biting their caudal fins. As a consequence, goldsinny spent only 1% of their time resting when they were cohabiting with 110 g lumpfish, compared to 28–36% of their time when they were with intermediate (70 g) or small-sized (32 g) lumpfish. The existence of size-dependent agonistic interactions means that small lumpfish may be able to cohabit with goldsinny, at least for some time. However, at some point, lumpfish would become much larger than goldsinny due to their superior growth rate (Imsland *et al.* 2014b; Nytro *et al.* 2014; Skiftesvik *et al.* 2014), particularly at lower water temperatures, and antagonistic feeding behaviour may increase as lumpfish size increases.

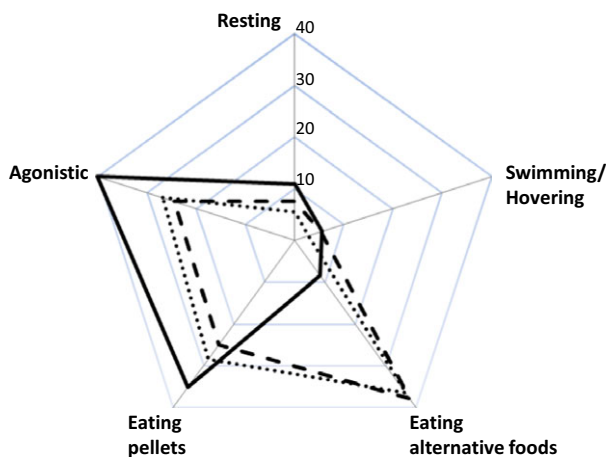


Figure 6 Size-dependent behaviour of lumpfish (% time spent) in the presence of goldsinny wrasse in land-based tanks. Large lumpfish spend significantly more time in agonistic interactions with goldsinny than small or intermediate-sized lumpfish (modified from Imsland *et al.* 2016a,b). (—) Large (110 g); (.....) Intermediate (70 g) and (---) Small (32 g).

Six species of wrasse are found in Norway, four of which have been used as cleaner fish for delousing salmonids, namely ballan wrasse; goldsinny wrasse; corkwing wrasse; *Symphodus melops* L.; and rock cook, *Centrolabrus exoletus* L. Their maximum reported size is 60 cm for ballan wrasse (Quignard & Pras 1986), 18 cm for goldsinny (Darwall *et al.* 1992), 28 cm for corkwing (Darwall *et al.* 1992) and 16.5 cm for rock cook (Sayer *et al.* 1996). The relative high levels of aggression exhibited by large lumpfish towards goldsinny may have been caused by the large size difference, so it is possible that larger wrasse species such as ballan wrasse may be able to cohabit with lumpfish better. However, as pointed out by Imsland *et al.* (2016b), the trial was performed in 1.5 m³ land-based tanks and behaviour may be different in large open-net pens where it might be easier for the two species of cleaner fish to avoid each other. No information is available on interspecific interactions between different species of cleaner fish in sea cages, and this is a research area that warrants further study. Also, the possible exchange of pathogens between lumpfish and wrasse when both are held in the same cages should be investigated.

Concluding remarks: strategies for advancing lumpfish aquaculture

The ultimate goal of the emerging lumpfish aquaculture industry is to produce disease-free juveniles that adapt well to deployment in salmon pens, and are efficient at delousing farmed salmon whilst maintaining the health and welfare of both salmon and cleaner fish. One approach towards achieving this goal might be to examine the development and challenges faced by the more mature wrasse farming industry as a precedent. A handbook on production of ballan wrasse has recently been published under the 'LeppeProd' project (Helland *et al.* 2014), and similar technical guidance would be very useful for lumpfish culture. To this end, our review has identified different levels of technology readiness (TRLs, Anon 2014b) and several steps that can be taken to increase sustainability in the use of lumpfish for sea-lice control (Fig. 7). These include improved collection techniques and transport of wild-caught spawners, until all broodstock are reared entirely in captivity, as well as improvements in reproduction, particularly with respect to control of maturation, gamete collection and storage. Currently, lumpfish production originates almost entirely from wild-caught broodstock, but in the future, commercial production will need to be derived entirely from selected farmed strains. For this, the breeding cycle needs to be closed in captivity (Anon 2015b). This is still a relatively new species for aquaculture, and no selective programme for lumpfish is currently in place, but the production of selected lines with desirable traits needs to be

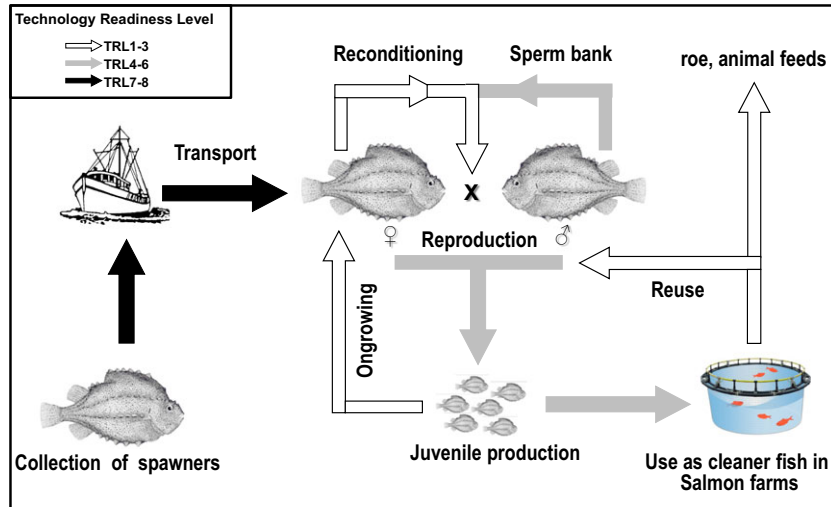


Figure 7 Strategies for the sustainable use of lumpfish in salmon farming showing level of technology readiness (TRL). Each stage shows areas where targeted research can be used to increase survival and improve sustainability.

developed. As lumpfish are not farmed for human consumption, but rather to remove sea-lice from salmon, the targets of artificial selection will differ from those applied to most other cultured fish which are typically selected for fast growth and high conversion efficiency (Vandeputte *et al.* 2009). In the case of lumpfish, commercial production will benefit from selecting individuals that show a high affinity for preying on sea-lice. Strains showing slow growth may also be advantageous, as lumpfish stop eating sea-lice when they reach a size of 300–400 g (Anon 2014a). The species spawns over a relatively long period (Anon 2003), and it may be possible – perhaps in combination with photoperiod manipulation – to select lumpfish lines that reproduce throughout the year to achieve year-round juvenile production. Larval production also needs to be optimized, and the selection of lines that adapt well in captivity, along with improved formulation of larval diets, should help to reduce the high post-weaning mortality currently associated with the transition from live to dry feeds.

Arguably, one of the most important considerations for commercial lumpfish production is to reduce the risk of disease transfer between cleaner fish and salmon, for example of IPNV, AGD and Vibriosis (Breiland *et al.* 2014; Haugland *et al.* 2016b; Murray 2016). Intensification of lumpfish production and close mixing with salmon creates favourable conditions for the emergence and transfer of diseases, in both lumpfish and salmon, so consideration must be given to general processes by which disease emerge in aquaculture (e.g. Murray & Peeler 2005; Murray 2016). Developing selected lumpfish lines that show increased disease resistance is therefore a strategy that should pay dividends. Vaccines, as well as more effective therapeutants, are

urgently required to combat emerging infectious diseases, particularly atypical furunculosis, AGD and VHS (Cockerill & Wallis 2015).

Not all lumpfish readily feed on sea-lice, and as some families appear better than others (Imstrand *et al.* 2016a), this suggests the existence of a genetic component for sea-lice consumption which can be used for the selection of strains with improved delousing performance. Better ways of monitoring attrition rates, delousing activity and welfare of lumpfish are also required, as developed for ballan wrasse (Leclercq *et al.* 2014, 2015). Survival of lumpfish in salmon cages needs to be better quantified, modelled and monitored under real conditions to achieve the most efficient de-lousing programmes. Likewise, the risk of cleaner fish escaping from open-net salmon pens and interbreeding with wild fish needs to be critically evaluated. In this sense, the production of monosex (Martin-Robichaud *et al.* 1994) or sterile lumpfish will aid in reducing the risk of potential gene introgression with wild fish and should be examined.

Re-use of lumpfish post-deployment is another important area where sustainability can be increased, as the current practice of culling lumpfish after just one salmon production cycle has been criticized as being wasteful and has welfare implications (Anon 2013b; Farm Animal Welfare Committee 2014). Opportunities for re-use may include the use of lumpfish post-deployment as broodstock for the selection of elite lines in captive breeding programmes, as well as the harvesting of lumpfish for use in animal feeds and perhaps also for human consumption (including roe production; Stevenson & Baird 1988). New markets for lumpfish have opened since Iceland banned

discards in 2011 (only the roe was formerly collected), and in recent years, the species has become a newly discovered delicacy for Asian food markets. Increasingly, large numbers of frozen whole and filleted lumpfish are now being exported to China, bringing more than €18 Million year⁻¹ to the Iceland economy (Thordarson 2013). Prices paid for frozen lumpfish have escalated and currently sell in the internet at over \$2 per kg. The reuse of lumpfish which have been feeding on sea-lice, hence, constitutes an attractive form of nutrient recycling, and might even represent a business opportunity, but for this vaccines and stringent health checks will need to be developed to prevent the risk of disease transmission, especially if cleaner fish or their offspring are to be used in more than one salmon production cycle (Murray 2016).

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References

- Adams MB, Crosbie PBB, Nowak BF (2012) Preliminary success using hydrogen peroxide to treat Atlantic salmon, *Salmo salar* L., affected with experimentally induced amoebic gill disease (AGD). *Journal of Fish Diseases* **35**: 839–848.
- Alarcón M, Gulla S, Røsaeg MV, Rønneseth A, Wergeland H, Poppe TT *et al.* (2016) Pasteurellosis in lumpsucker *Cyclopterus lumpus*, farmed in Norway. *Journal of Fish Diseases* **39**: 489–495.
- Albert OT, Torstensen E, Bertelsen B, Jonsson ST, Pettersen IH, Holst JC (2002) Age-reading of lumpsucker (*Cyclopterus lumpus*) otoliths: dissection, interpretation and comparison with length frequencies. *Fisheries Research* **55**: 239–252.
- Anon (2003) Lumpfish (*Cyclopterus lumpus*). Emerging Species Profile Sheets. Department of Fisheries and Aquaculture, Government of Newfoundland and Labrador, St. John's, Newfoundland.
- Anon (2013a) *MSC Assessment for Icelandic Gillnet Lumpfish Fishery*. The Fish Site and 5M Publishing.
- Anon (2013b) *Cleaner Fish Position Paper (mcsuk.org)*. Marine Conservation Society, 7 pp. [Cited 16 Oct 2016.] Available from URL: http://www.mcsuk.org/downloads/fisheries/Cleaner_Fish_Position_Paper.pdf.
- Anon (2014a) *Increasing Production of Farmed Cleaner Fish*. The Fish Site and 5M Publishing. 04 June 2014. [Cited 24 Jan 2016.] Available from URL: <http://www.thefishsite.com/fishnews/23319/increasing-production-of-farmed-cleaner-fish/>
- Anon (2014b) *Technology readiness levels (TRL)*. Horizon 2020 – Work programme 2014–2015. General Annexes. Commission Decision C(2014)4995. [Cited 16 Oct 2016.] Available from URL: https://ec.europa.eu/research/participants/data/ref/h2020/wp/2014_2015/annexes/h2020-wp1415-annex-g-trl_en.pdf
- Anon (2015a) *Lumpfish Identified as Possible Reservoir for IPN*. The Fish Site, 06 January 2015. 5M Publishing. [Cited 16 Oct 2016.] Available from URL: <http://www.thefishsite.com/fishnews/24865/lumpfishidentifiedaspossiblereservoirforipn/>
- Anon (2015b) *Arctoe Reports First Spawning of Captive Reared Lumpfishes*. The Fish Site and 15 May 2015. 5M Publishing. [Cited 16 Oct 2016.] Available from URL: <http://www.thefishsite.com/fishnews/25678/arctoe-reports-first-spawning-of-captive-reared-lumpfishes/>
- Badil S, Elliott DG, Kurobe T, Hedrick RP, Clemens K, Blair M *et al.* (2011) Comparative evaluation of molecular diagnostic tests for *Nucleospora salmonis* and prevalence in migrating juvenile salmonids from the Snake River, USA. *Journal of Aquatic Animal Health* **23**: 19–29.
- Bañón R, Garazo A, Fernández A (2008) Note about the presence of the lumpsucker *Cyclopterus lumpus* (Teleostei, Cyclopteridae) in Galician waters (NW Spain). *Journal of Applied Ichthyology* **24**: 108–109.
- Bellas J, Hilvarsson A, Granmo Å (2005) Sublethal effects of a new antifouling candidate on lumpfish (*Cyclopterus lumpus* L.) and Atlantic cod (*Gadus morhua* L.) larvae. *Biofouling* **21**: 207–216.
- Belova I (2015) Nutritional programming in lumpsucker, *Cyclopterus lumpus* – a transcriptomic approach. MSc in Aquaculture University of Nordland, 46 pages.
- Benfey TJ, Methven DA (1986) Pilot-scale rearing of larval and juvenile lumpfish (*Cyclopterus lumpus* L.), with some notes on early development. *Aquaculture* **56**: 301–306.
- Birkbeck TH, Reid HI, Darde B, Grant AN (2006) Activity of bronopol (Pyceze®) against bacteria cultured from eggs of halibut, *Hippoglossus hippoglossus* and cod, *Gadus morhua*. *Aquaculture* **254**: 125–128.
- Bjordal Å (1991) Wrasse as cleaner-fish for farmed salmon. *Progress in Underwater Science* **16**: 17–28.
- Blacker RW (1983) Pelagic records of the lumpsucker, *Cyclopterus lumpus* L. *Journal of Fish Biology* **23**: 405–417.
- Bornø G, Lie LM (2015) Fish Health Report 2014. The Norwegian Veterinary Institute, Harstad.
- Bornø G, Alarcón M, Linaker M, Colquhoun D, Nilsen H, Gu J *et al.* (2016) Akutt dødelighet hos rognkjeks (*Cyclopterus lumpus*) i 2015 [in Norwegian]. Veterinærinstituttets Rapportserie, The Norwegian Veterinary Institute, Oslo.
- Boxshall G (1974) Infections with parasitic copepods in North Sea marine fishes. *Journal of the Marine Biological Association of the United Kingdom* **54**: 355–372.
- Breck O (2015) An update from Norway. Proceedings of the Cleanerfish Workshop. Scottish Salmon Producers Organisation, Inverness, 1st December 2015.

- Breiland MSW, Mikalsen H, Johansen L-H (2014) Susceptibility of Lumpfish (*Cyclopterus lumpus*) to *Vibrio ordalii* and infectious pancreatic necrosis virus (IPNV). In: *European Aquaculture Society Conference*. Abstracts. [Cited 16 Oct 2016.] Available from URL: <https://www.was.org/easonline/AbstractDetail.aspx?i=3343>.
- Brown JA (1986) The development of feeding behaviour in the lumpfish, *Cyclopterus lumpus* L. *Journal of Fish Biology* **29**: 171–178.
- Brown JA, Somerton DC, Methven DA, Watkins JR (1992) Recent advances in lumpfish *Cyclopterus lumpus* and ocean pout *Macrozoarces americanus* larviculture. *Journal of the World Aquaculture Society* **23**: 271–276.
- Brown JA, Wiseman D, Kean P (1997) The use of behavioural observations in the larviculture of cold-water marine fish. *Aquaculture* **155**: 297–306.
- Cavin JM, Donahoe SL, Frasca S, Innis CJ, Kinsel MJ, Kurobe T et al. (2012) *Myxobolus albi* infection in cartilage of captive lumpfish (*Cyclopterus lumpus*). *Journal of Veterinary Diagnostic Investigation* **24**: 516–524.
- CEFAS (2016) *Aquatic animal health news and consultations*. Centre for Environment, Fisheries and Aquaculture Science. [Cited 16 Oct 2016.] Available from URL: <https://www.gov.uk/government/news/changes-to-formaldehyde-formalin-rules>
- Chilvers H (2013) Lumpfish: *the Latest Weapon in the Battle Against Sea Lice?* The Fish Site and 2 December 2013, 5M Publishing. [Cited 16 Oct 2016.] Available from URL: <http://www.thefishsite.com/articles/1787/lumpfish-the-latest-weapon-in-the-battle-against-sea-lice/>
- Clague GE, Cheney KL, Goldizen AW, McCormick MI, Waldie PA, Grutter AS (2011) Long-term cleaner fish presence affects growth of a coral reef fish. *Biology Letters* **7**: 863–865.
- Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology* **68**: 893–905.
- Cockerill D, Wallis T (2015) Health challenges with cleanerfish. Proceedings of the Cleanerfish Workshop. Scottish Salmon Producers Organisation, Inverness, 1st December 2015.
- Collins MAJ (1976) The lumpfish (*Cyclopterus lumpus* L.) in Newfoundland waters. *The Canadian Field-Naturalist* **90**: 64–67.
- Consuegra S, García de Leániz C (2007) Fluctuating sex ratios, but no sex-biased dispersal, in a promiscuous fish. *Evolutionary Ecology* **21**: 229–245.
- Consuegra S, Pooley C, Powell A, Keay A, Galloway G, Cockerill D et al. (2015) A traceability and genetic screening programme for sustainable breeding of lumpfish (*Cyclopterus lumpus*) for sea lice control in salmon farming. Proceedings of the Aquaculture Europe 2015, Rotterdam, 2015. European Aquaculture Society City, pp. 167.
- Costello MJ (2009) The global economic cost of sea lice to the salmonid farming industry. *Journal of Fish Diseases* **32**: 115–118.
- Daborn GR, Gregory RS (1983) Occurrence, distribution, and feeding habits of juvenile lumpfish, *Cyclopterus lumpus* L. in the Bay of Fundy. *Canadian Journal of Zoology* **61**: 797–801.
- Darwall WRT, Costello MJ, Donnelly R, Lysaght S (1992) Implications of life-history strategies for a new wrasse fishery. *Journal of Fish Biology* **41**: 111–123.
- Davenport J (1983) Oxygen and the developing eggs and larvae of the lumpfish, *Cyclopterus lumpus*. *Journal of the Marine Biological Association of the United Kingdom* **63**: 633–640.
- Davenport J (1985) *Synopsis of Biological Data on the Lump-sucker, Cyclopterus lumpus (Linnaeus, 1758)*, Vol. **147**. Food & Agriculture Organization, Rome.
- Davenport J, Bradshaw C (1995) Observations on skin colour changes in juvenile lumpsuckers. *Journal of Fish Biology* **47**: 143–154.
- Davenport J, Kjorsvik E (1986) Buoyancy in the lumpsucker *Cyclopterus lumpus*. *Journal of the Marine Biological Association of the United Kingdom* **66**: 159–174.
- Davenport J, Lonning S (1983) On the structure and function of the urogenital system of the female lumpsucker *Cyclopterus lumpus* L. (Teleostei: Scorpaeniformes). *Proceedings of the Royal Society of London B: Biological Sciences* **218**: 201–210.
- Davenport J, Rees EIS (1993) Observations on neuston and floating weed patches in the Irish Sea. *Estuarine, Coastal and Shelf Science* **36**: 395–411.
- Dawit BG (2015) Adaptive Humoral Immune Response in Lumpfish, *Cyclopterus lumpus* L. Master of Aquaculture Biology, University of Bergen, 111 pages.
- Deady S, Varian SJ, Fives JM (1995) The use of cleaner-fish to control sea lice on two Irish salmon (*Salmo salar*) farms with particular reference to wrasse behaviour in salmon cages. *Aquaculture* **131**: 73–90.
- Deevey ES Jr (1947) Life tables for natural populations of animals. *Quarterly Review of Biology* **22**: 283–314.
- Dulčić J, Golani D (2006) First record of *Cyclopterus lumpus* L., 1758 (Osteichthyes: Cyclopteridae) in the Mediterranean Sea. *Journal of Fish Biology* **69**: 300–303.
- Elliott JM (1989) Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. *Journal of Animal Ecology* **58**: 987–1001.
- Farm Animal Welfare Committee (2014) *Opinion on the Welfare of Farmed Fish*, 40 pp. Department for Environment, Food & Rural Affairs (DEFRA), London, UK. [Cited 24 Jan 2016.] Available from URL: <https://www.gov.uk/government/groups/farm-animal-welfare-committee-fawc>
- Freeman MA, Kristmundsson Á (2013) Ultrastructure of *Nucleospora cyclopteri*, an intranuclear microsporidian infecting the Atlantic lumpfish (*Cyclopterus lumpus* L.). *Bulletin of the European Association of Fish Pathologists* **33**: 194–198.
- Freeman MA, Kasper JM, Kristmundsson Á (2013) *Nucleospora cyclopteri* n. sp., an intranuclear microsporidian infecting wild lumpfish, *Cyclopterus lumpus* L., in Icelandic waters. *Parasites & Vectors* **6**: 1–13.
- Froese R, Pauly D (2014) *FishBase*. [Cited 16 Oct 2016.] Available from URL: www.fishbase.org, version (11/2014) edn. World Wide Web electronic publication.
- Garcia de Leaniz C, Fleming IA, Einum S, Verspoor E, Jordan WC, Consuegra S et al. (2007) A critical review of adaptive genetic variation in Atlantic salmon:

- implications for conservation. *Biological Reviews (Cambridge)* **82**: 173–211.
- Garcia de Leaniz C, Keay A, Frazao-Pires A, Powell A, Pooley CL, Lloyd R *et al.* (2015) Swansea Lumpfish Project. Optimisation of captive breeding of lumpfish for sea lice control in salmon farming. Proceedings of the Cleanerfish Workshop. Scottish Salmon Producers Organisation, Inverness, 1st December 2015.
- Gibson S, Sayer MD, Joyce JA (2015) A Report on the background and economic potential of Lumpfish Culture: Diversification using existing infrastructure (MAFF). Working Paper. 59 pp. [Cited 16 Oct 2016.] Available from URL: <https://ueaeprints.uea.ac.uk/id/eprint/14401>
- Goulet D, Green JM, Shears TH (1986) Courtship, spawning, and parental care behavior of the lumpfish, *Cyclopterus lumpus* L., in Newfoundland. *Canadian Journal of Zoology* **64**: 1320–1325.
- Grant B, Picchi N, Davie A, Leclercq E, Migaud H (2016) Removal of the adhesive gum layer surrounding naturally fertilised ballan wrasse (*Labrus bergylta*) eggs. *Aquaculture* **456**: 44–49.
- Grutter AS (1995) Relationship between cleaning rates and ectoparasite loads in coral reef fishes. *Marine Ecology Progress Series* **118**: 51–58.
- Gulla S, Sørnum H, Vågnes Ø, Colquhoun DJ (2015) Phylogenetic analysis and serotyping of *Vibrio splendidus*-related bacteria isolated from salmon farm cleaner fish. *Diseases of Aquatic Organisms* **117**: 121–131.
- Gulla S, Duodu S, Nilsen A, Fossen I, Colquhoun DJ (2016) *Aeromonas salmonicida* infection levels in pre- and post-stocked cleaner fish assessed by culture and an amended qPCR assay. *Journal of Fish Diseases* **39**: 867–877.
- Haugland GT, Rønneseth A, Eggsetøl HØ, Lunde HS, Wergeland HI (2016a) Immune responses in lumpfish (*Cyclopterus lumpus* L.) leukocytes upon bacteria challenge. *Fish & Shellfish Immunology* **53**: 123.
- Haugland GT, Olsen A-B, Rønneseth A, Andersen L (2016b) Lumpfish (*Cyclopterus lumpus* L.) develop amoebic gill disease (AGD) after experimental challenge with *Paramoeba perurans* and can transfer amoebae to Atlantic salmon (*Salmo salar* L.). *Aquaculture* doi: 10.1016/j.aquaculture.2016.04.001.
- Hedeholm R, Blicher ME, Grønkvær P (2014) First estimates of age and production of lumpsucker (*Cyclopterus lumpus*) in Greenland. *Fisheries Research* **149**: 1–4.
- Helland S, Dahle SW, Hough C, Borthen J (2014) Production of ballan wrasse (*Labrus bergylta*). Science and Practice. The Norwegian Seafood Research Fund (FHF), p. 136.
- Heuch PA, Øines Ø, Knutsen JA, Schram TA (2007) Infection of wild fishes by the parasitic copepod *Caligus elongatus* on the south east coast of Norway. *Diseases of Aquatic Organisms* **77**: 149–158.
- Higgins M, Kent M, Moran J, Weiss L, Dawe S (1998) Efficacy of the fumagillin analog TNP-470 for *Nucleospora salmonis* and *Loma salmonae* infections in chinook salmon *Oncorhynchus tshawytscha*. *Diseases of Aquatic Organisms* **34**: 45–49.
- Hjeltnes B (2014) *Farmed Fish Health Report 2013*. Norwegian Veterinary Institute, Oslo. [Cited 16 Oct 2016.] Available from URL: <http://www.vetinst.no/eng/Publications/Fish-Health-Report>
- Immsland AK, Reynolds P, Eliassen G, Hangstad TA, Foss A, Vikingstad E *et al.* (2014a) The use of lumpfish (*Cyclopterus lumpus* L.) to control sea lice (*Lepeophtheirus salmonis* Krøyer) infestations in intensively farmed Atlantic salmon (*Salmo salar* L.). *Aquaculture* **424–425**: 18–23.
- Immsland AK, Reynolds P, Eliassen G, Hangstad TA, Nytrø AV, Foss A *et al.* (2014b) Assessment of growth and sea lice infection levels in Atlantic salmon stocked in small-scale cages with lumpfish. *Aquaculture* **433**: 137–142.
- Immsland AK, Reynolds P, Eliassen G, Hangstad TA, Nytrø AV, Foss A *et al.* (2014c) Notes on the behaviour of lumpfish in sea pens with and without Atlantic salmon present. *Journal of Ethology* **32**: 117–122.
- Immsland AK, Reynolds P, Eliassen G, Hangstad TA, Nytrø AV, Foss A *et al.* (2015a) Assessment of suitable substrates for lumpfish in sea pens. *Aquaculture International* **23**: 639–645.
- Immsland AK, Reynolds P, Eliassen G, Hangstad TA, Nytrø AV, Foss A *et al.* (2015b) Feeding preferences of lumpfish (*Cyclopterus lumpus* L.) maintained in open net-pens with Atlantic salmon (*Salmo salar* L.). *Aquaculture* **436**: 47–51.
- Immsland AK, Reynolds P, Eliassen G, Mortensen A, Hansen ØJ, Puvanendran V *et al.* (2016a) Is cleaning behaviour in lumpfish (*Cyclopterus lumpus*) parentally controlled? *Aquaculture* **459**: 156–165.
- Immsland AK, Reynolds P, Eliassen G, Hangstad TA, Jónsdóttir ÓDB, Elvegård TA *et al.* (2016b). Investigation of behavioural interactions between lumpfish (*Cyclopterus lumpus*) and goldsinny wrasse (*Ctenolabrus rupestris*) under controlled conditions. *Aquaculture International* **24**: 1509–1521.
- Ingólfsson A (2000) Colonization of floating seaweed by pelagic and subtidal benthic animals in southwestern Iceland. *Hydrobiologia* **440**: 181–189.
- Ingólfsson A, Kristjánsson BK (2002) Diet of juvenile lumpsucker *Cyclopterus lumpus* (Cyclopteridae) in floating seaweed: effects of ontogeny and prey availability. *Copeia* **2**: 472–476.
- Iversen A, Hermansen Ø, Andreassen O, Brandvik RK, Marthinussen A, Nystøyl R (2015) Kostnadsdrivere i lakseoppdrett (Cost Drivers in Salmon Farming). No. 41/2015, 1–43. Nofima [in Norwegian].
- Jacobsen J, Gaard E (1997) Open-ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon (*Salmo salar* L.). *ICES Journal of Marine Science: Journal du Conseil* **54**: 1113–1119.
- Johannesson J (2006) *Lumpfish Caviar: From Vessel to Consumer*, Vol. **485**. Food & Agriculture Organization, Rome.
- Johansen R (2013) *Farmed Fish Health Report 2012*. Norwegian Veterinary Institute, Oslo. [Cited 16 Oct 2016.] Available from URL: <http://www.vetinst.no/eng/Publications/Fish-Health-Report>
- Jones PG, Hammell KL, Gettinby G, Revie CW (2013) Detection of emamectin benzoate tolerance emergence in different life stages of sea lice, *Lepeophtheirus salmonis*, on farmed

- Atlantic salmon, *Salmo salar* L. *Journal of Fish Diseases* **36**: 209–220.
- Jones AC, Mead A, Kaiser MJ, Austen MC, Adrian AW, Auchterlonie NA et al. (2015) Prioritization of knowledge needs for sustainable aquaculture: a national and global perspective. *Fish and Fisheries* **16**: 668–683.
- Kasper JM, Bertelsen B, Ólafsson HG, Holst JC, Sturlaugsson J, Jónsson SP (2014) Observations of growth and postspawning survival of lumpfish *Cyclopterus lumpus* from mark-recapture studies. *Journal of Fish Biology* **84**: 1958–1963.
- Kelly NI, Alzaid A, Nash GW, Gamperl AK (2014) Metabolic depression in cunner (*Tautoglabrus adspersus*) is influenced by ontogeny, and enhances thermal tolerance. *PLoS ONE* **9**: e114765.
- Kennedy J, Jónsson S, Kasper JM, Ólafsson HG (2014) Movements of female lumpfish (*Cyclopterus lumpus*) around Iceland. *ICES Journal of Marine Science: Journal du Conseil* **72**: 880–889.
- Khan R, Lee E, Barker D (1990) *Lernaecera branchialis*: a potential pathogen to cod ranching. *Journal of Parasitology* **76**: 913–917.
- Killen SS, Brown JA, Gamperl A (2007a) The effect of prey density on foraging mode selection in juvenile lumpfish: balancing food intake with the metabolic cost of foraging. *Journal of Animal Ecology* **76**: 814–825.
- Killen SS, Costa I, Brown JA, Gamperl AK (2007b) Little left in the tank: metabolic scaling in marine teleosts and its implications for aerobic scope. *Proceedings of the Royal Society of London B: Biological Sciences* **274**: 431–438.
- Kristmundsson Á, Freeman MA (2014) Negative effects of *Kudoa islandica* n. sp. (Myxosporea: Kudoidae) on aquaculture and wild fisheries in Iceland. *International Journal for Parasitology: Parasites and Wildlife* **3**: 135–146.
- Kyūshin K (1975) The embryonic and larval development, growth, survival and changes in body form, and the effect of temperature on these characteristics of the smooth Lump-sucker, *Aptocyclus ventricosus* (Pallas). *Bulletin of the Faculty of Fisheries Hokkaido University* **26**: 49–72.
- Lassen H, Lockwood S, Cappell R, Pedersen GM (2015) *Full Assessment Report*. Public Certification Report – Initial Assessment of the Greenland Lumpfish Fishery. Sustainable Fisheries Greenland. Report no.: 2014-018, rev. 5. Certificate no.: f-dnv-165369, 35 pp. [Cited 24 Jan 2016.] Available from URL: <https://www.msc.org/track-a-fishery/fisheries-in-the-program/fisheries-by-species/fisheries-by-species#lumpfish>
- Leclercq E, Grant B, Davie A, Migaud H (2014) Gender distribution, sexual size dimorphism and morphometric sexing in ballan wrasse *Labrus bergylta*. *Journal of Fish Biology* **84**: 1842–1862.
- Leclercq E, Zerafa B, Graham P, Migaud H. (2015) Development of best practices for the maintenance of cleaner fish in commercial Scottish salmon (*Salmo salar*) net-pens: supplementary feeding and 3D behavioural study. Proceedings of the Aquaculture Europe 2015, Rotterdam, 2015. European Aquaculture Society City, pp. 455–456.
- Lees F, Baillie M, Gettinby G, Revie CW (2008) Factors associated with changing efficacy of emamectin benzoate against infestations of *Lepeophtheirus salmonis* on Scottish salmon farms. *Journal of Fish Diseases* **31**: 947–951.
- Levsen A, Maage A (2016) Absence of parasitic nematodes in farmed, harvest quality Atlantic salmon (*Salmo salar*) in Norway – results from a large scale survey. *Food Control* **68**: 25–29.
- Liu Y, vanhauwaer Bjelland H (2014) Estimating costs of sea lice control strategy in Norway. *Preventive Veterinary Medicine* **117**: 469–477.
- Lorance P, Cook R, Herrera J, de Sola L, Florin A, Papaconstantinou C (2015) *Cyclopterus lumpus*. The IUCN Red List of Threatened Species 2015: e.T18237406A45078284. [Cited 22 Oct 2016.] Available from URL: <http://www.iucnredlist.org/details/18237406/1>
- Marcos-López M, Donald K, Stagg H, McCarthy U (2013) Clinical *Vibrio anguillarum* infection in lumpsucker *Cyclopterus lumpus* in Scotland. *Veterinary Record* **173**: 319–319.
- Marine Harvest (2015) *Salmon Farming Industry Handbook 2015*. 89 pp. [Cited 16 Oct 2016.] Available from URL: <http://hugin.info/209/R/1934071/696335.pdf>
- Marine Stewardship Council (2014) *Fisheries by Species*. [Cited 24 Jan 2016.] Available from URL: <https://www.msc.org/track-a-fishery/fisheries-in-the-program/fisheries-by-species/fisheries-by-species#lumpfish>
- Martin-Robichaud DJ, Peterson RH, Benfey TJ, Crim LW (1994) Direct feminization of lumpfish (*Cyclopterus lumpus* L.) using 17 β -oestradiol-enriched *Artemia* as food. *Aquaculture* **123**: 137–151.
- McVicar AH (2004) Management actions in relation to the controversy about salmon lice infections in fish farms as a hazard to wild salmonid populations. *Aquaculture Research* **35**: 751–758.
- Mikkelsen N, Pedersen T (2012) Invasive red king crab affects lumpsucker recruitment by egg consumption. *Marine Ecology Progress Series* **469**: 87–99.
- Mitamura H, Thorstad EB, Uglem I, Bjørn PA, Økland F, Næsje TF et al. (2007) Movements of female lumpsucker *Cyclopterus lumpus* in a Norwegian fjord during the spawning period. NINA Rapport 288: 20 pp. Norsk institutt for naturforskning (NINA), Trondheim. 288.
- Mitamura H, Thorstad EB, Uglem I, Bjørn PA, Økland F, Næsje TF et al. (2012) Movements of lumpsucker females in a northern Norwegian fjord during the spawning season. *Environmental Biology of Fishes* **93**: 475–481.
- Moran J, Kent M, Whitaker D (1999a) *Kudoa thyrssites* (Myxozoa: Myxosporea) infections in pen-reared Atlantic salmon in the northeast Pacific Ocean with a survey of potential non-salmonid reservoir hosts. *Journal of Aquatic Animal Health* **11**: 101–109.
- Moran J, Whitaker D, Kent M (1999b) Natural and laboratory transmission of the marine myxozoan parasite *Kudoa thyrssites* to Atlantic salmon. *Journal of Aquatic Animal Health* **11**: 110–115.
- Moring JR (2001) Intertidal growth of larval and juvenile lumpfish in Maine: a 20-year assessment. *Northeastern Naturalist* **8**: 347–354.

- Mullins JE, Powell M, Speare DJ, Cawthorn RJ (1994) An intranuclear microsporidian in lumpfish *Cyclopterus lumpus*. *Diseases of Aquatic Organisms* **20**: 7–13.
- Murray AG (2016) A modelling framework for assessing the risk of emerging diseases associated with the use of cleaner fish to control parasitic sea lice on salmon farms. *Transboundary and Emerging Diseases* **63**: e270–e277.
- Murray AG, Peeler EJ (2005) A framework for understanding the potential for emerging diseases in aquaculture. *Preventive Veterinary Medicine* **67**: 223–235.
- NERC (2015) *Sustainable Aquaculture Industry Workshop Report*. BBSRC-NERC, Edinburgh, 15 pp. [Cited 24 Jan 2016.] Available from URL: <http://www.nerc.ac.uk/innovation/activities/sustainablefood/aquaculture/aquaculture-workshop-report-2015/>
- Nodland E (2016) *Erlend Waatevik, EWA Consulting*. [Cited 16 Oct 2016.] Available from URL: <http://ilaks.no/godt-over-ti-millioner-rognkjeks-produisert-i-2015/>. *Ilaks* [in Norwegian].
- Norðberg G, Johannesen A, Arge R (2015) Cryopreservation of lumpfish *Cyclopterus lumpus* (Linnaeus, 1758) milt. *PeerJ* **3**: e1003.
- Norwegian Directorate of Fisheries (2015) *Sale of farmed cleaner fish 2012–2015*. [Cited 16 Oct 2016.] Available from URL: <http://www.fiskeridir.no/English/Aquaculture/Statistics/Other-marine-fish-species>
- Nytrø AV (2013) The effect of temperature and fish size on growth of juvenile lumpfish (*Cyclopterus lumpus* L.). Master's Degree Thesis in Fisheries Science, University of Tromsø, 80 pages.
- Nytrø AV, Vikingstad E, Foss A, Hangstad TA, Reynolds P, Eliassen G *et al.* (2014) The effect of temperature and fish size on growth of juvenile lumpfish (*Cyclopterus lumpus* L.). *Aquaculture* **434**: 296–302.
- Øines Ø, Heuch PA (2005) Identification of sea louse species of the genus *Caligus* using mtDNA. *Journal of the Marine Biological Association of the United Kingdom* **85**: 73–79.
- Øines Ø, Heuch PA (2007) *Caligus elongatus* Nordmann genotypes on wild and farmed fish. *Journal of Fish Diseases* **30**: 81–91.
- Øines Ø, Simonsen JH, Knutsen JA, Heuch PA (2007) Host preference of adult *Caligus elongatus* Nordmann in the laboratory and its implications for Atlantic cod aquaculture. *Journal of Fish Diseases* **29**: 167–174.
- Pampoulie C, Skirnisdottir S, Olafsdottir G, Helyar SJ, Thorsteinsson V, Jónsson SP *et al.* (2014) Genetic structure of the lumpfish *Cyclopterus lumpus* across the North Atlantic. *ICES Journal of Marine Science: Journal du Conseil* **71**: 2390–2397.
- Perry B, Treasurer JW (2015) An overview of cleanerfish production at Ardtoe. Proceedings of the Cleanerfish Workshop, Inverness, 1st December 2015. Scottish Salmon Producers Organisation.
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* **308**: 1912–1915.
- Picón-Camacho SM, Holzer AS, Freeman MA, Morris DJ, Shinn AP (2009) *Myxobolus albi* n. sp. (Myxozoa) from the gills of the common goby *Pomatoschistus microps* Krøyer (Teleostei: Gobiidae). *Journal of Eukaryotic Microbiology* **56**: 421–427.
- Pike AW, Wadsworth SL (1999) Sealice on salmonids: their biology and control. *Advances in Parasitology* **44**: 233–337.
- Pooley C, Consuegra S, Gray C, Tew I, Garcia de Leaniz C (2015) Genetic screening of lumpfish (*Cyclopterus lumpus*) for the control of sea lice in salmon farming. Proceedings of the Aquaculture Europe 2015 (Poster) Rotterdam, 2015. European Aquaculture Society, City.
- Poppe TT, Taksdal T, Skjelstad H, Svieland C, Vagnes Ø, Colquhoun DJ (2012) Nye arter – nye diagnostiske utfordringer (New species – New diagnostic challenges). *Norsk Veterinærtidsskrift* **124**: 19–21 [In Norwegian].
- Poppe TT, Colquhoun DJ, Taksdal T, Nilsen H, Alarcón M (2013) Rognkjeks i oppdrett-diagnostiske og dyrevelferdsmessige utfordringer (Farmed lumpsucker-diagnostic and welfare challenges). *Norsk Veterinærtidsskrift* **125**: 556–558.
- Powell A, Keay A, Pooley C, Galloway G, Scolamacchia M, Frazao-Pires A *et al.* (2015a) Optimization of captive breeding of the lumpfish (*Cyclopterus lumpus*) for sea lice control in salmon farming. Proceedings of the Aquaculture Europe 2015, Rotterdam, 2015a. European Aquaculture Society, pp. 647.
- Powell MD, Reynolds P, Kristensen T (2015b) Freshwater treatment of amoebic gill disease and sea-lice in seawater salmon production: considerations of water chemistry and fish welfare in Norway. *Aquaculture* **448**: 18–28.
- Quignard JP, Pras A (1986) Labridae. In: Whitehead PJP, Bauchor M-L, Hureau J-C, Nielsen J, Tortonese E (eds) *Fishes of the North-eastern Atlantic and the Mediterranean*, Vol. II, pp. 919–942. UNESCO, Paris.
- Rincón-Cervera MÁ, Suárez-Medina MD, Guil-Guerrero JL (2009) Fatty acid composition of selected roes from some marine species. *European Journal of Lipid Science and Technology* **111**: 920–925.
- Rolbiecki L, Rokicki J (2008) Helminths of the lumpsucker (*Cyclopterus lumpus*) from the Gulf of Gdańsk and Vistula Lagoon (Poland). *Oceanological and Hydrobiological Studies* **37**: 53–59.
- Rønneseth A, Ghebretnsae DB, Wergeland HI, Haugland GT (2015) Functional characterization of IgM+ B cells and adaptive immunity in lumpfish (*Cyclopterus lumpus* L.). *Developmental & Comparative Immunology* **52**: 132–143.
- Rønneseth A, Haugland GT, Brudal E, Colquhoun D, Wergeland HI (2016) Vaccination and adaptive immune response of lumpfish (*Cyclopterus lumpus* L.). *Fish & Shellfish Immunology* **53**: 122.
- Saleh M, Kumar G, Abdel-Baki AA, Dkhil M, El-Matbouli M, Al-Quraishy S (2014) Development of a novel in vitro method for drug development for fish; application to test efficacy of antimicrosporidian compounds. *Veterinary Record* **175**: 561–561.
- Sayer MDJ, Davenport J (1996) Hypometabolism in torpid goldsinny wrasse subjected to rapid reductions in seawater temperature. *Journal of Fish Biology* **49**: 64–75.

- Sayer MDJ, Reader JP (1996) Exposure of goldsinny, rock cook and corkwing wrasse to low temperature and low salinity: survival, blood physiology and seasonal variation. *Journal of Fish Biology* **49**: 41–63.
- Sayer MDJ, Gibson RN, Atkinson RJA (1996) Seasonal, sexual and geographical variation in the biology of goldsinny, corkwing and rock cook on the west coast of Scotland. In: Sayer MDJ, Treasurer JW, Costello MJ (eds) *Wrasse: Biology and Use in Aquaculture*. Blackwell Science, Oxford.
- Scyborska TA (1948) The parasitofauna of *Cyclopterus lumpus* in the White Sea. *Raboty Morsk biologii Stat Karelo-Finsk University* **1**: 145–151.
- Skiftesvik AB, Bjelland RM, Durif CMF, Johansen IS, Browman HI (2013) Delousing of Atlantic salmon (*Salmo salar*) by cultured vs. wild ballan wrasse (*Labrus bergylta*). *Aquaculture* **402**: 113–118.
- Skiftesvik AB, Blom G, Agnalt A-L, Durif CM, Browman HI, Bjelland RM et al. (2014) Wrasse (Labridae) as cleaner fish in salmonid aquaculture – the Hardangerfjord as a case study. *Marine Biology Research* **10**: 289–300.
- Skirnisdottir S, Olafsdottir G, Olafsson K, Jendrossek T, ap Dafydd Lloyd H, Helyar S et al. (2013) Twenty-two novel microsatellite loci for lumpfish (*Cyclopterus lumpus*). *Conservation Genetics Resources* **5**: 177–179.
- Skretting (2016) *Lumpsucker*. [Cited 16 Oct 2016.] Available URL: <http://www.skretting.com/en-GB/species/lumpsucker/>
- Småge SB, Frisch K, Brevik ØJ, Watanabe K, Nylund A (2016) First isolation, identification and characterisation of *Tenacibaculum maritimum* in Norway, isolated from diseased farmed sea lice cleaner fish *Cyclopterus lumpus* L. *Aquaculture* **464**: 178–184.
- Stevenson SC, Baird BJ (1988) The fishery for lumpfish [*Cyclopterus lumpus*] in Newfoundland waters. Canadian Technical Report of Fisheries and Aquatic Sciences, No. C/639.805 C35/1595, 26 p.
- Templeman W, Hodder VM, Fleming AM (1976) Infection of lumpfish (*Cyclopterus lumpus*) with larvae and of Atlantic cod (*Gadus morhua*) with adults of the copepod, *Lernaecera branchialis*, in and adjacent to the Newfoundland area, and inferences therefrom on inshore-offshore migrations of cod. *Journal of the Fisheries Board of Canada* **33**: 711–731.
- Thordarson G (2013) *Markets for lumpfish*. Coastal Fisheries Reports. Coastal Fisheries in the North Atlantic. [Cited 18 Oct 2016.] Available from URL: <http://www.coastalfisheries.net/>, <http://www.coastalfisheries.net/wp-content/uploads/2013/06/Export-value-of-lumpfish-products-from-Iceland-increase-around-300-million-IKR.pdf>.
- Towers L (2015) *Viral Hemorrhagic Septicemia Reported for First Time in Icelandic Fish*. The Fish Site and 5M Publishing. [Cited 16 Oct 2016.] Available from URL: <http://www.thefishsite.com/fishnews/26621/viral-hemorrhagic-septicemia-reported-for-first-time-in-icelandic-fish/>
- Treasurer JW (2002) A review of potential pathogens of sea lice and the application of cleaner fish in biological control. *Pest Management Science* **58**: 546–558.
- Treasurer JW (2013) *Use of wrasse in sea lice control*. Report to the Scottish Aquaculture Research Forum (SARF), Sarf068, 33 pp. [Cited 16 Oct 2016.] Available from URL: <http://www.sarf.org.uk/cms-assets/documents/124859-172398.sarf068.pdf>
- Vandendriessche S, Messiaen M, O'Flynn S, Vincx M, Degraer S (2007) Hiding and feeding in floating seaweed: floating seaweed clumps as possible refuges or feeding grounds for fishes. *Estuarine, Coastal and Shelf Science* **71**: 691–703.
- Vandeputte M, Baroiller JF, Haffray P, Quillet E (2009) Genetic improvement of fish: achievements and challenges for tomorrow. *Cahiers Agricultures* **18**: 262–269.
- Vasconcelos P, Monteiro CC, Santos MN, Gaspar MB (2004) First record of the lumpfish (*Cyclopterus lumpus* Linnaeus, 1758) off the Algarve coast (southern Portugal): southward extension of the species distributional range. *Journal of Applied Ichthyology* **20**: 159–160.
- Vestvik N (2013) *Lumpsuckers on the rise! Campbeltown: Aqua Kompetanse*. 7770 Flatanger. [Cited 16 Oct 2016.] Available URL: www.aqua-kompetanse.no.