REVIEW

A gap analysis on modelling of sea lice infection pressure from salmonid farms. I. A structured knowledge review

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ABSTRACT: Sustainability of aquaculture, an important component of the blue economy, relies in part on ensuring assessment of environmental impact and interactions relating to sea lice dispersing from open pen salmon and trout farms. We review research underpinning the key stages in the sea lice infection process to support modelling of lice on wild salmon in relation to those on farms. The review is split into 5 stages: larval production; larval transport and survival; exposure and infestation of new hosts; development and survival of the attached stages; and impact on host populations. This modular structure allows the existing published data to be reviewed and assessed to identify data gaps in modelling sea lice impacts in a systematic way. Model parameterisation and parameter variation is discussed for each stage, providing an overview of knowledge strength and gaps. We conclude that a combination of literature review, empirical data collection and modelling studies are required on an iterative basis to ensure best practice is applied for sustainable aquaculture. The knowledge gained can then be optimised and applied at regional scales, with the most suitable modelling frameworks applied for the system, given regional limitations.

KEY WORDS: Aquaculture · Salmon louse · Environmental interactions · Dispersal modelling · Population modelling

1. INTRODUCTION

The term 'sea lice' generally refers to a family of marine copepod crustaceans, Caligidae (Revie et al. 2009). Sea lice are ecto-parasites that depend on successful attachment to hosts for full maturation and reproduction in completion of their life cycle. There are many species of such parasitic copepods of fish

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(Kabata 2003), but the sea lice that infest salmonids are of particular economic and environmental concern. The most extensively studied species is *Lepeophtheirus salmonis* (Krøyer, 1837), often referred to as 'salmon lice', which are well documented to have a major impact on aquaculture sustainability (Krkošek et al. 2007, Costello 2009, Taranger et al. 2015, Abolofia et al. 2017, Forseth et al. 2017, Myksvoll et al. 2020, Johnsen et al. 2021, Bøhn et al. 2022). An important aspect of aquaculture sustainability, in the North Atlantic region, is moderating or minimising impact on wild fish stocks; thus it is important to understand the interactions between farmed Atlantic salmon *Salmo salar* L. and wild Atlantic salmon, sea trout *Salmo trutta* L. and Arctic char *Salvelinus alpinus* L. The success of wild salmon populations, in terms of numbers and sizes of fish returning from sea, depends on the magnitude and interactions of many pressures operating in both the freshwater and marine environments (Beaugrand & Reid 2012, Todd et al. 2012, Forseth et al. 2017, Olmos et al. 2020). Wild Atlantic salmon, which are in population decline (Chaput 2012), are subject to a wide range of pressures in the marine environment including sea lice (Dadswell et al. 2022, Utne et al. 2021, 2022), the impact of which needs to be urgently assessed and managed to bolster wild stocks in many salmon-producing countries.

Sea lice occur naturally in the marine environment and are commonly recorded on wild salmonids. However, the numbers of sea lice in coastal waters can be greatly inflated by the presence of salmon aquaculture (Dempster et al. 2021). Salmon smolts can tolerate sea lice as parasites with little consequence up to threshold levels, above which serious physiological damage and direct mortality can occur (Grimnes & Jakobsen 1996, Finstad et al. 2000, Wagner et al. 2003, Fjelldal et al. 2020). Wild salmon are particularly at risk from sea lice infection as they migrate towards the high seas due to the proximity of their migration paths to salmon farms, which are mostly located in the coastal zone (Bøhn et al. 2020, Johnsen et al. 2021, Vollset et al. 2023). By contrast, wild sea trout may be exposed to sea lice from aquaculture for months in coastal populations. Sea trout (those individual brown trout that migrate to sea) can return to freshwater (where salinities are below sea lice tolerance levels), where the parasite detaches from the host. However, this delousing behaviour may disrupt anadromy (the process of migrating from freshwater to sea and back) in sea trout over time (Bøhn et al. 2022); it may also reduce growth and compromise future fitness for individual fish (Serra-

Llinares et al. 2020). Impacts of sea lice in wild Artic char populations are less investigated; however, infestation in the short periods of marine migrations for feeding and storage of energy supplies can negatively impact their osmoregulatory control, growth and survivorship (Fjelldal et al. 2019).

Sea lice are difficult to control on farms due to their resistance to chemical treatments (Aaen et al. 2015) and their planktonic larval stages, which allow dispersal by currents over many kilometres (Asplin et al. 2014, Rabe et al. 2020, Huserbråten & Johnsen 2022). This dispersion of larval stages facilitates connectivity in lice populations within and between different salmon farms, with high infestation potential of farmed and wild fish host populations (Adams et al. 2015, Samsing et al. 2017, Cantrell et al. 2021, Huserbråten & Johnsen 2022, Harrington et al. 2023). Managing and minimising sea lice connectivity between farmed fish and wild stocks requires an understanding of the sea lice life cycle. The sea lice planktonic dispersal stages are particularly important for modelling the processes by which they are transported towards new hosts (e.g. Myksvoll et al. 2018, Murray et al. 2022a).

To understand sea lice populations and improve their management, dispersal models have been specifically developed in Norway, Scotland, Canada, Ireland and the Faroe Islands (Amundrud & Murray 2009, Jackson et al. 2012, Johnsen et al. 2016, Cantrell et al. 2018, Kragesteen et al. 2018). Generally, modelling sea lice distributions requires detailed hydrodynamic models with relevant regional meteorological forcing and highly resolved tidal, temperature, salinity and freshwater inflow forcing, and coupled to a regional model that provides realistic values of currents, salinity and temperature along lateral boundaries. Such computational models are then coupled with biological models accounting for sea lice behaviour (e.g. survival, stage development and swimming), and finally forced using regional aquaculture site locations, farm stocking and management of on-fish sea lice counts. Further inference can be made by developing a population model to account for on-farm treatments and physical site conditions (Kragesteen et al. 2021). However, many parameter values within physical components of dispersal models and details of larval behaviour, ecology and host–parasite interactions remain uncertain. Much of the empirical and modelling effort driving this field has taken place in Norway, with work also carried out in other areas, such as Scotland or Canada (Murray et al. 2022a). Questions remain open as to the most appropriate methods of validation and ana-

lysis of model outputs and their integration with sparce data sources for specific applications (Murphy et al. 2024, this volume). Furthermore, work to assess the optimal approach to combining models representing different components of the life cycle is also relatively underdeveloped (Cantrell et al. 2020).

Advances in modelling techniques have led to improvements in simulating aspects such as sea lice behaviour (e.g. McEwan et al. 2015, Johnsen et al. 2016), which can be coupled with wave−wind−tide interactions in 3D flow fields (e.g. Lewis et al. 2019). Given the importance of inter- and intra-annual weather-driven variability in dispersal (e.g. Myksvoll et al. 2020, Demmer et al. 2022), growing interest in aquaculture (Bostock et al. 2010) and the increase in coastal engineering projects (e.g. offshore wind farm colocation; Gimpel et al. 2015), it is important to review how these advances can be best utilised alongside other priority areas of research. Furthermore, dispersal modelling is becoming an increasingly important tool for Scotland's aquaculture industry. Applications to reduce impact of potential interactions between sea lice originating on farms and wild smolts at a site level have been developed (Moriarty et al. 2023a). This work is ongoing, drawing from best available research, as is the case in Norway (Sandvik et al. 2020, 2021a). This means there is a need for clearly defined and empirically justified protocols for sea lice population and dispersal models as they relate to management and regulatory objectives. Additionally, to ensure best adaptive management practices, there is a need to critically assess the information available on an iterative basis. A review of the data collected to describe biological parameters important to effective modelling has previously been made (Brooker et al. 2018). Thus, our purpose of reviewing information is to update and further investigate the nature of uncertainties and sensitivity of important biological processes and the parameter values chosen to represent sea lice larval biology. The ultimate aim is to improve distribution and abundance modelling (specifically, sea lice dispersal modelling and sea lice population and larval production assessment).

2. METHOD FOR LITERATURE REVIEW

The review is framed around the key stages in the infection process as categorised in Moriarty et al. (2023a). This process can be split into 5 stages (Fig. 1): (A) production of sea lice nauplii on farmed fish; (B) transport of the sea lice copepodids in the marine environment; (C) exposure and infestation of new host fish; (D) development and survival of the attached lice stages; and (E) impact on those host populations.

Therefore, we have carried out an evaluation of the literature by systematically reviewing the steps in Fig. 1 to assess where key knowledge gaps exist, in terms of both availability of data to reduce parameter variation and the importance of this variation for effective assessment and management of impacts of sea lice on wild salmonids (see Murphy et al. 2024 for details of stakeholder opinions). The conceptual framework presented in Fig. 1 simplifies the infection process into 5 main steps to guide our review; this is not intended as an all-encompassing diagram. Various models will span multiple stages outlined above, while others, such as interactions with wild fish, will not be well represented by Fig. 1, but are discussed in Section 3. Therefore each stage (A to E) is expanded graphically, while models, their characteristics and applications within the sea lice infection process are summarised in Table 1. These schematics and table are presented to aid understanding and simulate the discussion of key uncertainties and data gaps within the text.

3. REVIEW OF CURRENT STATE OF KNOWLEDGE

Research into sea lice dispersal modelling and sea lice population assessment is framed around the key stages in the infestation process (Fig. 1). Sea lice dispersal and population models are operational and effective in some national management plans (e.g. Norway) and are currently being integrated into
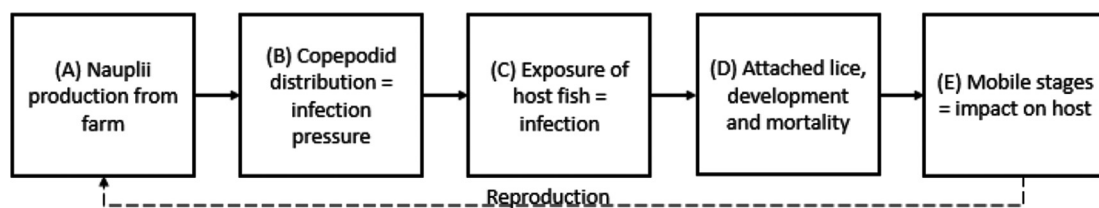

Fig. 1. Conceptual framework of infection processes from nauplii release to infestation (and beyond), adapted after Moriarty et al. (2023a) to include a specific step describing the attached lice development and mortality stage (Murray et al. 2022b), and highlighting the link from Stages E to A through reproduction (specifically fertility and fecundity)

Table 1. Types of models used in various stages of sea lice modelling, their classification and examples of their applications (updated after Groner et al. 2016a)

Model type	Model classification	Applications
Difference equations	Deterministic Discrete-time dynamics Spatially homogeneous Can include delays Often used within other models	Effects of sea lice infection and predation on salmon productivity Population growth models (e.g. Ricker 1954, Rogers et al. 2013)
Matrix models	Deterministic Balanced linear system of difference equations Can include stochastic effects	Age-structured population growth models used to describe dynamics of connected sea lice population network (e.g. Toorians & Adams 2020) Analysis of temperature-dependent sea lice demography (e.g. Groner et al. 2014)
Numerical ocean-circulation model	Deterministic Numerically solved complex dynamical system Includes hydrodynamic equations 3-dimensional transport and diffusion equations Realistic model for oceanic motion	Model for current, temperature and salinity patterns in marine environment (e.g. Asplin et al. 2020) Applied connectivity modelling using finite volume coastal ocean model (FVCOM) simulation of the spread of sea lice from salmon farms in Scotland (e.g. Rabe et al. 2020) See the National Partnership for Ocean Prediction (NPOP) for a growing list of coastal models and their applications (https://coastal.miraheze.org/)
Partial differential equations	Deterministic Continuous Time dynamics Advection-diffusion models Spatially heterogeneous	Timing and probability of arrival for sea lice dispersing between farms (e.g. Harrington et al. 2023) Stage structure global sea lice dynamics using partial differential and delay differential equations (e.g. Tian et al. 2018)
Stochastic processes	Discrete-time or continuous-time dynamics Stochastic Can include additional hierarchy Can be adapted for full system dynamic modelling	Exploring epidemiological factors affecting sea lice abundance on salmon farms (e.g. Jeong et al. 2021)
Regression models	Descriptive/correlational Statistical (GLM, GLMM, random effects, logistic regression, mixed effects linear regression) Can include spatial effects	Estimating sea lice dispersal among and within aquaculture sites (e.g. Parent et al. 2021) Identifying epidemiological factors effecting sea lice abundance on salmon farms (e.g. Revie et al. 2003) Associations between aquaculture and sea louse infections on sea trout (e.g. Middlemas et al. 2013)
Ordinary differential equations	Deterministic Continuous-time dynamics Spatially homogeneous Can include delays	Host–parasite models for sea lice–salmon dynamics, e.g. Anderson–May model (Anderson & May 1978) Sea lice model incorporating seasonal dynamics (e.g. Rittenhouse et al. 2016) Host–parasite models for sea lice–salmonid dynamics (e.g. Stien et al. 2005) and farm treatment effects on sea lice populations (e.g. Revie et al. 2005b) Parasite-mediated changes to predation (e.g. Peacock et al. 2014)
Individual-based (or agent-based) model	Can be deterministic and/or stochastic Particle tracking computer model Simulates actions and interactions of individuals within a system Includes physical advection and diffusion of particles Multiple stages of development	Lagrangian Advection and Diffusion Model (LADIM; https://github.com/bjornaa/ladim) Described in Myksvoll et al. (2018) and Sandvik et al. (2020) FISCM described in Ounsley et al. (2020) https://github.com/GeoffCowles/fiscm/tree/ounsley_et_al_2019) BioTracker described in Adams et al. (2016) UnPTRACK described in Gillibrand & Willis (2007) (https://github.com/gillibrandpa/unptrack) Predicting role of wild refugia in sea lice resistance (McEwan et al. 2015)
Survival functions and hazard functions	Statistical Descriptive Correlational	Survival analysis Impacts of sea lice on salmon survival in the NE Atlantic (Krkošek et al. 2013) Effects of salinity on sea lice survival on juvenile salmon (Connors et al. 2008) Timing and probability of arrival for sea lice dispersing between farms (e.g. Harrington et al. 2023)
Dose response analysis	Statistical Descriptive Correlational	Sea lice loads associated with reduced welfare (Ives et al. 2023) Emergence of chemotherapeutic resistance (e.g. Whyte et al. 2014)

others (e.g. Scotland). However, data for parameterisation of models is inevitably incomplete, with varying degrees of uncertainty in different components or processes that make up the model. This incompleteness leads to uncertainties in the assessment of infestation and impact on host fish, and thus in effective management. Table 1 summarises the characteristics and applications of the various models used to describe the information presented in Sections 3.1 to 3.5.

3.1. Stage A: production of sea lice larvae

Host-density dependence is an important factor in sea lice transmission dynamics (Fig. 2A; Krkošek 2010, Jansen et al. 2012, Kristoffersen et al. 2018, van Walraven et al. 2021) which reflects a tendency for more interactions when farms are closer together. When developing models of sea lice population dynamics, using basic stage-structured modes (Fig. 2B, Table 1), there is a need for experimental investigation of possible density-dependent effects on sea lice fecundity and survival (Stien et al. 2005). Increases in host density may trigger a transition from chronic to acute sea lice outbreak dynamics (Krkošek 2010, Jansen et al. 2012, Groner et al. 2016a). Thus, in an effort to provide information to manage this, sea louse abundance on farms (i.e. number of sea lice per fish, Fig. 2C) is routinely reported by companies and is highly variable among individual fish and among cages (Heuch et al. 2011). Sea lice sampling and reporting on salmon farms has improved over the past 2 decades to resolve issues around farm-level estimates that can be affected by pen-level clustering (Treasurer & Pope 2000, Revie et al. 2005a, 2007, Heuch et al. 2011). For example, in Scotland the counting regime is carried out by farm operators, and is based on at least 25 fish from a farm, taken from at least 5 pens (Scottish
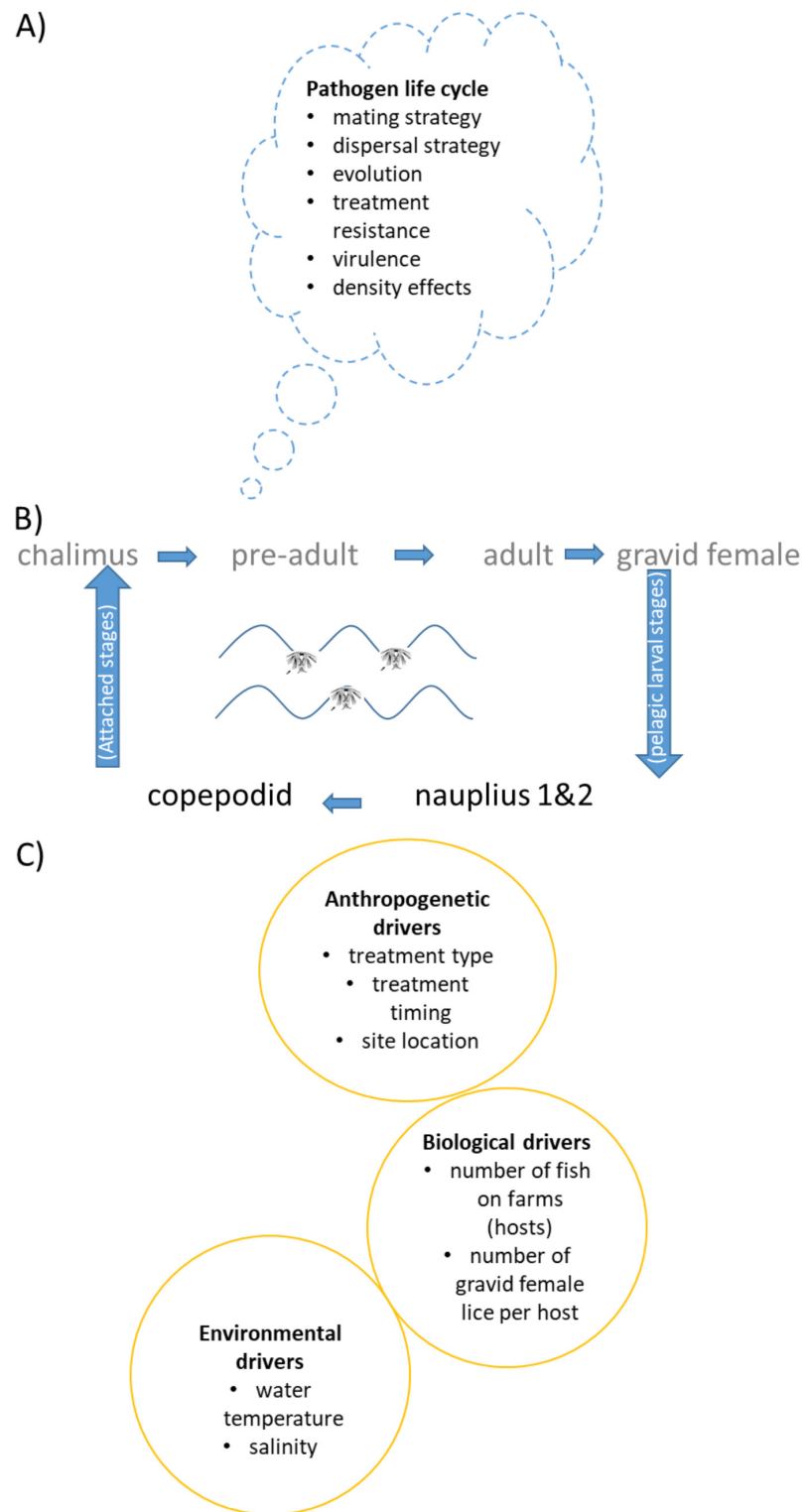

Fig. 2. Understanding nauplii production on farms requires knowledge of the sea lice life cycle. Here we highlight the key drivers impacting the pelagic larval stages as discussed in Section 3.1. (A) Summary of the parasite factors determining disease development. (B) Simplified sea lice life cycle focusing on the pelagic larval stages (black text). (C) Key drivers of nauplii production from farms

Salmon Producers' Organisation 2015). Adult females are reported to Scottish Government Fish Health Inspectors who also carry out audits. In Norway, the authorities require salmon farmers to report on key production statistics; this includes counting and reporting sea louse infestations weekly when water temperatures are above 4°C (Guarracino et al. 2018). Either 10 or 20 fish are required from every pen on a farm, in the winter/spring and summer periods, respectively (van Walraven et al. 2021). In the Faroe Islands, sea lice are counted on 20 fish in each net pen every 2 wk, by a third party (Fiskaaling), and data are reported to the authorities (Faroese Food and Veterinary Authority). For Norway and the Faroe Islands, sea lice stages are registered as adult females, large mobile stages, and small mobile stages, and adult *Caligus elongatus* are also reported. In most jurisdictions, counts are regularly audited by official inspectors, and while differences have been observed between self-reporting and auditor-based estimates, counts of adult females tend to be most accurate (Elmoslemany et al. 2013, Godwin et al. 2021), particularly for higher sea lice abundances. Sea lice tend to follow a negative binomial distribution at low sea lice prevalence on both farms (Jeong & Revie 2020) and in wild salmon populations (Murray & Simpson 2006), but tend towards binomial distribution at higher prevalence levels on farms (Heuch et al. 2011). Abundance of sea lice also varies considerably over time (McKenzie et al. 2004, Johnsen et al. 2021, Sandvik et al. 2021a), with a tendency to increase through production cycles (Revie et al. 2003, Lees et al. 2008), but with considerable short-term variation, particularly and as expected following treatment interventions (Gautam et al. 2017).

This leads to a key question, 'What is the precision of on-farm sea lice enumeration?' In this context, the fuller reporting of overall sea lice demographics (e.g. reporting of all sea lice numbers not only adult females) on salmon farms is more likely to aid in an accurate estimate of population-level infestation pressure. While the situation in Scotland has improved with weekly counts reported (as opposed to monthly mean abundances, prior to 2021), these are only for adult female lice attached to salmon. The rationale behind this approach appears sound in that this stage leads to larval populations that re-infest. Indeed, in some regions (e.g. Ireland), the requirement is to report only gravid female lice, i.e. those that have egg strings attached. However, one problem with this approach is that the more narrowly defined a metric becomes, particularly one that is also a target (as is the case in many regions where treatment 'thresholds' exist), the less useful it becomes from a data science perspective—an effect commonly referred to as 'Goodhart's Law', which appears to apply to sea lice reporting (Jeong et al. 2023). Reporting only the female adult stages, does not allow researchers to quantify the mortality and population dynamics in the chalimus, pre-adult and adult stages. This leaves gaps in our understanding of the full sea lice life cycle, with a paucity of data between the larval and adult stages including infectivity from pelagic larval concentrations, likely underestimates of the small and more easily hidden copepodid and chalimus stages, reproductive mate-guarding effectiveness in pre-adult stages and inter-stage mortality. However, quantification of the stages other than the adult female is demanding and requires a higher level of expertise, time and possibly additional equipment (e.g. microscope for counts on copepodids in gills). As underwater imaging of attached sea lice on fish and image processing using machine learning become increasingly adopted on farms, infestation estimates should improve, but it is unlikely that data on all attached life stages will be provided.

Further uncertainties arise in the precision of on-farm sea lice enumeration as the total number of lice on salmon farms depends on the number of fish on the farm (Fig. 2C). By legislation, all active farms in Norway must report the number of fish stocked monthly. Although the numbers are confidential and not published, they can be used for both research and advisory purposes. In Scotland, the numbers are also published, although fish weights and biomass have been reported historically, thus allowing numbers to be estimated (Salama et al. 2016). Two proxies for estimating fish numbers are farm-consented biomass (i.e. the maximum biomass allowed) and actual biomass on the farm, which are often publicly available data. In some ways, consented biomass is more useful as it is known for all farms prior to stocking, while actual biomass is only available retrospectively. An estimate of the number of fish can be made based on consented biomass, but it may be higher than the actual number stocked and will include farms that were not stocked or in operation during a study window. Moriarty et al. (2023a) apply the equation $F = sB/W_h$, where s is a multiplier used to account for overstocking for fish (F) that are harvested early or die during production, B is consented biomass (kg) and W_h is the average weight of the fish (kg) throughout the production cycle. In reality, the relationship between numbers of fish and biomass changes throughout the cycle as fish grow from a few hundred grams to 5 kg or more. This causes substantial uncertainties in the estimate of the num-

ber of fish, which a fixed estimate based on consented biomass reduces. However, for increased accuracy, modelling over shorter periods of time (2 to 3 mo) when the number of fish is relatively constant and estimating the average fish weight based on the stage of the production cycle may be preferable.

Precision in on-farm sea lice enumeration is important, as it leads to inferences being made within the sea lice population dynamics and dispersion in the larval stages. Sea lice larvae hatch directly into the water from egg strings attached to the gravid adult female on a fish host (Fig. 2B). Egg string lengths are correlated with the number of embryos contained within a string and vary according to many factors, including age of the louse, origin (wild or farmed host), farm treatment regimes and temperature (Brooker et al. 2018). However, the female louse can release egg strings if stressed due to crowding or delousing events and eggs will continue to develop normally after becoming detached (Eisenhauer et al. 2020), thus changing the dispersal dynamics. Occasional non-viable egg strings are produced, but these appear to be rare (Gravil 1996, Heuch et al. 2000). Longer egg strings but slower hatching rates are associated with lower temperatures (Samsing et al. 2016) and viability of eggs and embryos is affected by very low temperatures. In experimental work, larvae developing from hatched eggs were obtained for 100% at 20 and 15°C, 87 ± 3% (±SD) at 10°C, 90 ± 4% at 7°C, 85 ± 4% at 5°C, and 28 ± 4% at 3°C. All larvae successfully developed to the copepodid stage, with the exception of those eggs incubated at 3°C, where none developed to copepodids (Samsing et al. 2016). Egg viability is adversely affected by seawater with a salinity below 25 PSU. Larval hatching success has been reviewed by Brooker et al. (2018) and, in seawater with a salinity of 25 PSU and above, this can approach 100%. The production of eggs per ovigerous female louse is more variable compared with egg or embryo viability (Johnson & Albright 1991, Brooker et al. 2018). For modelling applications, rates of between 28 and 30 viable eggs per day are used, as a multiplication factor (for each adult female) and are applied as a default (e.g. Adams et al. 2021, Murray & Moriarty 2021) or may be specified as a function of temperature (e.g. Sandvik et al. 2020). However, this is an area where more detailed empirical data, following the approach by á Norði et al. (2016) or similar, and subsequent modelling could be useful, particularly if freshwater intrusions from nearby rivers occur in the modelled area. The freshwater influence will vary from system to system and region to region; in western Scotland and Ireland most rivers are relatively small and spring snow melt is less significant than in some other countries (Norway, Canada) where more snow accumulates through the winter.

3.2. Stage B: transport and survival of sea lice larvae in the marine environment

Planktonic larval sea lice dispersal depends on large-scale hydrodynamic processes (a to d in Fig. 3A,B), which can transport larval stages over many kilometres (Cantrell et al. 2019, Asplin et al. 2020, Rabe et al. 2020), and small-scale directed swimming of the sea lice larvae (e to h in Fig. 3A,B; Heuch et al. 1995, Heuch & Karlsen 1997, Crosbie et al. 2019, Szetey et al. 2021). Numerical ocean-circulation models are a key tool for synthesising the complex physical and biological drivers required for simulating the spread of sea lice from farms (Section 3.2.1, Table 1). Another important consideration in understanding dispersion is survival during the planktonic larval stages (Section 3.2.2).

3.2.1. Transport of planktonic larvae stages

The physical processes that affect sea lice dispersal vary over the coastal zone. In inshore waters, where the freshwater influence of hydrodynamics is significant, baroclinic (water density-driven) dynamics are important, together with the effects of wind stress, waves and tides (a to d in Fig. 3A,B). Further offshore, where freshwater influence is weaker, wind, wave, tidal energy and larger-scale ocean currents alone will be the predominant drivers of transport of larvae. In both nearshore and offshore environments, behavioural traits of sea lice, controlling their vertical position within a flow field (i.e. bio-physical processes), are an important contributor to dispersal, since the baroclinic circulation and wind-, wave- and tidally driven currents all have vertical profiles (e.g. Lewis et al. 2017).

Turbulence (i.e. instantaneous deviations to the mean flow) should be considered to impact dispersal through eddy viscosity, rather than viewed as a fine-scale transport feature (e.g. Rodriguez et al. 1995, Nickols et al. 2012). The bio-physical transport processes in shelf waters are described in e to h in Fig. 3A,B, which, alongside physical process interactions (e.g. wave–wind–tide interaction; a to d in Fig. 3A,B), can significantly affect transport and therefore dispersal. For example, larvae remaining close to the sea surface during the day will experi-
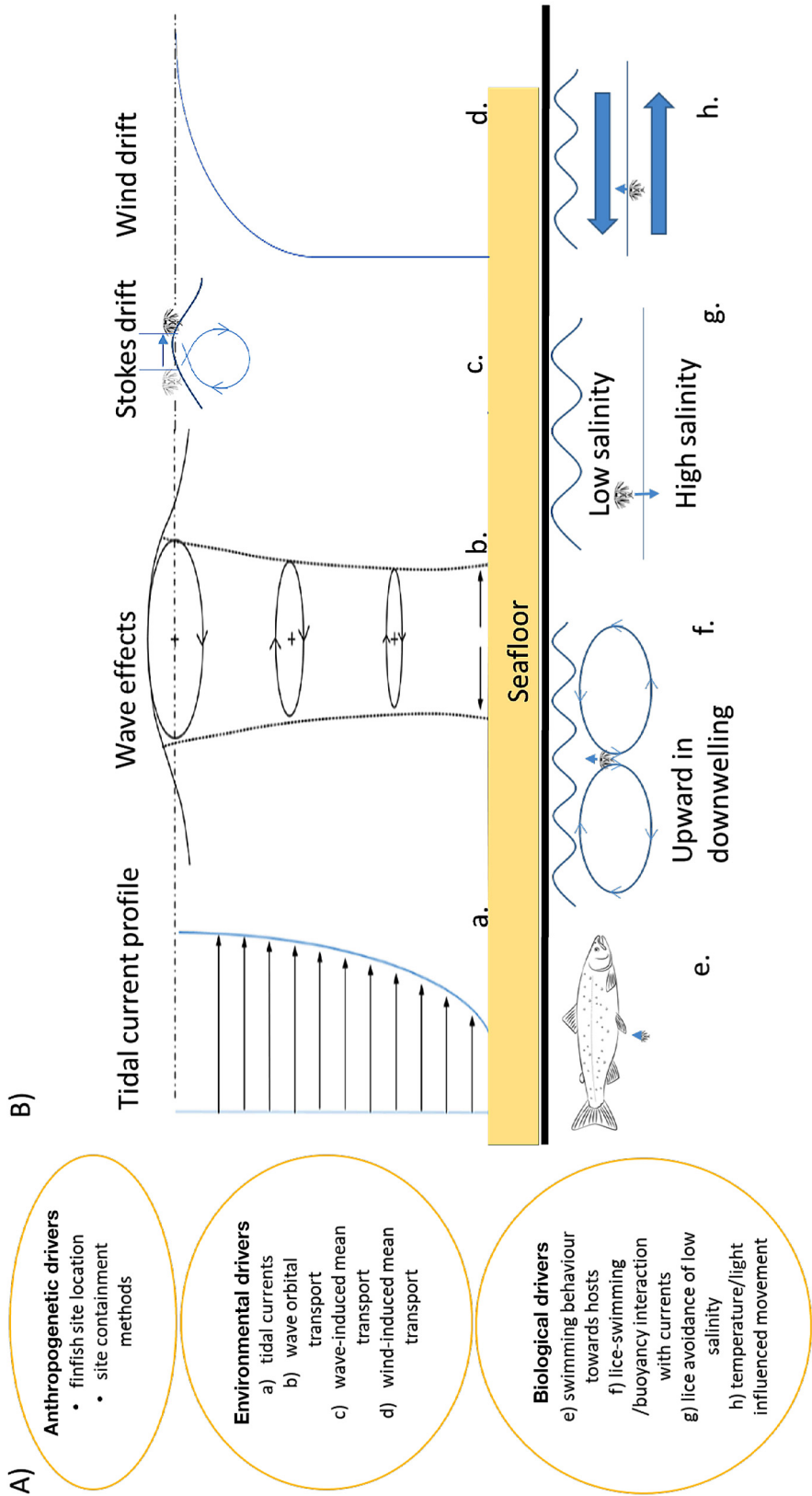
Fig. 3. (A,B) Describing the copepodid distribution requires an understanding of the bio-physical processes governing sea lice transport and dispersion in shelf water, including physical processes (a to d) and biological–physical interactions (e to h)

ence asymmetric transport from the phase-locked semilunar spring–neap tidal cycle (tidal currents that occur around a similar time of day; Macdonald et al. 2014, Roberts et al. 2014, Neill et al. 2016). Near-surface meteorologically driven currents, from wind and waves, will significantly differ from tide-only transport pathways (e.g. Lundquist et al. 2009, Demmer et al. 2022), whilst surface convergence features such as Langmuir cells (which form foam lines parallel to the wind), arise from variability in wind currents or 3D baroclinic current structures (e.g. Thorpe 2009, Robins et al. 2012, Röhrs et al. 2023), and can trap buoyant material such as phototactic (responsive to light) sea lice larvae. Therefore, resolving the variability of the current field (both spatio-temporal scales and physical processes) is a crucial step when mapping particle transport pathways along the coast. Previous work has established that the drift current at the ocean surface is generally estimated at ~3 % of the 10 m wind speed (e.g. van der Mheen et al. 2020). Wu (1983) showed that Stokes drift makes up two-thirds (~2 % of the wind speed) of the surface drift current. In contrast, more recent studies estimate lower values for surface Stokes drift, i.e. ~1 % of the wind speed (e.g. Clarke & van Gorder 2018).

In Norwegian waters, baroclinic current components in the upper 20 m are important for transporting plankton. This is due to the stratified Norwegian Coastal Current. Episodes of coastal wind will trigger mean unidirectional flow in the fjords lasting for several days, and such episodes occur at least monthly (Asplin et al. 1999, 2014, 2020). Similarly, in Scotland, the baroclinic (water density-driven) circulation arising from freshwater discharges along the coast will strongly influence larval transport and dispersal. In most Scottish lochs (not including lochs with a pronounced sill, e.g. Loch Etive; Edwards & Edelsten 1977), surface salinities are typically greater than 30 PSU, except during occasional transient freshwater discharge events, and sea lice larvae are expected to be found near the surface, at least during daylight hours. In stratified flow, vertical positioning in the water column becomes critical to transport and dispersal (Gillibrand & Willis 2007, Johnsen et al. 2014, 2016). The complex interactions between physical and biological processes imply a need for wave–wind–ocean-coupled 3D hydrodynamic modelling approaches (e.g. Lewis et al. 2014, 2019) to simulate sea lice dispersal at sea (Table 1). To date, modelling has focussed largely on inshore waters, where wave effects are perhaps less significant than the baroclinic and wind-driven circulation, and wave models have not generally been utilised.

Sea lice larval behaviour and movement allows them to control their mean position in a given current hydrodynamic field (Gravil 1996, Heuch & Karlsen 1997). Evidence for the ability of sea lice larvae to swim has been studied experimentally since the 1990s, and relevant literature (summarised in Table 2) comes from 2 sources: experimental tests in the laboratory and observations of sea lice larvae distribution in the natural environment. Nauplii and copepodids have different behaviours in response to environmental variables and cues of light exposure, salinity gradients, or the presence of a potential host. The nauplii strategy is to widely disperse in order to reach favourable habitats and conditions while copepodids specifically locate a suitable host (Crosbie et al. 2019). Few experimental studies have looked at copepodid swimming abilities and fewer have considered nauplii (Table 2). Heuch & Karlsen (1997) measured copepodid swimming velocities of 1.55 ± 0.17 mm s^{-1} (±SD) in an undisturbed system, while in response to mechanical stimulus an average burst swimming speed of about 13 mm s^{-1} for 1 to 3 s was recorded. However, Gravil (1996) found a mean swimming speed of 21.4 ± 2.4 mm s^{-1}, a burst swimming speed of 64.8 ± 25.6 mm s^{-1} and a maximum swimming speed of 102.3 mm s^{-1}. This range of copepodid swimming velocities is also reflected in the different sea lice numerical models. Gillibrand & Willis (2007) implement Heuch & Karlsen's (1997) value of 1.55 mm s^{-1} for copepodid vertical movements, while Johnsen et al. (2014) and Sandvik et al. (2020) use a lower swimming speed of 0.5 mm s^{-1}, based on the premise that this is a reasonable sustained swimming speed (Kiørboe et al. (2010).

Burst swim speed is important for infective copepodids to approach and attach to hosts (Murray & Moriarty 2021), but it is the ability to swim persistently that allows sea lice nauplii and copepodids to migrate vertically. Vertical position of sea lice in the water column is an important variable which affects their coastal dispersal by selecting horizontal currents to transport them (Gillibrand & Willis 2007, Johnsen et al. 2014, 2016, Sandvik et al. 2020), resulting in concentrations forming in areas with downwelling currents. Sea lice larvae have been found in high concentrations at considerable distances from their source, with copepodids found in higher concentrations compared to nauplii with distance from source (McKibben & Hay 2004, Penston et al. 2004, 2008). However, in other studies, the concentration of lice (mostly nauplii) declined with distance from source, as in Ardmore Bay, Ireland (Costelloe et al. 1996). In Killary Harbour, Ireland, sporadic concen-

Table 2. Summary of movements of sea lice in literature, as discussed in Section 3.2.1. Values are presented as mean (± SD) when reported by author; nd: no data reported; na: not applicable to the experiment

Parameter	Reference	Copepodid	Nauplius
Active swimming	Heuch & Karlsen (1997)	1.55 mm s^{-1} (±0.17)	nd
	Gravil (1996)	Swim with 'hop' of 21.4 mm s^{-1} (±2.4)	Swim with 'hop' of 12.5 mm s^{-1} (±1.6)
Sinking velocity	Bricknell et al. (2006)	1–1.4 mm s^{-1}	nd
	Gravil (1996)	Swim with 'hop' of 1.0 mm s^{-1} (±0.3)	Swim with 'hop' of 0.9 mm s^{-1} (±0.1)
Mechanical stimulus	Heuch & Karlsen (1997)	17–90 mm s^{-1} burst speed	na
Semiochemical	Bailey et al. (2006)	Active approach hosts	na
Surface light	Heuch et al. (2009)	To surface/sink in dark	nd
Light	Novales Flamarique et al. (2000)	Actively moved towards the light	Did not swim towards light
Salinity	Heuch (1995)	Avoid <20 PSU	nd
Salinity	Crosbie et al. (2020)	Avoid <20 PSU	Avoid <30 PSU
Thermocline	Crosbie et al. (2020)	No effect	10–12°C
Large enclosure	Heuch (1995)	Migrate to surface in light/fall in dark	Less diurnal movement
Light/dark experimental column	Szetey et al. (2021)	Remain at surface light and dark	Migrate to surface in light/fall in dark
Light	Solvang & Hagemann (2018)	1 mm s^{-1}	nd
Light	Nordtug et al. (2021)	Attracted by even weak light	nd
Field Shieldaig/Scotland 0 or 5 m	Penston et al. (2008)	More at 0 m	More at 5 m
Field Shetland/Scotland	Salama et al. (2018)	72% surface night and day	65.6% surface night, 34% day
Field Bay of Fundy/ Canada	Nelson et al. (2018)		1–6 m night, 10–17 m day

trations were found at the river mouth (Costelloe et al. 1998). Penston et al. (2008) sampled 2 depths and found more nauplii at 5 m and more copepodids at 0 m, although depth structure varied between sampling stations. Similar inference was found in the Faroe Islands, where copepodid spatial distribution was influenced by wind direction, suggesting they are near surface (á Norði et al. 2015).

Vertical position of sea lice is influenced by 4 main environmental stimuli: light, salinity, temperature and pressure. Heuch (1995) observed diel vertical migration of copepodids in a 1 m Perspex column, where they gathered at the surface after 1 h of light exposure and migrated down over 4 h of darkness. Sampling in large enclosures also revealed photo-positive behaviour of copepodids with difference in day and night distribution (Heuch et al. 1995). Sound has been suggested to impede sea lice movement, and in its absence, sea lice moved at 1 mm s^{-1} over 10 min towards a light source (Solvang & Hagemann 2018). Even very low light intensity (1.5 µmol m^{-2} s^{-1}) attracts copepodids, especially blue and white light (Nordtug et al. 2021). With salmon staying in deep

water during the day and gathering at the surface during the night, it has been suggested that the vertical migration of copepodids enables them to intercept potential hosts (Heuch et al. 1995). However, nauplii moved relatively little with light cues (Heuch et al. 1995, Novales Flamarique et al. 2000).

Conversely, more recent experimental work found that copepodids remained near the surface in light and dark, while nauplii showed diurnal migration to the surface with increasing light intensity (Szetey et al. 2021) supporting previous field studies (Nelson et al. 2018, Salama et al. 2018). Conflicting results on the swimming behaviour of the sea lice stages may be explained by an evolutionary shift due to their new habitat on farms which encourage daytime surface water feeding in the salmon (Szetey et al. 2021). A robust piece of evidence to support copepodid presence in near-surface waters is that salmon kept in relatively shallow waters (0 to 4 m depth) are more infested than fish kept deeper, with artificial light around fish farm cages further enhancing this difference (Hevrøy et al. 2003). The effectiveness of sea lice barrier (e.g. 'skirting' and 'snorkel barriers') management practices on

farms in minimising sea lice levels on hosts is further evidence that sea lice accumulate in surface waters (e.g. Geitung et al. 2019); these methods have consequently been widely developed and deployed around salmon cages with the effect of reducing the number of sea lice entering farms (Stien et al. 2016, Oppedal et al. 2017). However, sea lice may evolve and alter their depth selection behaviour in response to widespread use of such methods, and more studies are needed to see if swimming depth is a heritable trait (Coates et al. 2020).

Where salinity gradients exist in stratified water bodies, copepodids have been shown to aggregate at or just below the halocline, actively resisting further travel towards the surface (Heuch 1995, Crosbie et al. 2019). This has been corroborated further by Crosbie et al. (2019), with additional evidence showing that nauplii avoid salinity less than 30 PSU. At lower salinities, e.g. around river mouths, copepodids sink passively or swim downward to find higher salinities at which their infective ability is not reduced (Bricknell et al. 2006). Temperature changes also influence the movement of nauplii, which were found to move to warmer waters when exposed to <10°C and cooler waters at >12°C, while copepodid behaviour was not affected by temperature (Crosbie et al. 2020). Field data are sparse, but in the Faroe Islands, samples of nauplii indicated that nauplii preferred warmer waters: they were more present in the warmer deeper water during winter, while during summer, they stayed in the surface waters, which are the warmest (á Norði et al. 2015). This temperature preference is now implemented in a few sea lice models (Samsing et al. 2016, Crosbie et al. 2020). Additionally, pressure stimuli of a near-field acceleration (as produced by a fish swimming nearby) have been shown to produce a swimming burst behaviour in copepodids (Heuch & Karlsen 1997), allowing infective sea lice to locate and approach a host. Exposing copepodids to increased pressure at lower depth triggers an upward swimming response to reach surface waters (Coates et al. 2020).

Sea lice modelling can be a powerful tool to understand the importance of each swimming behaviour in describing pelagic sea lice distribution. To achieve this purpose, models need to provide a close representation of the observations while being as simple as possible to give a clear vision of the underlying processes at play and their interactions. Over the last few years, sea lice modelling has gradually increased the complexity of the biological behaviour they implement. Earlier models chose to keep sea lice within the surface layer (Murray & Gillibrand 2006, Amund-

rud & Murray 2009, Adams et al. 2012, Salama et al. 2018), motivated by observations showing that fish infections by sea lice occur mostly at depths of 0 to 4 m (Hevrøy et al. 2003), and the assumption that sea lice dispersal is mainly achieved by circulation of surface water since their swimming capacity is slow compared to the horizontal advection of currents (Murray & Gillibrand 2006, Amundrud & Murray 2009). However, studies implementing sea lice behaviour of diel vertical migration and low salinity (<30 PSU) avoidance (Crosbie et al. 2019) gave new insights into how they can heavily impact dispersion patterns. In Hardangerfjord, Norway, simulations showed a shorter dispersion distance for sea lice fixed at the surface compared to those that applied diel vertical migration (Johnsen et al. 2014). Vertical migration of sea lice can also influence their retention in a coastal inlet via selective tidal stream transport (Tully & Nolan 2002) and therefore increase the predicted surface density (Gillibrand & Willis 2007). However, Stucchi et al. (2011) observed no major difference in the spatial pattern of dispersion between simulations with sea lice fixed at 0 to 4 m depth and those without diel vertical migration, only a lower concentration for passively transported sea lice compared to a scenario including diel vertical migration. Similarly, Amundrud & Murray (2009) found that as long as sea lice experience surface circulation, introducing a diel vertical migration behaviour produced a horizontal dispersion pattern that did not differ much to the one resulting from particles transported by surface motion. However, since fjordic systems in Norway and Scotland often experience stratified water and wind-driven circulation with strong current shear of surface water (Murray & Gillibrand 2006, Inall & Gillibrand 2010, Asplin et al. 2014, Dalsøren et al. 2020), vertical migration behaviour still should be considered for horizontal dispersion of sea lice. Finally, sea lice larval transport pathways are sensitive to other parameters such as vertical swimming velocity (Johnsen et al. 2016), vertical turbulence (Johnsen et al. 2016) and new mechanisms of salinity avoidance (Sandvik et al. 2020), and their implementation in sea lice modelling is currently being explored.

In summary, there is good evidence that larval sea lice avoid low salinity water, particularly nauplii, although copepodids may migrate into slightly lower salinity water during host searching behaviour. Whilst temperature gradients do not affect depth selection by copepodids, nauplii do prefer water between 10 and 12°C. There is robust evidence that sea lice larvae are found predominantly in the surface

layers, and physical barrier management measures can be highly effective at sites without a brackish layer or strong vertical mixing (Barrett et al. 2020). Selection of near-surface waters means sea lice are exposed to wind-driven currents that aid their transport, whereas sea lice remaining below a halocline to avoid low salinity water may move in the reverse direction to that predicted from surface currents, owing to counter currents in nearshore shallow environments. Therefore, it is important to understand the specific swimming behaviour in space and time of the larval stages in order to better parameterise models.

3.2.2. Survival of the planktonic stages

Transmission of larval sea lice depends not only on transport to suitable habitats, but also on survival for long enough periods to actively infect fish hosts. Both depend on predation, starvation, mortality and senescence between the 2 nauplii stages and the infective copepodid stage. Sea lice larvae are likely to be consumed by planktonic grazers, such as larger zooplankton, jellyfish, benthic organisms (scallops/ mussels) or some species of fish (Molloy et al. 2011, Webb et al. 2013, Brooker et al. 2018). Seasonal and environmental variability in high-latitude spring bloom systems leads to a difference in survival of plankton (Eiane & Ohman 2004). Variations in regional distributions and seasonality in the populations of such grazers, due to events such as spring blooms, is likely to have a significant impact on sea lice larval predation rates. Sea lice larvae do not feed until they attach to a host. The larval survival period and infectivity depend on lipid energy reserves (Dalvin et al. 2011, Skern-Mauritzen et al. 2020, Taccardi et al. 2021). In addition, metabolic rate is dependent on ambient temperature, which will affect how rapidly these reserves are exhausted (Hamre et al. 2013, Samsing et al. 2016, Hamre et al. 2019, Taccardi et al. 2021). Since sea lice numbers and viability decline over time, generally specified as a 1% mortality per hour or 17% per day (Murray et al. 2022a), relatively few larval sea lice reach the starvation limit. Thus infection pressure is not particularly sensitive to starvation time (Murray & Moriarty 2021, Sandvik et al. 2021b). Starvation is qualitatively different to mortality, since the latter represents an exponential decay that can continue indefinitely, while starvation occurs at some point after lipid reserves are exhausted. Starvation results in a finite limit on transmission time and hence transmission distance. Mortality rate

and senescence can be combined into a single decay process, and many models use 1% h^{-1} (Amundrud & Murray 2009, Salama et al. 2018) or 17% d^{-1} for all free-living stages in Norwegian sea lice dispersion modelling (Sandvik et al. 2016, Myksvoll et al. 2018, Sandvik et al. 2021b). These values are widely used in sea lice dispersal models with validation of predicted distributions against field observations (Table 1; Salama et al. 2018, Sandvik et al. 2020). However, this simple parameter, while functional, can be broken down into different processes. In particular, mortality rate becomes much higher as salinity drops below 29 PSU, or where temperature drops below 3°C or rises above 24°C (Johnson & Albright 1991, Bricknell et al. 2006, Brooker et al. 2018, Dalvin et al. 2020). Consequently, there is potential for more sophisticated modelling of the mortality parameters, i.e. increased mortality in low salinity with low salinity avoidance behaviours (Crosbie et al. 2019, Sandvik et al. 2020), and incorporation of the effects of temperature (Jeong et al. 2021). Although there is considerable scope to make the modelling of sea lice survival, senescence and predation pressure more realistic, and possibly determine seasonality, the empirically derived values already being used in Scotland (1% h^{-1}, ~21% d^{-1}) and Norway (17% d^{-1}) currently provide good fits to observations under a variety of circumstances. Sea lice are highly adaptable; for example, experimental work assessing sea lice tolerance of projected future ocean acidification scenarios indicate that they have mechanisms to compensate for increased concentration of pCO$_2$ (Thompson et al. 2019). This indicates that more experimental work and modelling are required to unpick fundamental ecological relationships as the climate changes (Coates 2023).

3.3. Stage C: exposure and infection of new hosts

Thus far we have focused on the interaction of pelagic sea lice stages with the environment. However, development of parasitic infection depends on finding and attaching to a suitable host salmonid (Fig. 4). Under experimental conditions, copepodids display a variety of behaviours that may aid in positioning them within the marine environment at a location where the probability of encountering a fish host is increased (Heuch 1995, Heuch et al. 1995). From a management perspective, understanding the rate of sea lice infection on wild smolts is important. However, laboratory-based experiments do not give a rate of infection in the en-
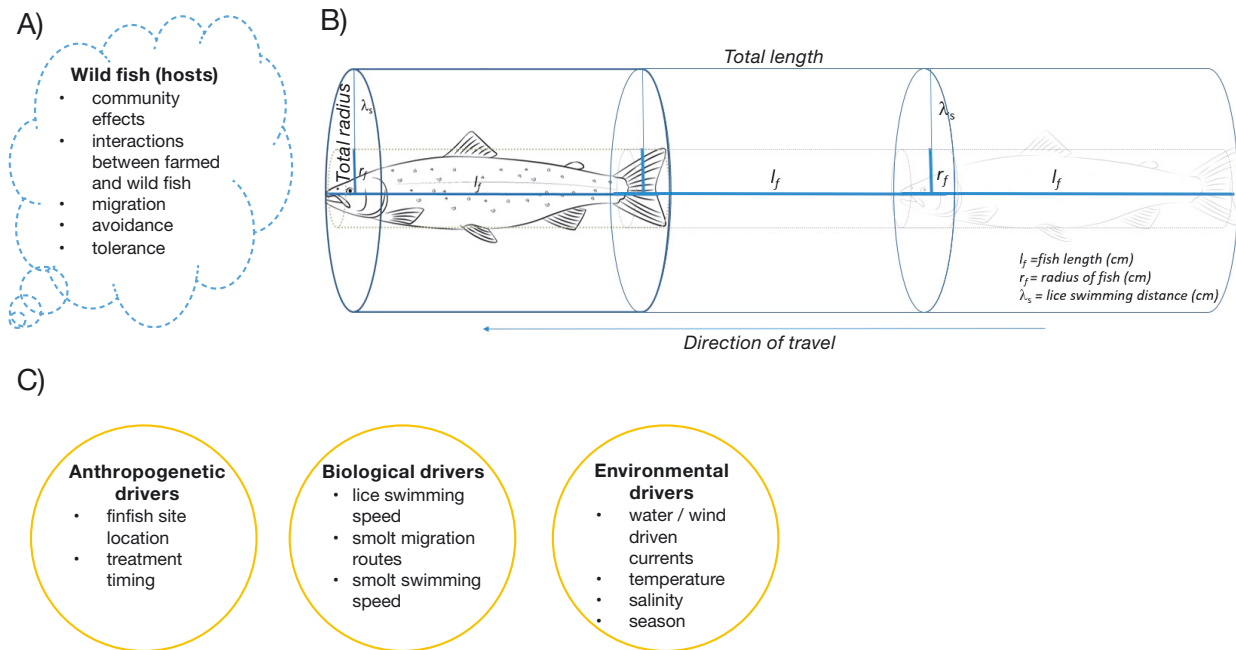
Fig. 4. Exposure of host fish to copepodids can lead to infection. (A) Summary of wild fish factors determining disease development. (B) Conceptualisation of the effective surface area for host encounters between salmonids and sea lice copepodids for a fish moving at 3 body lengths per second; water volume and fish are treated as cylinders for simplicity (Murray & Moriarty 2021). (C) Key drivers of sea lice infection of wild fish, which is dependent on lice concentrations in the environment and the movement of fish

vironment. Infection rates can be derived by comparing modelled larval concentrations in the vicinity of sentinel cages to numbers of sea lice on sentinel caged fish (Sandvik et al. 2020), and from first principles of interaction of copepodids and smolt movements in wild fish populations (Murray & Moriarty 2021). Modelling from sentinel cage data from Norway estimates that critical threshold concentrations of around 2 copepodids m^{-2} (Sandvik et al. 2020) could result in damaging levels of infection (equating to 10 lice per fish) within the exposure time to copepodids of sentinel caged fish. While this threshold concentration is consistent with contact deduced from first principles (Murray & Moriarty 2021), it is very sensitive to sea lice swimming behaviour, velocity and duration (Fig. 4B), and the link with modelled pelagic sea lice density will also be dependent on the specific model implementation.

Attachment is a critical component of infection which is sensitive to salinity (Bricknell et al. 2006) and temperature (Dalvin et al. 2020), as there is a reduced sea lice infestation success and post-attachment survival rate at lower temperatures (Ugelvik et al. 2022). Furthermore, both contact rates and exposure times are sensitive to salmon swimming be-

haviour. This has been investigated in the vertical distribution and swimming speed of smolts and shown to impact the encounter rate with sea lice, ultimately affecting infection success (Samsing et al. 2015). Faster swimming smolts are exposed for less time to the elevated larval numbers in fjords and coastal waters (Kristoffersen et al. 2018, Johnsen et al. 2021). Smolt movements can be assessed using modelling and field tracking data (Ounsley et al. 2020). A full review of salmon swimming behaviour is outside the scope of this paper. However, it is important to consider migration paths and timing in the arrival of wild salmonids as these affect sea lice infection rates. There is currently considerable uncertainty and more data are required to constrain models. Data may come from various sources: challenge trials to directly measure rates of attachment; more detailed understanding of salmonid smolt swimming behaviour (Jensen et al. 2022); and linking of simulated sea lice concentrations to infestation rates measured in sentinel cages or on wild-caught salmonids (Johnsen et al. 2021).

The migration of post-smolts has been linked to environmental cues, from simulating migration routes based on behaviour and hydrodynamic data (e.g. Mork et al. 2012, Ounsley et al. 2020, Vollset et al.

2021) and documented regional differences in migratory behaviour in relation to environmental cues (Jensen et al. 2022), while others suggest a preferred migration route (Newton et al. 2021). Advancements in acoustic telemetry have led to clearer interpretations of salmonid migration patterns in Norway (e.g. Thorstad et al. 2012, 2015, Halttunen et al. 2018) and Scotland (e.g. Middlemas et al. 2017). Acoustic telemetry studies on salmon smolts in Norway indicate that fairly direct routes are taken through fjords towards the ocean, but fjords vary in length and smolts will spend between a few days to weeks in the fjords before leaving the coast (Thorstad et al. 2012, Halttunen et al. 2018, Bjerck et al. 2021, Jensen et al. 2022). Salmon post-smolts have been found to migrate in both nearshore and pelagic habitats (Thorstad et al. 2007, Davidsen et al. 2009), primarily swimming in the upper 3 m of the water column (Davidsen et al. 2009, Plantalech Manel-la et al. 2009).

Acoustic tracking of sea trout in Loch Torridon, Scotland (Middlemas et al. 2013), showed that behaviour and space use at sea varied substantially among fish from different rivers and within populations from each river. Similar observations have been made in sub-Arctic Norway (Strøm et al. 2021). In addition, sea lice infections affect the behaviour of sea trout, as they remain closer to fresh or brackish waters in seasons with high infection pressure (Halttunen et al. 2018) and when infected (Serra-Llinares et al. 2020). These studies emphasise the need for good locally relevant data, particularly in the case of sea trout. It is not yet clear whether more generic movement models will suffice for salmon migrations, many of which are believed to move rapidly through the inner coastal zone. However, the variation in movement rates among individuals in both salmon and sea trout populations is very important for modelling risks to sea lice infestation and implications for population-level impacts.

More salmon and sea trout movement data are required in Scotland at a range of spatial scales to better inform accurate modelling efforts for sea lice management. Very localised fish behaviour determine likelihood of infestation at any given density of sea lice (Murray & Moriarty 2021), since this depends on swimming speed. Movements at the larger scale of traversing a sea loch or fjord, for example, determine the total time that salmon remain in high sea lice-risk areas. Migrations across bigger distances, for example moving through the Minch on the west coast of Scotland, will influence the time fish spend within the zone where sea lice are likely to be concentrated due to salmon farms.

3.4. Stage D: development and survival of attached lice stages

Reducing the abundance of sea lice in the marine environment in areas of aquaculture production requires effective sea lice control, and integrated sea lice management is a strategy adopted by many salmon companies (Treasurer & Bravo 2022). Effective sea lice control on farms through medicinal and non-medicinal treatments, biological controls and preventative methods limits the opportunities for infestations on wild fish (Treasurer & Bravo 2022). The efficacy of subjecting wild salmon smolts to parasite treatment in terms of the marine survival of returning adults has reduced over time (Vollset et al. 2023), due to sea lice resistance to medicinal control methods (Aaen et al. 2015). Understanding the sea lice life cycle (Fig. 5B) is an important component of control, as interrupting it before eggs hatch and are released into the environment is preferable for wild fish populations (Jeong et al. 2021). The settled or attached stages of sea lice refer to the chalimus, pre-adults, adult males and females, and gravid (egg-bearing) females (Fig. 5B; Revie et al. 2005b, Hamre et al. 2013, 2019, Adams et al. 2015, Rittenhouse et al. 2016, Toorians & Adams 2020). Development, maturation and survival for these sea lice stages have been described by both Hamre et al. (2019) and Stien et al. (2005). The infection pressure and attachment rate of copepodids and their development and survival to attached chalimus are key biological processes that are still data-deficient (Pike & Wadsworth 1999, Brooks 2005, Genna et al. 2005).

Sea lice population models describe the abundance and population structure of attached stages over time (Fig. 5B; Buffoni & Pasquali 2007). The approaches to building a useful population model depend on the physical and biological parameters that drive the growth and decline of the sea lice population (Fig. 5C). For sea lice, population dynamics are generally stage structured (see Table 1, Aldrin et al. 2019), leading modellers to use either matrix ordinary differential equations (Frazer et al. 2012, Groner et al. 2014, 2016b, Toorians & Adams 2020) or delay-differential-based equations (Revie et al. 2005b, Gettinby et al. 2011, Adams et al. 2015, Rittenhouse et al. 2016, Tian et al. 2018, Kragesteen et al. 2019).

3.5. Stage E: impact on host populations

Sea lice inherently cause damage to the fish they infest by feeding off the mucus, compromising the
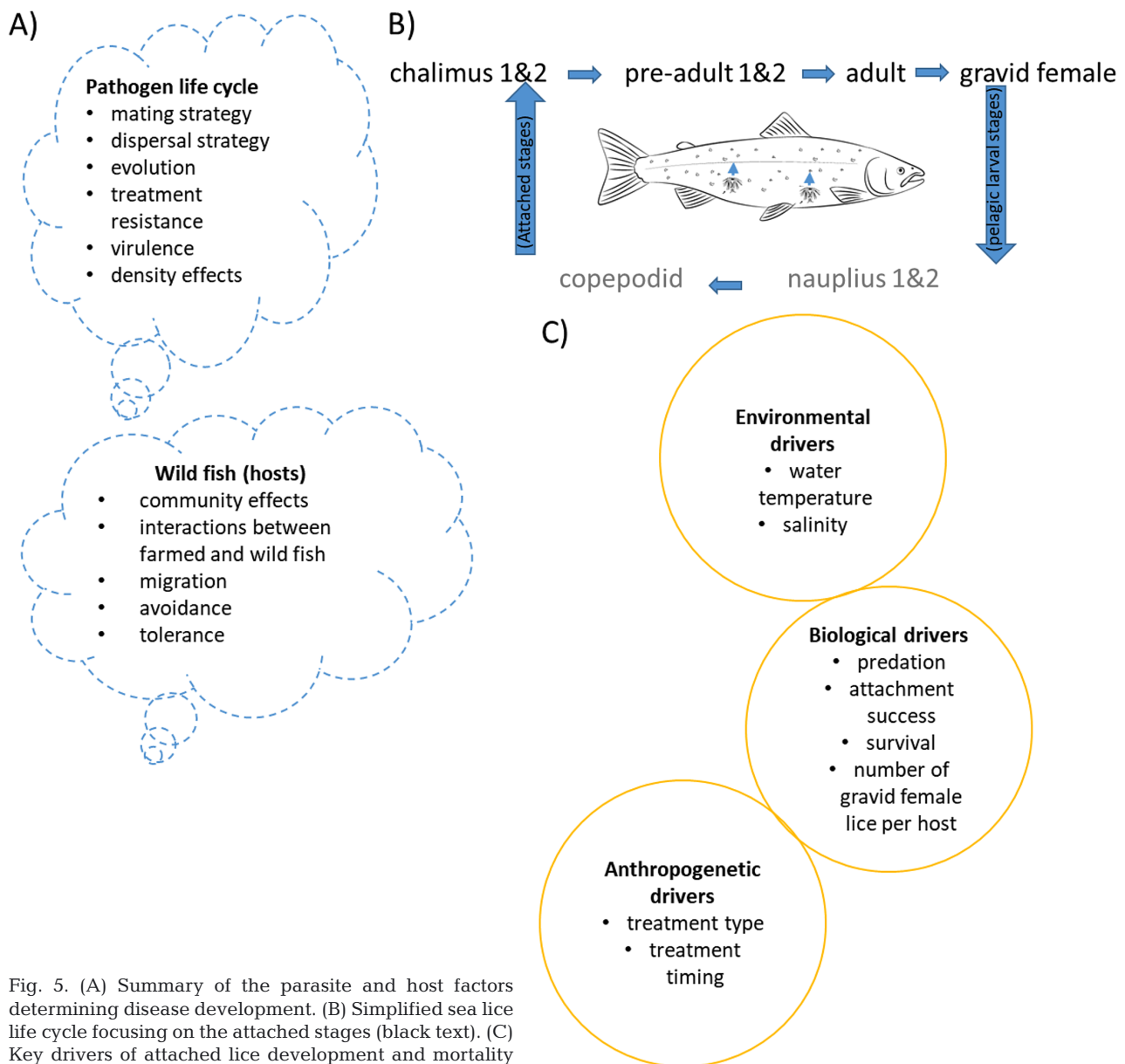
Fig. 5. (A) Summary of the parasite and host factors determining disease development. (B) Simplified sea lice life cycle focusing on the attached stages (black text). (C) Key drivers of attached lice development and mortality

fishes first line of defence against infection, and introducing secondary infections, and at severe levels causing skin and blood loss (Fig. 6). The damage can range from superficial, such as that seen from small numbers of lice, which is generally limited to localised surface wounds (e.g Long et al. 2019), to lethal, where large numbers of sea lice can lead to mortality of the host (Fig. 6; e.g. Grimnes & Jakobsen 1996). Host response to infection is due to a combination of many factors, including the life stage of both the host fish and sea lice, and the environmental conditions, particularly temperature and salinity (Fast & Braden 2022 and references herein). Understanding specific thresholds of impact on hosts is a critical

component of management and modelling frameworks (e.g. Murray & Moriarty 2021). Risk of mortality at the individual level translates to proportional mortality at the population level. For instance, the Norwegian traffic light system uses thresholds based on levels of expected mortality where 20%, 50%, and 100% levels of mortality are proposed to occur at sea lice concentrations of 0.1–0.2, 0.2–0.3 and >0.3 g^{-1} wet weight of host, respectively (Taranger et al. 2012, 2015). Researchers are now suggesting the use of a 'welfare threshold' in place of a purely mortality-based system (Ives et al. 2023). This threshold, set at 0.08–0.1 g^{-1}, is based on experiments measuring physiological and performance-related responses
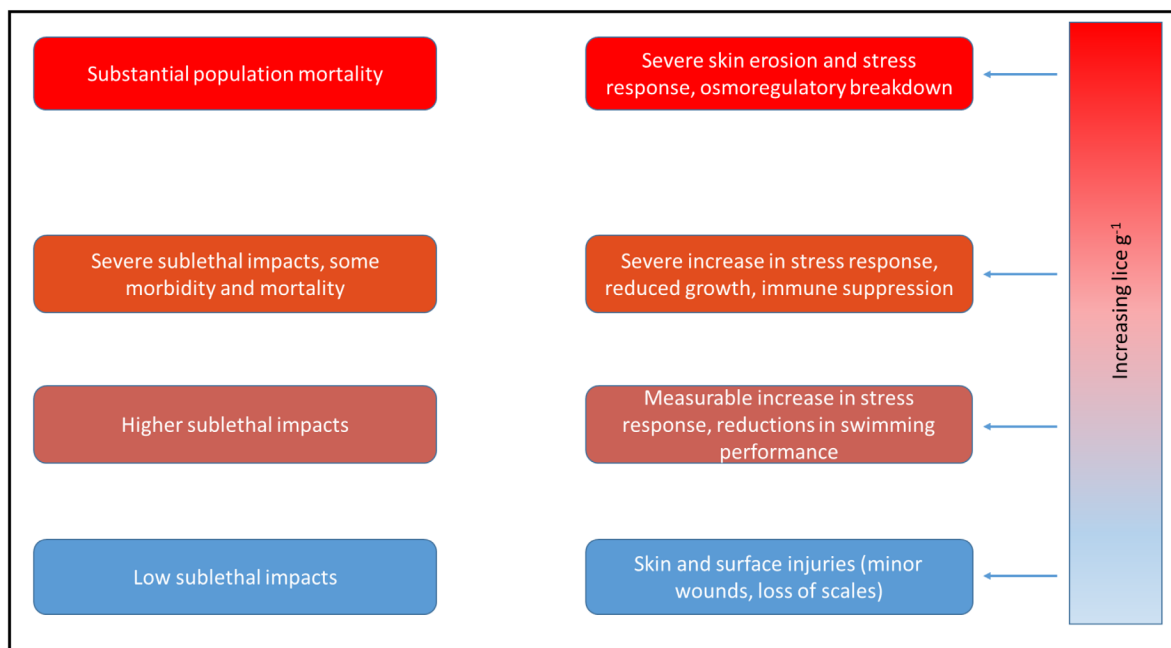
Fig. 6. The severity of the impact of sea lice infestation on juvenile hosts increases with the number of lice per gram (after Ives et al. 2023)

of salmon, decreases in cardiac output and haematocrit (the proportion of red cells in blood), and a 22% reduction in swimming performance (Wagner et al. 2004, 2008). These reductions in performance are likely to lead to further risk of sea lice infestation due to longer periods spent in infested areas and greater risk of successful attachment by copepodids (Moriarty et al. 2023a). As sea lice concentrations rise beyond this level, further physiological impacts are measured with a specific population mortality occurrence probability of 50% calculated at 0.24 g^{-1} (Ives et al. 2023). The lice g^{-1} values from Ives et al. (2023) broadly support the lower 2 thresholds used in the Norwegian traffic light system, albeit for different biological reasons (Eliasen et al. 2021).

Pre-adult and adult lice are most likely to impact host welfare (Ives et al. 2023). The average value for survival to these stages (pre-adult and adult stages) was found to be 65% by Tucker et al. (2002), meaning that 35% die before they have a significant impact on their host, although variability of sea lice survival is high in both laboratory and field work. While Tucker et al. (2002) have considerable data on mortality of the different stages, the experiment at the time considered 4 chalimi stages, rather than the now described 2 chalimi stages (Hamre et al. 2013). The effect of having a greater number of stages is resolved by compounding total mortality over the development to pre-adult. However, additional re-

search may help to better differentiate the mortality levels at each stage. A further factor is that, whilst the sea lice mature from copepodid to chalimus to preadult, the host is also growing (Moriarty et al. 2023a). This effectively reduces the ratio of sea lice to grams of host and, therefore, reduces the number as a proportion of fish size. However, growth of host fish is negatively impacted by sea lice infections (Fjelldal et al. 2019, 2020).

The overall impacts of sea lice on wild fish have been investigated using randomised control trials, measuring return rate of salmon from smolt releases treated with sea lice parasiticides compared to untreated smolt releases. A meta-analysis of Norwegian studies by Vollset et al. (2016) found an overall risk ratio of 1.18 (CI 1.07–1.30); an 18% reduction in return rate of treated fish in comparison with untreated control fish. This is corroborated by studies in Ireland (Jackson et al. 2013, Krkošek et al. 2013), Scotland (Penston et al. 2004), and other studies in Norway (Hvidsten et al. 2007, Skilbrei et al. 2013), which outline that sea lice infestation can have a significant impact on returning smolt numbers, accounting for between 34% (Jackson et al. 2013, Krkošek et al. 2014) and 39% (Krkošek et al. 2013) reduction in returning smolts. Vollset et al. (2023) have shown that wild salmon returns to the Vosso River (Norway) are negatively correlated with sea lice levels during their out-migration year. Similar correlative studies

are lacking in other regions, which limits the ability to detect the impact of sea lice management decisions on wild fish stocks, which is a major source of uncertainty.

4. DISCUSSION

The body of literature summarised in the review of the current state of knowledge serves as a guide to how advanced our understanding of the key stages in the sea lice infection process already is. Regular reviews of the state of our science are important for successful adaptive management of natural resources, helping to uncover areas of uncertainty (Lindenmayer & Likens 2009, Williams & Brown 2014, 2018). This provides ways to reduce or remove uncertainties in modelling through management and institutional learning as evidenced in Murphy et al. (2024) or through improved monitoring (see Pert et al. 2022), which in turn helps develop and improve our models.

Much of the modelling of sea lice production, transmission and impact is already well developed and models are widely used in many salmon-producing countries to advise on management. Models have been developed for Scotland (Salama et al. 2018, Gillibrand et al. 2023, Moriarty et al. 2023b), the Faroe Islands (Kragesteen et al. 2018), Canada (Stucchi et al. 2011), and primarily for Norway (Johnsen et al. 2016, Myksvoll et al. 2018, Sandvik et al. 2020), where they are firmly integrated into finfish aquaculture management through controls on permitted sea lice densities (Taranger et al. 2015, Johnsen et al. 2021, Sandvik et al. 2021a). In Norway, an operational coastal current model, the NorKyst800 based on the ROMS model (Asplin et al. 2020), is run daily in a collaboration between the Institute of Marine Research and the Norwegian Meteorological Institute, producing results covering the whole coast of Norway in a 120 h forecast. These results are used to estimate the weekly copepodid abundance and distribution (www.lakselus.no) and provide background information to the Norwegian traffic light system. Routinely, the results are validated against current observations showing reasonable performance of the model (e.g. Dalsøren et al. 2020). Recent developments to improve the results include data assimilation capability and routines for improving resolution by a 2-way nesting of the numerical grid. The philosophy behind the NorKyst800 model is to be open source and readily downloadable (https://thredds.met.no), thereby improving the development of the model and strengthening the credibility of the results.

Tools that allow parasitic traceability are not discussed within our review; however, genetic studies have attempted to characterise the population structure of sea lice in the North Atlantic with limited success, due to high levels of gene flow (Todd et al. 2004, Tjensvoll et al. 2006, Nolan & Powell 2009, Glover et al. 2011). Recently, Jacobs et al. (2018) used more sophisticated genetic fingerprinting and machine learning to distinguish between samples taken from sites in Ireland, Scotland and Norway. Data generated using such techniques have the potential to provide validation for hydrodynamic/dispersal modelling predictions on regional scales (such as the west coast of Scotland (Corrochano-Fraile et al. in press).

The usefulness of any model depends, in part, on the accuracy and reliability of the output. However, as models are normally encumbered by inadequate comprehension of the process, and precise environmental observations are rarely available, the certainty of model output values are difficult or impossible to determine (Skogen et al. 2021). This means there is an inter-dependence between data accuracy, process understanding and uncertainties in modelling output. The focus of this review was to investigate the nature of uncertainties and sensitivities in sea lice biological processes, and the parameter values chosen to simulate distributions and abundance (specifically, sea lice dispersal modelling and sea lice population assessment). Figs. 2–6 and Table 1 summarise the modelling information outlined in the review, highlighting the strength in our current knowledge base.

Improved parameter estimates will increase the accuracy of model outputs for particle tracking of larval stages and population models describing attached stages of sea lice. The combination of particle tracking models and population models has been noted elsewhere as a research area of interest (Adams et al. 2015, Kragesteen et al. 2021). A combined model with improved parameter estimates would offer a new tool in describing the dynamics of sea lice on farm sites, give insight into critical thresholds of connectivity (Toorians & Adams 2020), and further inform the most effective timing of treatments to reduce abundance on farms, improve fish welfare and reduce costs (Groner et al. 2014, Rittenhouse et al. 2016, Kragesteen et al. 2021). A combined modelling approach would also further illustrate key points in the marine salmonid production cycle that could be disrupted to reduce transmission and abundance of sea lice on both farmed and wild salmonids (Peacock et al. 2016, 2020, Toorians & Adams 2020). Combined modelling would allow further refinement

or calibration of model parameters. Integrating this into a forecasting system would be a useful advance for the aquaculture industry.

The reviewed literature highlights that work that seeks to test the underlying biological, ecological and physical processes, make comparisons between different models or develop 'benchmark' exercises for specific tools is required to increase confidence in model usage. Water movements in the coastal zone occupied by aquaculture have a wide range of drivers, and there are still likely to be small-scale features that are poorly resolved by present regional models (Morro et al. 2022). Careful implementation of model packages therefore remains important. Coherent methods for studying sensitivity of model outputs to design choices, and the variability between simulation packages, would permit better understanding of the scope within which model predictions can be considered fit-for-purpose.

5. CLOSING REMARKS

The types of model and associated data gathering required for their calibration and validation identified here are diverse (e.g. hydrodynamic, sea lice dispersal, sea lice population, salmon population, salmon smolt migration). They are also variable in the amount of research that is required to achieve outputs to plug the gaps. Prioritisation of research gaps in Scotland as ranked by stakeholders in various sectors pertaining to modelling and data are investigated further in our companion paper by Murphy et al. (2024). Monitoring options were recently reviewed by Pert et al. (2022). The aquaculture sector is vitally important for global food security (FAO 2020); active research in terms of modelling and empirical data collection is therefore critical to strengthen our knowledge base, identify emerging issues and mitigate against them for sustainable industry expansion.

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