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Abstract

Host behaviour can prevent infection and moderate the fitness of parasites. Anti-parasite behaviours are prevalent in many host-parasite systems, and occur over fine- or broad-scales. With global growth in aquaculture production and the associated proliferation of parasites in farming systems, the behaviour of the fish being farmed has seldom been investigated in relation to parasites. Epidemics and outbreaks of parasites are prevalent in most aquaculture systems, and behaviour could be harnessed in concert with current methods to prevent and control parasites and pathogens. However, this requires a systematic understanding of the behaviours of hosts, their capacity for resistance, and their interaction with the environment and the parasite. Herein, we present evidence for how behaviour could be used in aquaculture, and discuss the possibility for behaviour to be used in aquaculture as a) an indicator of welfare status, b) a tool in prevention or control, and c) to maintain or improve welfare. We apply this framework to a case study of a highly problematic parasite, the salmon louse (*Lepeophtheirus salmonis*), on farmed Atlantic salmon (*Salmo salar*). We present the current state of the system, and the drawbacks of current control or prevention methods. We synergise current knowledge on host behaviours, and show how behaviour could be incorporated into current and new approaches for prevention and control. Through this first evaluation of the possibilities behaviour presents in disease management, we aim to facilitate a shift in the current disease control paradigm from reactive-based post-infection control to pre-infection prevention approaches.

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Aquaculture on the rise, with diseases and parasites hitching a ride

From humble beginnings, the farming of aquatic species in basic pond systems has developed into a multi-billion dollar global industry with farming methods that incorporate special cage designs, artificial feed, and advanced water treatment methods (Lucas and Southgate 2012). The development and success of aquaculture technologies has led to aquaculture becoming one of the primary sources of animal protein (Ashche 2008, Teletchea and Fontaine 2014, Ottinger *et al.* 2016), surpassing cattle in global biomass production (Larsen and Roney 2013). Despite all its successes and rapid expansion, aquaculture has concurrently experienced major setbacks associated with diseases and parasites (Molnár 1987, Meyer 1991, Seng 1997, Scholz 1999, Bondad-Reantaso *et al.* 2005, Blaylock and Bullard 2014, Buchmann 2015), and its history is considered a chain of victories over diseases (Sindermann 1990). For example, commercial culture of Japanese yellowtail (*Seriola quinqueradiata*) commenced in 1961 and has subsequently overcome epidemics caused by vibriosis (1963), nocardiosis and ichthyophoniasis (1967), pseudotuberculosis (1969), streptococcosis (1974), and lymphocystis (1975; Egusa 1983, Lafferty *et al.* 2015).

A broad spectrum of parasites and diseases affect aquaculture, from bacterial, fungal and viral infections, to endo- and ectoparasites (Meyer 1991, Shao 2001, Blaylock and Bullard 2014). The success of fish aquaculture is hindered by the need for efficient disease and parasite control, which adds to the economic and technical constraints of farming (Sindermann 1990, Lafferty *et al.* 2015). Even with modern technologies and information distribution, entire industries have collapsed due to a pathogen outbreaks. For example, Chilean salmon aquaculture operations suffered drastic losses from infectious salmon anaemia (ISA), which devastated the industry (Asche *et al.* 2009) and damaged public perception of salmon farming (Hansen and Onozaka 2011). As such, parasites and disease are considered the primary bottleneck that restrains the “Blue Revolution” (Blaylock and Bullard 2014).

The common toolbox for treating parasites (and why it doesn't always work)

Pathogen and parasite management is one of the major hurdles for intensive fish farming (Schlag 2010), and given the diverse range of species to repel, there is a wide repertoire of treatment approaches. Proactive prevention techniques such as quarantine measures, maintaining water and environmental quality, and optimising nutrition have always been prevalent in aquaculture management (Meyer 1991), yet diseases and parasites inevitably find their way through these barriers. Thereafter, aquaculture relies on reactive treatments centred on chemotherapeutants (Molnár 1987, Sindermann 1990, Seng 1997, Shao 2001). However, the long-term sustainability of such approaches is jeopardised by drug resistance and reduced sensitivity (Wolstenholme *et al.* 2004, Aaen *et al.* 2015), and there is concern about these chemicals permeating into surrounding ecosystems and harming non-target animals (Burridge *et al.* 2010). Parasites and pathogens retain life-history traits to ensure success in a wide variety of environments, and the conditions provided by intensive fish farming have pushed their evolution towards increased transmission and virulence (Mennerat *et al.* 2010, Kennedy *et al.* 2016). The use of chemotherapeutants in aquaculture creates a strong selection pressure, and the fast generation time of parasites and pathogens allows for rapid adaptation to treatments (Boots 2015, McNair 2015). The use of chemotherapeutants to limit and combat disease and parasites is, thus, unlikely to remain effective in areas where genetic resistance can penetrate the population quickly (e.g. Kreitzman *et al.* 2017).

Aquaculture may be able to benefit from long-standing agricultural practices and strategies to cope with disease and parasites. Although terrestrial and aquatic farming differ due to the age of industry (aquatic domestication lags about 8000 years behind; Ashche 2008, Nash 2011), farming medium (land vs. water), innate species-specific differences, and the general approach (self-contained terrestrial species vs. reliance on wild populations in aquaculture; Teletchea & Fontaine 2014), parallels can be drawn in terms of welfare and disease management. Molento (2009) describes the pressing need for a paradigm shift in terrestrial agriculture from the current chemical warfare, to using alternative methods of control such as integrated pest management or selective breeding for host resistance. We echo these sentiments, and also push for behaviour to be incorporated into methods to prevent and control infectious diseases and parasites within aquaculture.

Incorporating behaviour into prevention and treatment

Animal behaviour has long been utilised in agriculture to enhance husbandry practices and animal welfare (Fraser and Broom 1997). The behaviours of fish have shifted with the introduction of intensive aquaculture systems (Huntingford 2004), where much of the environment is under the control of humans (Lien and Law 2016). Consequently, there are substantial differences in the environments experienced by cultured and wild fish. Farmed fish are spatially restricted, provided with diets high in protein and fat, protected against predators, treated for sickness, and provided with mates without competition (Gross 1998, Price 1999). Phenotypic changes are inevitable when species are domesticated, but how behaviour is altered in captive environments is less straightforward (Price 1999). Normal behaviours may be lost (such as competing for food) or adapted to suit the captive environment (such as schooling), yet whether these changes are advantageous or deleterious remains largely unknown (although see Huntingford and Adams 2005, Fernö *et al.* 2011).

Generally, domesticated animals have traits that are beneficial in captivity, such as disposition, minimal stress responses to their created habitat, and successful reproduction (Diamond 2002). Behaviours suited to domestication confer advantage to the animals themselves and the humans farming them, and are often enhanced through deliberate selective breeding or co-selected for when focusing on other traits (Price 1999). In terrestrially farmed species, early generations were selected for growth and behaviour, whereas aquaculture primarily focused on species that were attractive for human consumption and could complete their reproductive cycle in captivity whilst demonstrating an acceptable welfare profile (Duarte *et al.* 2007, Teletchea and Fontaine 2014). As behaviours of aquatic animals under culture were not at the forefront of the characteristics by which species are selected for domestication, selection for growth and reproduction is likely to have secondarily promoted behaviours that represented positive welfare status (Price 1999, Huntingford 2004).

With this approach to domestication, we have limited understanding of the behaviours of fish in aquaculture compared to terrestrial agriculture species. As aquaculture is one of the fastest growing global primary industries (Teletchea and Fontaine 2014), better understanding the behaviours of the species we farm could facilitate optimal husbandry and welfare (Martins *et al.* 2012). In particular, understanding behaviours may help us confront the parasites and pathogens which plague production (Blaylock & Bullard 2014). While much research has focused on behavioural development and social organisation of fish (Magnhagen *et al.* 2008), behaviour in response to parasites and pathogens has been generally overlooked in an aquaculture context. Broad research on fish-parasite systems in the wild identifying the effects

of parasites on fish welfare (Barber *et al.* 2000, Barber 2007) can be collated and translated to provide useful knowledge for aquaculture applications. Thereafter, a comprehensive understanding of fish behaviour within aquaculture settings is required before options for integrating behaviour into effective preventative or control can be identified.

We propose that behaviour can be a useful tool in three ways: (1) as a welfare indicator of infection status; (2) as a means to enhance resistance to diseases and parasites; and (3) to improve welfare outcomes via encouraging behaviours through adaptive learning. We first assess the evidence from across marine and terrestrial systems for these approaches before we present a specific case study of the salmon-salmon louse host-parasite system.

Behaviour as a welfare indicator of infection status

Using behaviour to assess welfare status in aquaculture is underutilised. In addition to improving animal health status, social interactions, and nutrition (Gonyou 1994), behaviour is a simple, non-invasive indicator for welfare, providing information on needs and internal states of animals (Dawkins 2003, Smulders *et al.* 2006, Appleby and Hughes 2011). Changes in the frequency or the suppression of preferred behaviours can indicate reduced welfare, which can then be improved through management practices. Identifying abnormal behaviours is invaluable for veterinary clinicians when evaluating an animal's condition, as it allows prediction of compromised welfare or health without the need for physical examination. For example, pigs that no longer defended themselves against tail- or ear-biting pen-mates were suffering from infected wounds inflicted upon them previously (Smulders *et al.* 2006). Identifying behaviours associated with infection or disease is common practice for terrestrial livestock and lab animals, and health concerns are often linked with infectious diseases or parasites in synergy with poor housing conditions (Fraser and Broom 1997).

There is relatively limited knowledge of the behavioural responses of cultured fish to disease and parasite infection, likely due to the fact that using behaviour as an indicator for health and welfare in fish is inherently more difficult. Terrestrial farm animals are generally more distinguishable given their larger body size, and identifiable colour and markings, which can help farmers identify sick individuals or non-normal behaviours (Fraser and Broom 1997). In contrast, the relatively smaller cultured fish are commonly held in greater numbers and higher densities than larger terrestrial livestock, and identifying or following individuals is practically unfeasible without expensive technologies or invasive methods. In fact, the

ability to monitor individual behaviour with precision has only recently been developed for terrestrial livestock production (Berckmans 2014) and is in its infancy for aquaculture (Fore et al. 2017).

Consequently, using behaviour as a welfare indicator within aquaculture must focus at the group level, and incorporate knowledge of natural behaviours as well as those present in the captive environment. This may include identifying and cataloguing changes to normal behaviour that can be attributed to the group's internal state, such as feeding behaviours, spatial position in the holding tank or cage, school structure, or response to negative stimuli (Martins *et al.* 2012). For example, reduced swimming speeds or abnormal school structure could indicate infection (Wagner and McKinley 2004, Barber 2007, Bui *et al.* 2016a). Despite the ease of focusing at the group level compared to identifying individuals, behaviour is often a manifestation of individual processes. Parasites and disease pathogens operate on the individual, as do selective processes, and thus changes in the behaviour of individuals is equally as important as the group level. Understanding the behavioural profile of individuals will form the knowledge base for drivers of group behaviour (i.e. Robinson 2009). Using behaviour as an additional measure of welfare will facilitate prompt actions to alleviate infestation or infection when needed. Behaviour is, thus, an advantageous indicator that can be quick and simple to assess by farmers provided with the right tools and training, and can be continuously surveyed.

Behaviour as a tool to enhance resistance to diseases and parasites

As the issue of animal welfare and chemical resistance in parasites is becoming more apparent, focus is shifting away from chemical and medicinal methods of parasite control towards alternative methods (Molento 2009, McNair 2015). Since behaviour is the first line of defence against parasites and disease (as it can limit exposure to infective parasites or deter successful infection; Hart 1990, Hart 1992, Hart 2011), it could be used to enhance host resistance (e.g. Hoste *et al.* 2010, Bui *et al.* 2013, Hosey *et al.* 2013, Frenzl *et al.* 2014, Kearney *et al.* 2016). The prevention of endo- and ectoparasitic infections or the transmission of infectious diseases can be achieved by manipulating animal behaviour; however, the effectiveness of such practices is largely anecdotal. For example, the current method of farming goats is analogous to that of sheep, where they are held in fields for grazing. In the wild, goats selectively browse and forage pastures which, in contrast to sheep, results in an

intermittent, and thus lower, risk of nematode ingestion (Hoste *et al.* 2010). Hence, goats have an evolved response to nematodes whereby they exhibit self-medicating behaviour and select foraging locations to avoid the parasite (Hoste *et al.* 2010), and have, thus, been ineffectively farmed as they are subject to the grazing habits of sheep.

Behavioural resistance in wild fish largely comes in the form of spatial and temporal avoidance of parasites. Individuals can detect and avoid parasite-risky habitats, infected conspecifics or sick prey (Barber 2005), and groups can make better avoid parasites, indicating the benefit of social interaction and group behaviour (Mikheev *et al.* 2013). Several major fish parasites have specific depth-related infection patterns. For example, copepodids of *Caligus rogercresseyi*, the main parasite of farmed salmon in South America, are most abundant in surface waters (Molinet *et al.* 2011). Similarly, the infectious stages of the skin fluke *Neobenedenia girellae* concentrate in surface waters where most infections of farmed kingfish *Seriola quinqueradiata* occur (Shirakashi *et al.* 2013). Farm-scale manipulations to spatially separate parasites and hosts, reducing encounter rates, could be effective in preventing infection. Few examples of behaviours to evade and deter parasites exist for fish, potentially due to the limited research because of the difficulties in observing behaviour at relevant scale in the wild. Behavioural resistance in cultured fish species is a promising tool for controlling parasites and diseases in aquaculture and warrants further investigation.

Teaching fish behaviours to promote welfare

By teaching animals to accept and adapt to their environment, behaviour has been used as a tool to improve welfare in zoos, laboratories and agricultural systems (Hemsworth *et al.* 1996, Price 2002, Hemsworth 2003, Fraser *et al.* 2013, Hosey *et al.* 2013). As a secondary outcome of improved welfare, behavioural adaptation also reduces stress and confers prevention against parasites and disease (Conte 2004) through positive hygiene practices, feeding habitats and social experiences (Wechsler and Lea 2007). Four pathways to investigate methods to facilitate learning in farm animals to improve husbandry procedures have been proposed (Wechsler and Lea 2007): to utilise i) innate preferences regarding relevant cues, ii) previous experience of the animals, iii) information transfer through social learning and interaction, and iv) eliciting interest and appropriate timing of reinforcements.

Although learning in farm animals has long been recognised as a tool to facilitate human-animal interactions or acclimatisation to infrastructure (Wechsler and Lea 2007), it has

gained little attention in aquaculture. This is linked to the common perception that fish have a limited capacity to learn. At the crux of discussions concerning our interactions with fishes (e.g. as pets, recreational fishing, etc.) is the debate on whether fish feel pain (Rose 2002, Braithwaite 2010, Sneddon 2011, Rose *et al.* 2014, Brown 2015). Arguments showing that fish indeed feel pain and suffering draw attention to the neural and cognitive abilities of fish (Braithwaite 2010), highlighting the many examples of deeper cognition through learning, spatial orientation, social interactions and cooperation (Brown *et al.* 2006). Recognising the learning capacity of fish can have positive implications for production systems (Salvanes and Braithwaite 2006). For example, commercial fish can be conditioned to aversive stimulus, thereby reducing stress responses and, if desirable, fish can be taught to display attraction to the stimulus through anticipating a positive reward (e.g. feed) associated with the stimulus (Bratland *et al.* 2010, Fernö *et al.* 2011). By reducing negative responses to aversive stimuli and improving fish's coping ability, maintaining welfare status could be promoted intrinsically. Taking this further, innate behavioural resistance to infection could be promoted through encouragement and operant learning at an early life-history stage of cultured fish, or adaptive behaviours could be taught at the individual level that subsequently permeate through a group via social information transfer (Couzin *et al.* 2005, Couzin 2009).

Fish have the potential for habituation or learning, a topic little explored in the context of aquaculture. Current knowledge often comes as a surprise finding within other research aims. For example, a study investigating the diet preferences of cod taught fish to activate a feeder using their mouth (a natural behaviour for cod; Millot *et al.* 2012), however, some individuals learnt that food could be delivered by activating the feeder using the external t-bar tag protruding from their back instead, and continued to deliberately use this method (Millot *et al.* 2014). This form of learnt feeding innovation further enforces the fact that fish have an underestimated cognitive ability. Therefore, in addition to using behaviour as a method to gauge the health status of fish and enhance disease and parasite resistance, beneficial behaviours could be taught as a passive means to promote welfare.

Case study: Sea lice in salmon aquaculture

The main parasitic culprit affecting aquaculture is the salmon louse *Lepeophtheirus salmonis*, which is widely distributed throughout the Atlantic salmon farming countries and the west coast of Canada (Costello 2006). Analogous to *L. salmonis* from the northern

hemisphere, species of the *Caligus* genus are at the crux of Chile's aquaculture parasite problem (Hamilton-West *et al.* 2012). Salmon lice are a crustacean copepod that feed on the blood, skin and mucous of their host (Costello 2006). In high densities, the cost of infestation by lice on host fitness and welfare is considerable (Grimnes & Jakobsen 1996; Finstad *et al.* 2000; Wagner & McKinley 2004; Wager, Fast & Johnson 2008; Finstad *et al.* 2011). Aside from direct impacts to salmon, sea lice also impose a remarkable cost to the salmon aquaculture industry through management actions and treatment regimes (Costello 2009), with profit reductions predicted to be between 16.1 to 17.9% in Norway (Liu and Bjelland 2014). Scientific literature relating to sea lice acquire the highest impact of all the pathogens in salmon aquaculture, and thus quantitatively, this parasite is the most important in the industry (Murray *et al.* 2016). Sea lice also generate considerable public conflict and controversy because of the broader ecological and social impacts the parasite causes (Bocking 2012, Klinger and Naylor 2012, Lafferty *et al.* 2015), such as its alleged role in the decline of wild salmonid populations as a result of lice spillback from farms (McVicar 2004, Heuch *et al.* 2005, Krkošek *et al.* 2013, Torrissen *et al.* 2013, Taranger *et al.* 2015, Shephard and Gargan 2017). In Canada, this has led to extensive interaction between government, industry, environmental groups and the local community to determine the progression of salmon aquaculture (Bocking 2012). A similar scenario is occurring in Norway, the global leader in salmon production, where their government has stated that sea lice are one of the indicators for regional environmental sustainability, and have imposed restrictions on biomass production linked to parasite levels reported on farms within a site; companies that maintain low parasite abundance on fish over time are permitted to produce greater biomasses (Svåsand *et al.* 2016). Consequently, considerable research and investment has gone into prevention and treatment methods.

What does the current toolbox look like?

The current toolbox for the prevention and treatment of sea lice in salmon aquaculture integrates multiple approaches (Costello 1993, Rae 2002, Igboeli *et al.* 2013, Torrissen *et al.* 2013; Fig. 1), but, similar to terrestrial farming, has largely focused on the use of chemicals or drugs to remove parasites post-infection (Igboeli *et al.* 2014). One of the most common methods to eradicate sea lice is bathing, whereby drugs are administered to fish completely immersed in an enclosed net pen or a well-boat (Svåsand *et al.* 2016). The array of active compounds in chemotherapeutants include organophosphates, pyrethrin or pyrethroid

compounds, oxidising agents or avermectins (Roth 2000, Grant 2002, Rae 2002, Grave *et al.* 2004, BurrIDGE *et al.* 2010, Murray 2015). In Norway, these compounds are used in rotation to reduce the build-up of resistance in sea lice populations (Svåsand *et al.* 2016). Bathing infected salmon in freshwater is an alternative method, typically used in combination with mechanical washing methods. However, the use of freshwater is not considered entirely effective, particularly against older lice stages (Stone *et al.* 2002a, Wright *et al.* 2016). In-feed or oral treatment is also frequently used to medicate salmon (Johnson and Margolis 1993, Stone *et al.* 2002b), and is considered advantageous due to its passive implementation, which avoids stress and mechanical harm to the fish. In countries with high salmon production, resistance is greater and therefore the medication is used as one of the many treatment approaches. This control method was more prevalent in earlier stages of salmon farming, however currently, it is used more in countries that still have treatment-sensitive lice populations (Saksida *et al.* 2011). Although a vaccine is being developed against sea lice (Raynard *et al.* 2002), it remains elusive and will not be 100% effective if it eventuates, as few vaccines are. Nevertheless, vaccination resistance is less likely to develop when compared to the rate of resistance to drugs and chemical therapeutants (Kennedy and Read 2017).

Chemical- and drug-free approaches to combating sea lice are becoming increasingly popular within the industry, such as placing cleaner fish that feed on the attached adult lice (e.g. the ballan wrasse *Labrus bergylta* or lumpfish *Cyclopterus lumpus*) in the cage with salmon (Treasurer 2002, Imsland *et al.* 2014a, Powell *et al.* 2017). Adapted from terrestrial agriculture, fallowing has also been adopted in salmon farming as a means for lice control (Bron *et al.* 1993, Werkman *et al.* 2011, Groner *et al.* 2016). Larger companies or interconnected farm sites will coordinate a plan that uses fallowing with all-in-all-out production cycles to reduce the infection pressure in their region by removing the adult lice from the system (Bron *et al.* 1993, Saksida *et al.* 2011).

Methods to prevent lice infestations that include additions or modifications to the sea-cage (Fig. 2), such as plankton skirts (Lien *et al.* 2014, Frank *et al.* 2015), snorkels (Stien *et al.* 2016), fully-submerged cages (Dempster *et al.* 2009), submerged feeding and lights (Frenzl *et al.* 2014), or moving cages offshore (Fredheim and Langan 2009), have been thoroughly investigated in relation to efficacy and fish welfare issues, and are being used throughout the industry in Norway. More recently, novel methods to reduce infestation are being employed but largely lack sufficient quantitative evidence of their efficacy. For

example, methods in early stages of development or use include using heated water up to 30°C to kill and remove attached lice (www.steinsvik.no/en/products/e/seaculture/fish-health/thermolicer), optical delousing with lasers (www.stingray.no), or mechanical removal (whereby lice fall off after rough handling of the fish or washing with water jets; www.flis.no/no/avluser). These applications still require methodical testing of their efficacy and the potential negative welfare impacts before being considered for commercial use. Finally, interest in genomics and selective breeding of parasite-resistant salmon is increasing (Jones 2011, Yáñez *et al.* 2014, Gharbi *et al.* 2015), but is still in the exploration phase.

Drawbacks of the current tools

Under the current landscape of parasite epidemics in salmon farming, the perception is that fish cannot avoid infection and thus the industry's focus has been reactive control of outbreaks (Nowak 2007). The most extensively used methods of treatment are chemical-based, with the quantities of chemotherapeutants increasing due to the growing number and size of farms, the rise of ineffective treatments, and the build-up of chemical resistance in lice (Grave *et al.* 2004, Jimenez *et al.* 2012, Torrissen *et al.* 2013, Murray 2015; Fig. 3). The sensitivity of parasites to treatment agents has reduced across many of the available drugs (Bravo *et al.* 2013, Aaen *et al.* 2015, Helgesen *et al.* 2015, Marin *et al.* 2015). Pesticide resistance is linked to the frequency and dosage of treatments in farms, and the population structure of lice (Denholm *et al.* 2002, McEwan *et al.* 2015), with the rate of evolved resistance likely to exceed the development of new drugs. In fact, no new chemotherapeutants have been approved for use in the industry since 1999 (Aaen and Horsberg 2016). Still, the evolution of resistance to chemotherapy remains a major obstacle for the sustainable growth of salmon aquaculture, which has driven the research community and industry to look elsewhere for solutions.

In addition to broader environmental concerns over the use of chemotherapeutants (BurrIDGE *et al.* 2010), a less publicised issue is the welfare implications of chemotherapeutants to the salmon themselves. Current bathing procedures negatively affect the health and welfare of fish through withholding feed prior to, and crowding and oxygen deprivation during, bathing (Burka *et al.* 1997, Conte 2004, Vera and Migaud 2016). Among aquaculturists, there is an unspoken understanding that it is the treatment, and not the sea lice, that cause many of the large-scale mortality events (Svåsand *et al.* 2016). The current

legislative threshold for lice levels in Norwegian farms (0.5 adult females per fish; imposed by the Norwegian Food Safety Authority) is well below the level that induces severe physiological effects in large salmon (Wagner *et al.* 2008). Therefore, salmon are exposed to treatments capable of inflicting substantial stress and physical harm well before their infection can. In Norway, there were 16 836 accounts of acute and delayed mortality events in cages following bath treatments between 2012–2015 (Svåsand *et al.* 2016). The majority of these mortality events were greater than 1% cage mortality, with some surpassing 50% mortality.

A severe oversight by the governing bodies is the lack of research into best-practice methods of treatment, and subsequently, a lack of proper legislation and regulations for farms to abide by. Farmers currently follow the basic guidelines provided by drug manufacturers, rarely taking into account fish size, behaviour, or environmental preferences. Furthermore, factors such as cage volume (in terms of its fluctuations), hydrodynamic mixing, or water temperature are not accurately incorporated when calculating dose rates. Anecdotally, fish will crowd to their own detriment in a small volume of the available space during bath treatments. As the chemical does not disperse evenly within the enclosed space, a portion of the group will not be exposed to the appropriate dosage, creating circumstances that assist the development of resistance in the parasites. Without legislative guidelines, the often-ineffective application of chemotherapeutants is aiding increased resistance in lice and subsequently reducing the efficacy of treatments.

In-feed treatments avoid the negative welfare issues associated with bath treatments, and are intended to be effective against all stages of sea lice through the inhibition of chitin synthesis (Stone *et al.* 1999). However, the active ingredient often disperses into the wider environment through waste output from salmon farms and settles in sediments where it impacts non-target benthic fauna. (Telfer *et al.* 2006). The efficacy of in-feed treatments also varies spatially and temporally (Lees *et al.* 2008), and as with chemotherapeutants, lice resistance to the active compound is increasing in many salmon farming regions (Espedal *et al.* 2013, Jones *et al.* 2013).

An increasingly popular treatment method being utilised in concert with chemotherapeutants, albeit with varying success levels, are cleaner fish (Costello 1996, Treasurer 1996, Treasurer 2002, Skiftesvik *et al.* 2014). The success of this approach is largely dependent on a suite of factors, both within the control of the farmers (e.g. chemical treatment regimen, cleaner fish habitat, and net condition, shape and size), and reliant on environmental variables (water temperature, hydrodynamics for parasite transmission between

farms, and site location; Costello 1996, Treasurer 1996). Although there are models that predict cleaner fish densities required to meet targets of parasite load reduction (Groner *et al.* 2013), these have not been verified at commercial scale. In addition, the use of cleaner fish faces issues associated with their culture and capture fisheries (Skiftesvik *et al.* 2014), and welfare concerns. For example, over 10 million wild wrasse are extracted from the Norwegian coast each year with unassessed ecological consequences. Ultimately, fundamental knowledge of cleaner fish biology and ecology is drastically lagging behind their use in salmon aquaculture.

Finally, the alternative methods discussed previously, such as heat-treatments and optical laser de-lousing, have not been tested under controlled experimental conditions or at commercial-scales, largely due to technological constraints (Lekang *et al.* 2016). Industrial developers or suppliers are almost rushed to produce new solutions, through the urgent need for alternative methods. The logistical effort needed to conduct this research can be exceedingly difficult (e.g. Lien *et al.* 2014) and may prove to have a negative effect on production (Stien *et al.* 2012).

Alternative prevention & control methods for the future toolbox

Current methods to mitigate disease and parasites within aquaculture are expensive and largely ineffective, and can harm the culture species and the wider environment. Alternative methods to reduce parasite prevalence, without relying solely on chemotherapeutants, are therefore important to the future sustainability of aquaculture (Aaen *et al.* 2015, McNair 2015). Atlantic salmon aquaculture presents an unparalleled opportunity to consider and research the usefulness of utilising behaviour to help combat the welfare and economic costs of sea lice. Behaviour could be a useful tool in aquaculture via three applications: as an indicator for health and welfare, as a method of prevention or resistance to parasites, or as a means of prevention in combination with practical solutions (Fig. 4). This framework can provide multiple, non-chemical approaches to the salmon lice issue.

Behaviour as a welfare indicator of infection

Current methods of estimating lice loads on salmon in sea cages are unlikely to be representative of the group (Heuch *et al.* 2011), as many factors influence the vertical

distribution of fish (such as preference, infestation status, and body size; Oppedal *et al.* 2011a, Folkedal *et al.* 2012, Bui *et al.* 2016b) and sample fish are mostly captured from the surface. Infestation levels are intrinsically linked to the welfare status of salmon, and therefore behaviour can be used as an indicator for health and welfare if there is comprehensive understanding of how and why fish behave, coupled with knowledge of the mechanisms of such behaviours (Martins *et al.* 2012). Stress indicators in fish include swimming activity, group or individual spatial distribution, and social interactions (Lima and Dill 1990, Martins *et al.* 2012). Thus, observations of locomotion, school structure, flashing behaviour or swimming speed could help identify compromised welfare in salmon (e.g. Fraser and Broom 1997, Barber *et al.* 2000). To determine the cause of such behavioural profiles we need to quantify behavioural responses to specific stimuli. For example, within the first few days of infestation by sea lice, sea trout (*Salmo trutta*) exhibit higher rates of flashing (lateral turning), erratic swimming behaviour, and jumping (Birkeland and Jakobsen 1997, Wells *et al.* 2006). Atlantic salmon also display increased jumping behaviours in net pens with increasing sea lice load (Fernö *et al.* 1988, Furevik *et al.* 1993), and farmers could use an increase in flashing or jumping behaviour as a sign of greater parasite intensity. These types of behaviours could be assessed by the farmer through standardised surveillance (e.g. daily periods of visual behavioural recording) or through more advanced methods such as evaluating shoaling behaviour from video recordings (e.g. Stien *et al.* 2007, Sadoul *et al.* 2014).

Compared to uninfected or lightly infected fish, salmon in sea cages carrying high lice loads swim deeper at night time and avoid the upper 4 m of water where infective lice aggregate (Bui *et al.* 2016b). Wild salmonids swim in shallow brackish waters during early stages of out-migration (Plantalech Manel-La *et al.* 2009, Thorstad *et al.* 2012) to facilitate their transition to seawater and orientation towards the ocean, but also to potentially avoid the freshwater sensitive sea lice (Tucker *et al.* 2000, Bricknell *et al.* 2006, Wright *et al.* 2016). Sea trout carrying high parasite loads exhibit movement patterns to reduce infection levels, by swimming in the shallow, low-saline waters or prematurely returning to rivers (Gjelland *et al.* 2014, Thorstad *et al.* 2015). Thus, salmon with higher parasite loads are likely to swim deeper in sea cages, which could provide information on health status. However, swimming depth is strongly associated with environmental factors such as temperature or light (Johansson *et al.* 2006, Oppedal *et al.* 2011a), so it cannot be used as a welfare indicator in isolation. Nevertheless, continuous monitoring of environmental conditions (particularly temperature

and oxygen levels) could be combined with current knowledge on behaviour to build an index to identify parasite-related divergence in depth preference. Group swimming depth can be assessed using visual aids such as submerged cameras in the sea cage or monitoring equipment such as echosounders suspended beneath the cage (described in Bjordal *et al.* 1993, use reviewed in Oppedal *et al.* 2011a).

Behaviour as a method to enhance resistance to diseases and parasites

Atlantic salmon have co-evolved with *L. salmonis*; if behaviours exist that deter infection in wild fish, they may be retained in cultured fish as farmed strains have only been selectively bred for 12 generations (Gjedrem *et al.* 1991). To encourage behavioural resistance in farmed salmon, we must first determine their behavioural profile in tanks and sea cages, and draw on knowledge from wild salmon. Recent work has shown that when compared to an altered behavioural phenotype, salmon capable of exhibiting their normal suite of behaviours displayed approximately 6.5 times more jumping behaviours, 2–3 times more burst swimming, and were 50% less active, and consequently, acquired 26–31% fewer sea lice (Bui *et al.* 2017). As salmon have an open swim bladder, they must control their buoyancy by ‘swallowing air’ at the surface (Fänge 1953). When access to the surface is removed for a short period (submergence) and reinstated, an increase in jumping and rolling behaviours is observed (Dempster *et al.* 2008). Therefore, these behaviours could be encouraged through temporary submergence, ultimately reducing the attachment of parasites (Dempster *et al.* 2011, Bui *et al.* 2013).

The ability of salmonids to mediate their parasite load through swimming depth preference (Gjelland *et al.* 2014, Bui *et al.* 2016b) can be encouraged or enhanced in farmed salmon through minor alterations to the production method or infrastructure. For instance, by using deeper net pens, fish could be given the opportunity to avoid infective lice by swimming deeper. Salmon lice aggregate in shallow waters if there is no halocline in the water column due to their phototactic nature and host-searching behaviour (Heuch 1995, Heuch *et al.* 1995). Using the innate preferences of salmon, light or feed stimuli could be used to lure the fish away from the surface. Salmon are attracted to low levels of light and submerged lamps are already utilised in commercial farms to prevent sexual maturation and influence swimming depth (Juell and Fosseidengen 2004, Oppedal *et al.* 2007). If positioned deeper in the cage, salmon would follow the preferred coloured light towards deeper waters

during the day and night, and spend less time at the parasite-risky surface (Hevrøy *et al.* 2003, Juell *et al.* 2003, Føre *et al.* 2013, Stien *et al.* 2014, Wright *et al.* 2015; Fig. 2). Submerged feeding is a more recent development and could provide additional encouragement for salmon to swim deeper and avoid infective copepodids (Frenzl *et al.* 2014; Fig. 2). In addition, adding a freshwater layer inside the cage (e.g. by using a snorkel cage, skirt, etc.) or placing cages at sites with natural haloclines or brackish layers could allow self-motivated delousing. Utilising and encouraging salmon's natural behavioural preference for escaping parasite risky areas could promote welfare through decreased requirement for handling and treatments.

The ecology of host-parasite interactions for both terrestrial and aquatic host species can provide examples that can carry across to farmed salmon and provide the foundation for harnessing behavioural traits that can deter infection. Animals will often choose their companions based on the groups' infection status, avoiding parasitised conspecifics (Hart 1990, Barber *et al.* 2000). High host density is typically associated with greater parasite intensity and prevalence (Arneberg *et al.* 1998, Patterson and Ruckstuhl 2013). However, the direction of host-parasite relationships depend on the mode of transmission, with host density causing a dilution effect with mobile parasites compared to contagious parasites (Côté and Poulin 1995). High fish densities in aquaculture may restrict the space required to display anti-parasite behaviours. Samsing *et al.* (2014) showed that salmon swimming at densities of 7.9 kg m^{-3} acquired 8.4 times less sea lice than when stocked at 68.5 kg m^{-3} , however infection prevalence was higher in the lower-density group. Therefore, optimal management of stocking densities could facilitate a reduction in new infections and parasite transmission by diluting the availability of hosts (current legislative threshold is a density of 25 kg m^{-3}). Importantly, nominal stocking densities rarely reflect observed densities as fish are not distributed evenly throughout the cage; observed salmon group densities are typically 1.5 to 5 times higher than stocking densities as they shoal together at preferred depths (Oppedal *et al.* 2011a). Group density in salmon aquaculture is a sensitive issue, in that welfare status is closely associated with observed group density as opposed to stocking density (Adams *et al.* 2007, Oppedal *et al.* 2011b). Issues with hypoxia and physical damage can arise when observed group densities occur at high levels, which often occurs due to environmental preferences resulting in fish crowding themselves (Oppedal *et al.* 2011a, Oppedal *et al.* 2011b). Comprehensive investigation into this relationship could provide more useful guidelines for host density thresholds, which if applied across multiple farms within a

geographical region, could facilitate the control of parasites through allowing natural anti-parasite behaviours (Krkosek 2010).

Host swimming speed also plays a large role in the attachment success of planktonic copepodids (Genna *et al.* 2005, Samsing *et al.* 2015). Although the swimming speed of salmon is driven by internal preferences and current velocity (Drenner *et al.* 2012), methods could be explored that temporarily increase host swimming speeds to provide brief protection against infestation. Increased swimming speeds could be encouraged through new lighting technologies, or through ‘push cage’ systems (whereby cages are forced through the water, propelled by boats; Fredheim 2016) that act on the salmon on a scale of hours to days. This could be particularly effective if combined with data on predicted copepodid infection pressure from ocean modelling and particle simulations (Asplin *et al.* 2014, Sandvik *et al.* 2016).

Fishes can display linked behavioural traits that form a personality (or behavioural syndrome), and these profiles can differ in susceptibility and exposure to parasites (Barber and Dingemanse 2010, Poulin 2013). Consistently displaying coupled behaviours, such as boldness and aggression, are considered a personality, and these profiles have been linked to an ability to cope with stressors (Koolhaas *et al.* 1999). Coping styles in salmon influence the level of stress experienced, and individuals that consistently respond negatively to stressors also have a higher risk of infection (Fevolden *et al.* 1993, Castanheira *et al.* 2015). In addition, personality and skin pigmentation are related in salmon (Kittilsen *et al.* 2009), and both factors have been correlated to susceptibility to sea lice, whereby fish with fewer skin spots were more prone to stress and more likely to acquire parasites (Kittilsen *et al.* 2012, Øverli *et al.* 2014). As behavioural competence reduces transmission risk (Barron *et al.* 2015), coping styles or beneficial personalities could be selectively bred to enhance resistance traits (Gjedrem and Rye 2016). Similar goals have previously been achieved in cattle, where tick infections were reduced through selective breeding to enhance grooming behaviours (Norval 1992).

Teaching fish behaviours to promote welfare

Salmon could be taught to acclimatise to infrastructure or cage manipulations before they are put to sea, or soon after their transfer. This could facilitate earlier adjustment to new set-ups so that appropriate behaviours are displayed and welfare status is maintained.

Environmental enrichment such as increasing the complexity of the holding environment has been used on salmonids produced in hatcheries to augment wild stocks to improve their survival when released (Brown and Day 2002). Farmed salmon could be similarly prepared for the next stage of production through priming. For example, the implementation of snorkel cages, where the upper metres of the sea cage are inaccessible to fish except through an impermeable ‘snorkel’ tube, has great promise in preventing lice infestations (Stien *et al.* 2016). The snorkel prevents fish swimming at depths where lice copepodids are expected to be distributed, yet still allows salmon to access the surface to refill their swim bladder. If the snorkel was installed after the fish had been held in the cage for a long period, however, they avoid the structure and do not use the snorkel (*pers. obs.*), which could have negative welfare implications (Korsøen *et al.* 2009). Use of the snorkel could be improved if salmon were taught to use a snorkel-like structure while in tanks as smolts, if the snorkel was present in the cage before the fish were transferred to sea, or if they were encouraged to swim within the snorkel using feed or lights. The efficacy of the snorkel cage could be further improved if the chamber was filled with freshwater, and the fish taught to delouse themselves by swimming within the snorkel for a short period (Wright *et al.* 2016). As snorkels of only 4 m depth can reduce new infections by up to 65% (Stien *et al.* 2016), implementing this technology commercially would be significant in preventing infections, as long as the welfare of the salmon was maintained.

The use of wrasses and other cleaner fish species is already prevalent in salmon aquaculture (Powell *et al.* 2017). Importantly, salmon do not often interact with the cleaner fish and any benefits are, thus, driven by the activity of the cleaner fish (Imsland *et al.* 2014b). However, salmon in sea cages have been observed to visit the shelters or hides of the cleaner fish they are housed with (Fosseidengen, J.E. *pers. comm.*), which could represent host desire for parasite removal by cleaners (Grutter 2001). This behaviour has not been officially described in wild salmon, although anecdotal evidence was convincing enough to promote the initial use of cleaner fish in salmon aquaculture. The biological control of parasites using cleaning fish could be improved if salmon were taught to visit cleaner stations and encouraged to interact, which would promote cleaning occurrences but also deter the cleaner fish from feeding on other things in the cage (such as net biofouling or food pellets; Imsland *et al.* 2014b). Individual salmon could be primed in an early life-history stage to be attracted to cleaner fish hides (using positive stimuli such as food or dim lighting), and groups of cleaner fish-trained salmon could be introduced into cages with larger numbers of cleaner

fish-naïve salmon to transfer their experience to the larger school in the sea-phase (e.g. Couzin *et al.* 2005).

Conclusion

The current approach to dealing with parasites and disease in aquaculture is based on waiting for infection to occur, then reacting with treatments. For salmon lice, the selective pressure of the culture environment and their fast generation time has led to rapid evolution to out-manoeuvre anti-parasite treatments. Industry management approaches are often short-term, short-sighted solutions, and do not take into account ecological or behavioural factors. There needs to be a paradigm shift away from the current control-dominated approach, towards preventative methods that inhibit initial infections, or methods that improve the efficiency of reactive treatments. Both approaches should lead to better welfare outcomes for the fish. These methods need to incorporate a thorough understanding of the host-parasite system, so that predictions of parasite population dynamics can assist pre-emptive actions by farmers and provide early warning signs of potential outbreaks or resistance build-up (e.g. Murray and Peeler 2005). The current strategy of parasite control only just restrains outbreaks with a tenuous leash, but future growth of the industry is stymied. Recognising the farmed animal as a species with an evolutionary history, and utilising the behaviours or already developed responses to parasites or disease pathogens, will facilitate management of their health and welfare in production systems.

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Figure Captions

Fig. 1. Current and possible future methods of sea lice prevention and control.

Fig. 2. Examples of cage modifications for the prevention of salmon lice infestations, with particular focus on depth-related designs. Shown are a standard polar ring cage (A), a cage in an exposed site with higher current velocities (B), the snorkel cage (C), a cage with a lice skirt (D), submerged feeding (E), submerged lights (F), a submerged cage with air provided through an air dome (G), and a fully submerged cage (H).

Fig. 3. Use of sea lice medications in Norway from 2006 – 2016. Source: Norwegian Institute of Public Health, 2016 (www.fhi.no/en).

Fig. 4. The suggested framework and examples of how behaviour could be used in the toolbox to combat salmon lice in Atlantic salmon aquaculture.

CHEMICAL/ PHARMACEUTICAL	NON- CHEMICAL	MECHANICAL	CAGE STRUCTURE	<div> <div>Not used commercially or at present</div> <div>Commercially used</div> </div>
IN-FIELD (BOMB STIMULANTS)	EALLOWING		CAGE SKIRT	PREVENTION (OF NEW INFESTATION)
	SELECTIVE BREEDING		SNORKEL	
IN-FIELD (AVERMECTIN)	VACCINATION		EXPOSED AQUACULTURE	
ORGANIC PHOSPHATES		LASER SYSTEM		TREATMENT (REACTIVE REMEDIATION, POST INFESTATIONS)
CYTHROMETERINS	FRESHWATER	MICROBIAL REMOVAL		
PERMETHROINS	HEATED WATER	CLEANER FISH		
HYDROGEN PEROXIDE				

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