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REVIEWS IN Aquaculture

REVIEW

A decision support tool for parasite management in fish aquaculture

Kate Suzanne Hutson[1,2] | Allan James Mooney[3] | Ingo Ernst[4] | Alexander Karlis Brazenor[2,5] | Max Scheel[1] | Javier Atalah[1]

[1]Cawthron Institute, Nelson, New Zealand

[2]Marine Parasitology Laboratory, Centre for Tropical Sustainable Fisheries and Aquaculture, College of Science and Engineering, James Cook University, Townsville, Queensland, Australia

[3]Independent, Canberra, ACT, Australia

[4]Biosecurity Animal Division, Department of Agriculture, Water and the Environment, Aquatic Pest and Health Policy, Canberra, ACT, Australia

[5]Biosecurity Animal Division, Department of Agriculture, Water and the Environment, Marine and Aquatic Biosecurity, Canberra, ACT, Australia

Correspondence
Kate Suzanne Hutson, Cawthron Institute, 98 Halifax Street East, Nelson 7010, New Zealand.
Email: kate.hutson@cawthron.org.nz

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Abstract

A decision support tool was developed to aid management of problematic parasites in marine fish aquaculture. The tool provides biologically relevant treatment intervals to interrupt the life cycle of ectoparasitic flatworms that occur in global kingfish and amberjack (*Seriola* spp.) aquaculture. Temperature-dependent life cycle parameters for the 'skin flukes', *Benedenia seriolae* and *Neobenedenia girellae*, and the 'gill fluke', *Zeuxapta seriolae*, were derived from published data and modelled using non-linear regressions. Increasing temperatures shortened the duration of most life cycle parameters of all parasites. Salinity had no effect on the timing of life cycle parameters but limited hatching success in hypo- and hypersaline conditions. The tool, named BeNeZe after the first two letters of each parasite genera, enables rapid determination of treatment intervals for two consecutive medicinal immersion or 'bathing' treatments—the first to kill adult flatworms attached to fish and the second to prevent maturity of new parasite recruits. As temperature increases, the interval between treatments and the 'window' within which the second treatment should be applied is reduced. The tool can be used for multi-species infections. The inclusion of parasite taxonomy, biology and behaviour as part of an integrated management strategy is reviewed. Available through an open access app, BeNeZe is intended to be applied in conjunction with farm biosecurity, surveillance, management measures and recognition of independent management units. BeNeZe can be used to reduce infection burdens, improve fish welfare and production and reduce treatment number and frequency.

KEYWORDS
amberjack, Carangidae, integrated parasite management, Monogenea, *Seriola*, treatment

1 | INTRODUCTION

Knowledge of parasite biology and how environmental conditions affect parasite development can help design effective aquaculture management strategies. Innovation in parasite prevention benefits from deep knowledge of biology and behaviour of both fish hosts and parasites.[1–7] Yet, the fish aquaculture industry continues to have to rely to a large extent on medicinal baths or osmotic shift to

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treat ectoparasitic protozoans, flatworms and sea-lice.[8–12] Medicinal baths are more effective if they are applied when parasite infection intensities are low and when they are timed to interrupt parasite life cycles (i.e., treatment intervals or therapeutic windows). Repeated use of chemotherapeutants drives the development of resistance in ectoparasites given their high fecundity and short life cycles,[13] thus strategically timed treatments are important because they alleviate treatment frequency and limit the amount of chemicals permeating into surrounding ecosystems.

Strategically timed medicinal bath treatments can account for temperature being a key influential factor for marine parasite life cycle parameters. In ectoparasitic flatworms (Monogenea: Platyhelminthes), temperature influences egg size, egg energy content, egg embryonation period, hatching success, larva (oncomiracidia) longevity, parasite size, development rate, fecundity and period of oviposition.[14–16] The direct life cycle of monogeneans can be interrupted using two successive bath treatments to kill parasites attached to fish (Figure 1).[17,18] The first treatment kills adult parasite populations on fish and the second kills immature, juvenile parasites that infect treated fish from eggs and larvae (oncomiracidia) resident in and around the system or farm. Timing of the second treatment is important because it can be coordinated so that all eggs in the vicinity have hatched and so that it kills new parasite recruits before they mature, commence laying eggs and contaminate the environment (Figure 1). While individual systems can be treated in recirculating aquaculture facilities, for maximum benefit in open aquaculture, every sea pen on each farm (or independent management unit [IMU]) must be treated within a short time frame.[18,19]

Global aquaculture of kingfish and amberjacks (*Seriola* spp.) is impacted by numerous pathogens and parasites[20] with monogenean ectoparasites considered to be particularly limiting for industry expansion. The *Seriola* industry comprises four main species including *Seriola quinqueradiata* Temminck & Schlegel, 1845, *S. lalandi* Valenciennes, 1833, *S. dumerili* (Risso, 1810) and *S. rivoliana* Valenciennes, 1833 which are predominantly farmed in net pens (e.g., Japan, China, US, Chile and Australia), while production in recirculating aquaculture systems (RASs) on land is also gaining momentum (e.g., Europe, South Africa, Chile and New Zealand; Figure 2). *Seriola quinqueradiata* rank third in world production volume for farmed marine finfish species following Atlantic salmon and rainbow trout[21] with considerable potential for further growth. Three parasite species are particularly problematic for production of *Seriola* spp. —the 'skin flukes', *Benedenia seriolae* (Yamaguti, 1934) Meserve, 1938 and *Neobenedenia girellae* (Hargis, 1955) Yamaguti, 1963, and the 'gill fluke', *Zeuxapta seriolae* (Meserve, 1938) Price, 1962, which occur in most regions where *Seriola* are farmed (Table 1). *Neobenedenia girellae* is widespread geographically and able to infest many different host fishes, including species that support commercial fisheries, aquaculture and the ornamental trade.[22]

Monogeneans that live on the skin can cause mechanical damage to fish epidermis and can lead to secondary infection,[23–26] while high gill monogenean burdens cause host anaemia.[27] Monogeneans are commonly treated using hydrogen peroxide baths (75–100 ppm for up to 1 h) to kill parasites attached to fish.[8,27,28] The eggs of these species bear long filamentous strands that tangle in aquaculture structures,[5,14,29] so filter changes, net changes or net cleaning aid in removing parasite eggs and other biofouling. Previously proposed strategically timed treatments for *B. seriolae* and *Z. seriolae* were suggested by Tubbs et al.[17] at three temperatures in New Zealand, while in South Australia knowledge of factors that influence the *B. seriolae* life cycle has been applied to minimise infections in farmed yellowtail kingfish, *S. lalandi*.[18,30] Brazenor and Hutson[16] developed an online tool for fish farmers to determine appropriate treatment times for the cosmopolitan parasite *N. girellae* that accounted for a range of temperatures and salinities using barramundi, *Lates calcarifer* (Bloch, 1790; Latidae) as the host model (http://www.marineparasites.com/paratreatmentcal.html). Nevertheless, the information required to make informed parasite management decisions for the *Seriola* industry has not been previously consolidated and is not available in open access or a format easily accessible to industry.

Expansion and retraction of aquaculture ventures around the globe can result in the loss of industry corporate knowledge. The

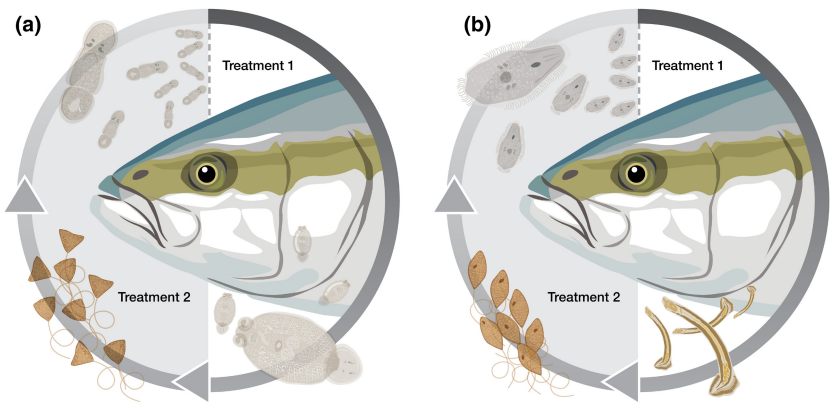

FIGURE 1 Schematic diagram showing key parasite life stages and representation of treatment schedules of (a) 'skin fluke' (i.e., *Benedenia seriolae*) and (b) 'gill fluke', *Zeuxapta seriolae*. Treatment 1 kills juvenile and adult stages attached to fish, while the biologically timed Treatment 2 is delivered when all eggs in the environment have hatched and oncomiracidia have infected fish but have not reached sexual maturity

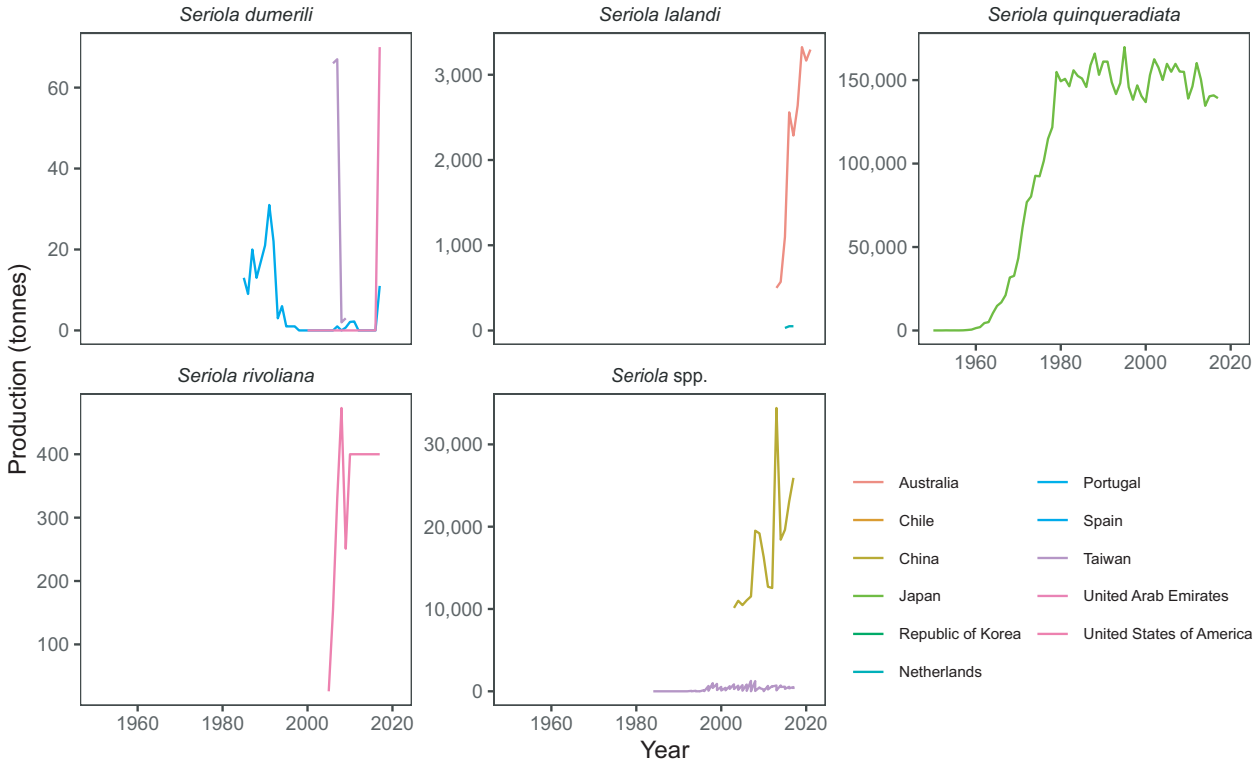

FIGURE 2 Production statistics for global *Seriola* aquaculture obtained from FAO statistics[21] and Clean Seas Seafood Limited Annual Reports.[110] Currently, New Zealand does not have commercial scale production; however, a 600 t/annum recirculating aquaculture system *for S. lalandi* is under construction[111]

implementation pathway for scientific data to enable change in industry practice needs to be founded in open access literature and on other platforms readily accessible to and understood by farm managers. Indeed, several mobile phone apps have been developed for the salmonid industry to assist with sea lice management including tools to help predict sea-lice development and infection pressure, treatment dosing and fish welfare during mechanical de-lousing processes.[31,32] The aim of this review was to assimilate published and previously unpublished data for *B. seriolae*, *N. girellae* and *Z. seriolae* life cycle parameters at various temperatures and salinities to determine appropriate timing of treatments to interrupt parasite life cycles. This information formed the basis of a decision support tool provided through an open-access app, BeNeZe (https://beneze app.cawthron.org.nz/) and website (https://beneze.cawthron.org.nz/). BeNeZe (Ben'easy; named after the first two letters of three monogenean parasite genera), provides guidelines for treatment of single and multi-species infections, parasite species diagnosis and surveillance. It is intended that the tool could accommodate changes and develop in its complexity and applicability as more information becomes available on monogenean life history parameters.

2 | METHODS: PARASITE LIFE CYCLE PARAMETERS AND MODELS

Life cycle parameters (i.e., time to first hatch, time to last hatch, oncomiracidia longevity and time to maturity) measured at various temperatures and salinities were compiled for *Benedenia seriolae*, *Neobenedenia girellae* and *Zeuxapta seriolae* from available published literature and previously unpublished data (Figure 1, Table 2). Given limited life cycle data available, parasite data were combined irrespective of host species and country of origin (Table 2). No data were available for *B. seriolae* oncomiracidia longevity. Life cycle parameters were obtained for a range of seawater salinities and temperatures, ranging between 10 and 50 ppt and 6 and 36.3°C, respectively. To provide conservative extension of the tool, proposed thermal tolerance limits were assigned 1°C either side of the lowest and highest experimental temperatures where egg hatching was observed for each species (Table 3). For example, *N. girellae* eggs hatched at 18°C, but not at 15°C, and the proposed lower thermal tolerance limit was 17°C (Table 3). In the event the proposed thermal tolerance exceeded the true thermal tolerance limit, the extension was not applied. This occurred in one instance for *B. seriolae* eggs that hatch at 29.7°C ± 0.3°C,[33] while Ernst et al.[14] did not observe hatching at 30°C. Thus, 30°C is likely the true upper thermal tolerance limit for this species (Table 3). Hatching success (= egg viability) data were compiled for salinities ≥24 ppt to provide an estimate of optimal hatching temperature but were not included as a parameter in the tool (Figure 3). Thermal hatching optima were estimated as the maximum predicted value by 95% quantile polynomial regressions with hatching success as function of temperature. Where the day of hatching was estimated by authors the data were omitted and where the salinity of seawater was not indicated, it was assumed as 35 ppt. Oncomiracidia longevity data obtained ≤25 ppt were not used.

TABLE 1 *Seriola* hosts and localities for *Benedenia* spp., *Neobenedenia* spp. and *Zeuxapta seriolae*

Parasite species	Host *Seriola* spp.	Location (Ocean, Country)	Origin	Key sources
Benedenia seriolae	*Seriola dumerili*	NW Pacific, off Japan	Captive	88
	Seriola hippos	Southern, off Australia	Wild	89
	Seriola lalandi	Indian, off Australia	Captive	90
		Southern, off Australia	Captive and wild	86,89
		SW Pacific, off Australia	Captive and& wild	(KSH pers obs; 91)
		SW Pacific, off New Zealand	Captive and wild	17,92
		NW Pacific, off Japan	Captive	60
	Seriola quinqueradiata	NW Pacific, off Japan	Captive	88,93
Benedenia humboldti[a]	*Seriola lalandi*	SE Pacific, off Chile	Wild	59
Benedenia sp.	*Seriola lalandi*	NE Pacific, off California	Captive	94
Neobenedenia girellae	*Seriola dumerili*	NW Pacific, off Japan	Captive	88
		NE Atlantic, off Canary Islands	Captive	25
	Seriola lalandi	SE Indian, off Australia	Captive	22
		NW Pacific, off Japan	Captive	61
	Seriola rivoliana	NE Pacific, off Hawaii	Captive	22
	Seriola quinqueradiata	NW Pacific, off Japan	Captive	88
Neobenedenia sp.	*Seriola lalandi*	SE Pacific, off Chile	Captive and wild	95
	Seriola lalandi	NE Pacific, off México	Captive	96
		NE Pacific, off California	Captive	94
	Seriola rivoliana	Land-based, México	Captive	97
		NE Atlantic, off Canary Islands	Captive (wild sourced)	98
Zeuxapta seriolae	*Seriola dumerili*	Mediterranean, off Spain	Captive and wild	99,100
		Mediterranean, off Greece	Captive	9
		NW Pacific, off China	Captive	101
		NW Pacific, off Taiwan	Captive	102
		NW Pacific, off Japan	Captive	8,88[b]
	Seriola lalandi	SE Indian, off Australia	Captive and wild	103
		Southern, off Australia	Captive and wild	80,89
		SW Pacific, off Australia	Wild	67,91
		SW Atlantic, off Brazil	Wild	68
		SE Pacific, off Chile	Captive and wild	72
		SW Pacific, off New Zealand	Captive and wild	17,92
		NE Pacific, off California	Captive	104
		SW Indian, off South Africa	Captive	105
	Seriola rivoliana	E Atlantic, off Portugal	Wild	106

Note: Seriola lalandi exhibits population subdivisions between some geographics areas and the reinstatement of *Seriola aureovittata* for the Northwest Pacific, and *Seriola dorsalis* for the Northeast Pacific is a point of contention in the scientific community; parasite–host records are provided as listed in the key sources indicated and in most cases identification through morphology or molecular means was not the primary aim of these reports.

[a]Synonymous with *B. seriolae* of Sepúlveda and González 2014.

[b]As syn. *Zeuxapta japonica*.

The effect of temperature on the duration of four parasite life cycle parameters, namely time to first hatch, time to last hatch, oncomiracidia longevity and time to sexual maturity, was tested using non-linear least squares models. The best fit for the models was obtained using power regressions fitted using the formula:

$$y = a \cdot t^{b},$$

where y is the number of days for each species to first, last hatch, oncomiracidia longevity or sexual maturity at a water temperature t in °C, a is the number of days to first, last hatch, longevity or maturity at a water temperature of 0°C and b is a constant describing how quickly each life cycle parameter decreases with temperature. Models were validated by inspecting standardised residuals.

TABLE 2 Source of temperature and life cycle parameter data for monogenean parasites *Benedenia seriolae*, *Neobenedenia girellae* and *Zeuxapta seriolae* indicating host fish species and locality

Parasite species	Host fish species	Location	Source	Reference no.
B. seriolae	*Seriola lalandi*	Australia	Lackenby et al. 2007	30
		New Zealand	Tubbs et al. 2005	17
	S. quinqueradiata	Japan	Ernst et al. 2005	14
			Kearn et al. 1992	107
			Hoshina and Matsusato 1967	33
	S. dumerili		Hirazawa 2019	45
N. girellae	*Lates calcarifer*	Australia	Brazenor and Hutson 2015	16
			Brazenor et al. 2020	15
	Verasper variegatus	Japan	Hirazawa et al. 2010	108
	S. dumerili		Hirazawa 2019	45
	Paralichthys olivaceus		Bondad-Reantaso et al. 1995	109
Z. seriolae	*S. lalandi*	Australia	AJM, unpublished data	
		New Zealand	Tubbs et al. 2005	17

TABLE 3 Assumed lower and upper thermal tolerance limits for monogenean parasites *Benedenia seriolae*, *Neobenedenia girellae* and *Zeuxapta seriolae*. Thermal tolerance limits were assigned 1°C below the lowest and 1°C above the highest experimental temperatures where egg hatching has been previously observed. Optimal thermal conditions were estimated based on egg-hatching success ≥25 ppt (see Figure 3)

Parasite species	Lower thermal tolerance (°C)	Upper thermal tolerance (°C)	Optimal thermal conditions (°C)
Benedenia seriolae	11.5	30[a]	21.9
Neobenedenia girellae	17	35	27.5
Zeuxapta seriolae	9	29	18.1

[a]True upper thermal tolerance limit based on available data.

The lower and upper limits of treatment times in days were then calculated using:

$$\text{Lower treatment limit} = \text{time to last hatch} + (\text{oncomiracidia longevity} \times 0.5),$$

$$\text{Upper treatment limit} = (\text{time to sexual maturity}) - 24\ \text{h}.$$

The lower treatment limit presents the maximum time for all eggs in the surrounding environment to hatch and for oncomiracidia to infect fish. Assumptions were that documented oncomiracidia longevity is not equivalent to infectivity (AJM unpublished data).[34] As such, oncomiracidia infectivity was estimated as 50% of their documented lifespan.[35] In the absence of longevity data for *B. seriolae*, infectivity was applied as per *Z. seriolae*, which occurs at a similar thermal tolerance range (Table 3).

The upper treatment limit represents the minimum time that parasites reinfect the fish and before they attain sexual maturity. Assumptions were that oncomiracidia and/or eggs at a later stage of development may be present in the environment and that parasites can infect fish immediately following the initial treatment. This is supported by laboratory experiments which showed that *N. girellae* oncomiracidia can infect fish immediately post-hatch (i.e., within 15 min).[36] A conservative approach to time to sexual maturity was suggested through the deduction of 24 h to allow for natural variation in the population where a small proportion of individuals may mature more quickly. Treatment limits for multiple species infection (i.e., two or three parasite species present in a farm) were determined from the range where species treatment intervals overlapped at a given temperature.

Temperature ceilings were applied to the decision support tool to ensure its suitability to real-world applications. A minimum low temperature was applied at 10°C to accommodate winter sea surface temperatures (e.g., *S. lalandi* farms Spencer Gulf, South Australia, Australia) while the maximum summer sea surface temperatures was applied at 30°C (e.g., *S. dumerili* farms Penghu Island, Taiwan). When using the tool, health managers should assess water temperature on the farm regularly and accommodate for changes in water temperature to the treatment plans as informed through surveillance. For example, seasonal changes such as winter to spring will result in accelerated parasite development (see Appendix S1, BeNeZe manual).

Based on the modelling predictions and calculated treatment time limits, an interactive open-source web tool, BeNeZe (https://

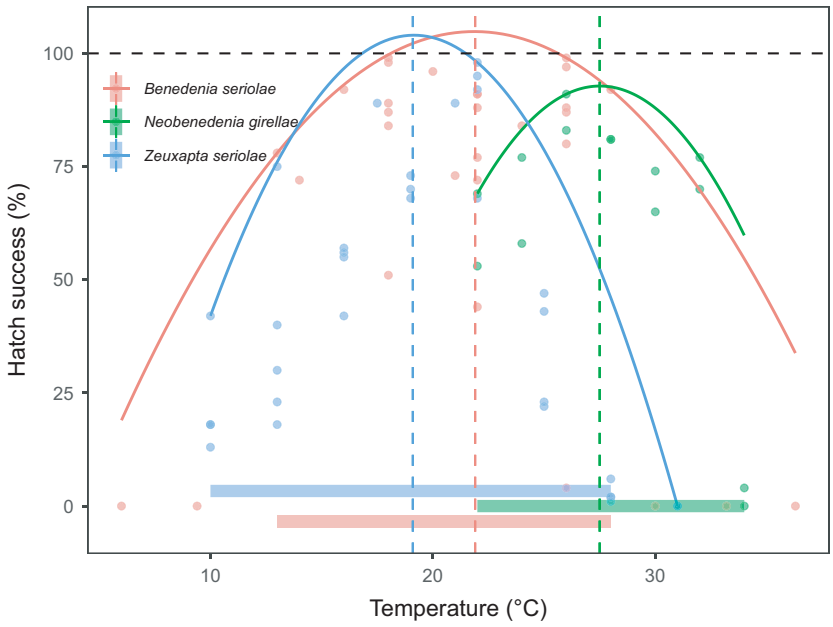

FIGURE 3 Hatching success of *Benedenia seriolae*, *Neobenedenia girellae* and *Zeuxapta seriolae* between 6 and 36.3°C. Data include hatching success measured at salinities ≥25 ppt. A quantile polynomial regression was fitted for each species to estimate optimal hatching temperature indicated by the dashed lines (see also Table 3). The horizontal bars represent the hatching temperature range for each species

benezeapp.cawthron.org.nz/), and website (https://beneze.cawthron.org.nz/) was written and developed by the authors and Cawthron support staff. The BeNeZe app is a single page application written in the progressive JavaScript framework vue.js. The app allows for the selection of parasite species, temperature and date for the initial treatment. It quickly provides the user with the determined time frames and durations for the consecutive relevant life cycle parameters and treatment events. The tool is configured for desktop computers, tablets and mobile phone devices. All data and scripts are available at https://doi.org/10.5281/zenodo.5701475. While the app could stand alone, it is embedded in a shorthand story web page to provide the reader with further information (https://beneze.cawthron.org.nz/). The main website hosts the tool and includes photographs and video to aid parasite identification and suggested use of the tool. A BeNeZe user manual, available as a Supplementary document (see Appendix S1) and on the website, provides broader background information on the biology of the three species, descriptions of the parasite life cycle and recommended techniques for farm surveillance.

3 | PARASITE LIFE CYCLE DURATION, THERMAL TOLERANCE, THERMAL OPTIMUM AND TREATMENT WINDOWS

Parasites exhibited a wide thermal tolerance range (9–35°C, Table 3). *Zeuxapta seriolae* exhibited the widest thermal tolerance, followed by *B. seriolae* and *N. girellae* (Table 3). Concurrent infections of *B. seriolae* and *Z. seriolae* are most likely to occur above 12°C, while infection of all three species is possible above 17°C in regions where parasite species cooccur (Table 3). *Zeuxapta seriolae* and *B. seriolae* are unlikely to persist above 30°C, while *N. girellae* may survive at slightly higher temperatures, potentially up to 35°C (Table 3). Thermal hatching optimum was 18.1°C for *Z. seriolae*, 21.9°C for *B. seriolae* and 27.5°C for *N. girellae* (Table 3, Figure 3). Given that hatching success increases towards the thermal optimum, farms that operate around these temperatures may experience heightened parasite burdens.

Regression analyses showed that life cycle duration was generally significantly reduced with increasing water temperature (Table 4, Figure 2). *Benedenia seriolae* and *Z. seriolae* exhibited an exponential decline in the time to first and last hatch and time to sexual maturity with increasing water temperatures, as evidenced by negative *b* parameters ranging between −4.9 and −0.37 ($p < 0.05$; Table 4, Figure 4). Temperature had weak effect on time to first hatch (b = −0.8, $p = 0.03$, Table 4, Figure 4) and sexual maturity (b = −0.9, $p = 0.007$; Table 4, Figure 4) of *N. girellae*, and it had no effect on time to last hatch (b = 0.5, $p = 0.26$; Figure 4, Table 4). *Zeuxapta seriolae* oncomiracidia longevity was significantly higher (3.95 ± 0.7 days) than for *N. girellae* (0.7 ± 0.6 days), but it was reduced at a slower rate with increasing temperatures ($p < 0.05$, Table 2, Figure 4).

BeNeZe can be applied in multi-infection scenarios (Figure 5), assuming the treatment used is effective against all target parasite species. Considerable overlap in the timing of life cycle parameters between *B. seriolae* and *Z. seriolae* means that the tool can be applied between 12 and 29°C to treat concurrent infections. Treatment windows for administering the second treatment to provide coverage for all three species were considerably limited with increasing seawater temperatures (Figure 5). While all three species can potentially co-infect fish at temperatures between 17 and 29°C (Table 3), there is no treatment window that applies to all three ≤22°C given the rapid development of *N. girellae* compared to *B. seriolae* and *Z. seriolae* (Figure 5). While a single treatment window is available between

TABLE 4 Results of non-linear regressions testing the relationship between time to first hatch, time to last hatch, oncomiracidia longevity and time to sexual maturity in days and sea surface water temperature (°C) for three parasite species: *Benedenia seriolae*, *Neobenedenia girellae* and *Zeuxapta seriolae*. Regression term 'a' is the number of days to first, last hatch or maturity at a water temperature of 0°C, and 'b' is a constant describing how quickly each life cycle parameters decrease with temperature. No data were available for *B. seriolae* oncomiracidia longevity

Model	Species	Term	Estimate	SE	*p*
First hatch	*Benedenia seriolae*	a	2208.8	595.3	0.001
		b	−1.9	0.1	<0.001
	Neobenedenia girellae	a	63.6	68.6	0.365
		b	−0.8	0.3	0.030
	Zeuxapta seriolae	a	2825.9	786.2	0.001
		b	−2.1	0.1	<0.001
Last hatch	*Benedenia seriolae*	a	2182.7	635.6	0.001
		b	−1.8	0.1	<0.001
	Neobenedenia girellae	a	1.3	1.8	0.486
		b	0.5	0.4	0.260
	Zeuxapta seriolae	a	1437.8	215.1	<0.001
		b	−1.7	0.1	<0.001
Oncomiracidia longevity	*Neobenedenia girellae*	a	6,688,027	11,773,692	0.58
		b	−4.9	0.56	<0.001
	Zeuxapta seriolae	a	11.53	4.62	0.05
		b	−0.37	0.14	0.05
Sexual maturity	*Benedenia seriolae*	a	6754.4	1498.4	0.006
		b	−1.9	0.1	<0.001
	Neobenedenia girellae	a	187.0	186.6	0.328
		b	−0.9	0.3	0.007
	Zeuxapta seriolae	a	6955.3	7300.2	0.384
		b	−1.9	0.4	0.004

23 and 29°C against all three species, the opportunity is short and may be challenging to meet in open aquaculture scenarios (Figure 5).

4 | SALINITY

There was no effect of salinity on the development rate for all three species (Figure S1). The effect of salinity on oncomiracidia longevity was not examined due to limited data. Given that salinity did not affect life cycle parameter durations, it is not relevant to the timing of treatments and was not incorporated in the BeNeZe tool. Hypo- and hypersalinity reduced egg viability (Figure S1) which is particularly relevant for more complex epidemiological models in open aquaculture systems for predicting parasite infection pressure. Furthermore, hyposalinity has been used to eradicate parasites in RASs.[37]

5 | BENEZE: APPLICATION AND ASSUMPTIONS

Strategically timed treatments can break the life cycle of ectoparasites in farm systems (Figures 1 and 6). As temperature increases, the number of days or the 'window' for application of a second, timed treatment is greatly reduced for management of ectoparasitic monogeneans on *Seriola* farms. When managing infestations in cooler water temperatures in winter, there is more scope for accommodating logistical considerations (e.g., weather in open aquaculture, staff availability) compared to summer. Treatments that aim to manage concurrent infections by all three species are challenging given limited overlap in the timing of life cycle parameters for *N. girellae*; however, co-infections of *B. seriolae* and *Z. seriolae* exhibit reasonable and achievable treatment windows for small-scale farms (Figure 5, Figure 6). Note that *N. girellae* has been recorded from several host fishes and host fish families,[22] and thus selection of this species from the tool may also be effective in public aquaria, research facilities, the ornamental fish trade and hobbyist aquaria. Life cycle parameter estimates should be validated to confirm tsuitability at various farming locations globally.

BeNeZe assumes that the infection source is from within the farm, that treatments are coordinated across the farm, that each treatment has complete efficacy and that parasite eggs cannot go dormant. Many of these assumptions may be met in land-based hatcheries and RASs and are highly applicable to the growing RAS-based *Seriola* industry in the Netherlands, South Africa, Chile and

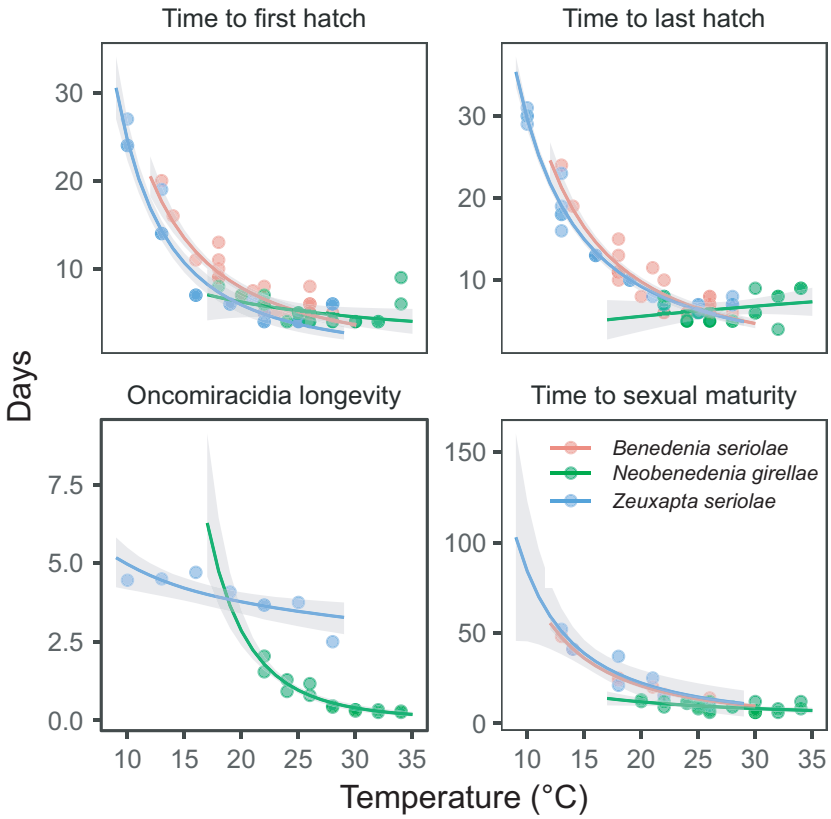

FIGURE 4 Exponential curves showing predicted changes in time to first hatch, time to last hatch, oncomiracida longevity and time to sexual maturity in days for *Benedenia seriolae*, *Neobenedenia girellae* and *Zeuxapta seriolae* in relation to sea surface water temperature in degrees Celsius. No data were available for *B. seriolae* oncomiracidia longevity

New Zealand. Assumptions are more difficult to meet in open systems, such as sea pens, where once a monogenean population is established, conditions within the net pen are favourable for transmission and establishment of additional populations within and between pens. The large scale and dynamics of commercial net pen farm operations introduce several challenges to parasite management because immersion treatments are reliant on suitable weather conditions which may not correspond with BeNeZe recommended treatment intervals. Furthermore, wild or escaped fish infected with monogeneans can associate with sea pens and introduce viable eggs and larvae into the system or they may be transported with ocean currents.[19,38] Nevertheless, without any intervention, parasites can potentially spread to all fish within a pen, to other pens on the farm and to pens located on other nearby farms, which can lead to mass mortality of fish stocks. In open systems, integrated management strategies will not eradicate infections, but can be used to reduce parasite burdens and treatment frequency.

For maximum benefit in open aquaculture, every sea pen on each farm (or IMU) must be treated within a short time frame.[18,19] The spatial area inclusive of all component parasite communities connected or influenced by the transmission process, termed an IMU, may be identified by epidemiological studies that consider the parasite life history, parasite–host interactions, the analysis of spatial and temporal transmission patterns and hydrodynamics.[19,39] Where these boundaries encompass multiple farms, cooperation between farm managers is required for effective and efficient parasite management. Several complex connectivity models have been developed to aid the management of sea-lice in salmonid aquaculture.[40] Data provided for the BeNeZe tool on egg embryonation period (time to first and last hatch) and egg viability (Figure 4) are essential for incorporation into more complex particle tracking models and ultimately the delineation of farm biosecurity zones, leases or locations that would benefit from targeted surveillance.

6 | BEHAVIOUR AND BIOLOGY: FURTHER CONSIDERATIONS FOR INTEGRATED PARASITE MANAGEMENT

Parasite behaviour and biology are important farm management considerations for the successful application of BeNeZe. Some monogeneans exhibit arrested development or dormancy during winter and hatch when temperatures rise in spring.[41] While dormancy has not yet been investigated for *B. seriolae*, *N. girellae* or *Z. seriolae*, it would be prudent for fish farmers to conduct net or filter changes to remove entangled eggs at the end of winter, prior to spring temperature increases. Subsequent identification of egg dormancy and the temperature triggers under which it occurs can be incorporated into the BeNeZe model to enhance accuracy and applicability. Another consideration is that some adult monogeneans, including *Z. seriolae*,

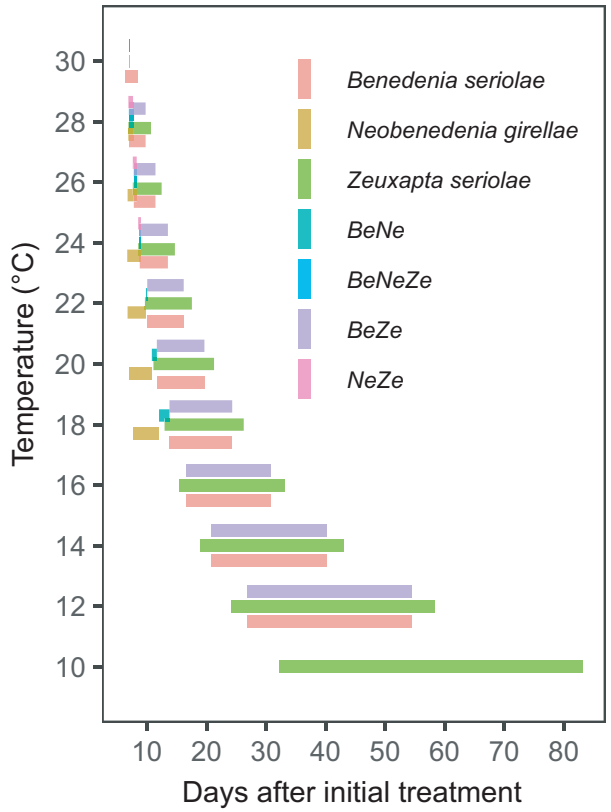

FIGURE 5 Treatment windows in days after initial treatment for *Benedenia seriolae*, *Neobenedenia girellae*, *Zeuxapta seriolae* and multiple species in relation to sea surface water temperature (°C). Treatment windows indicate the period from when all eggs have hatched and all oncomiracidia have infected fish to 24 h before the reach sexual maturity. Treatment 2 is administered during these treatment windows to break the parasite's life cycle. Treatment windows for multiple species are indicated by the first two letters of the genus for each combination (e.g., *B. seriolae* and *Z. seriolae* concurrent infection management is shown as 'BeZe'). Treatment windows were calculated based on modelled life cycle parameters (see Methods section for details)

release their eggs when disturbed or dying.[42,43] As such, immersion treatments targeted to kill adult *Z. seriolae* attached to fish could induce mass, simultaneous release of viable parasite eggs into the farm environment. In hatcheries or RASs, these eggs could be captured on filters or parasite egg collectors and removed.[44] In open aquaculture, it may be more difficult to capture eggs, but net changes conducted in conjunction with the initial immersion treatment may assist to reduce the frequency of fish handling and limit reinfection.

While monogenean eggs are highly resistant to short immersion in freshwater and hydrogen peroxide,[45–47] Boylan[37] found that prolonged hyposalinity at 20 ppt can be used to eradicate *Neobenedenia* sp. in large public display aquaria without compromising marine fishes. Shirakashi and Hirano[5] found *N. girellae* eggs tend to accumulate on net pens near the surface and suggested net emersion to kill the eggs through desiccation.[14,46] It has also been shown that high infection of *N. girellae* occurs near the surface,[48] thus 'snorkel' cages used in salmon production in Norway to limit interactions near the surface between salmon and sea-lice[49] may have applicability for the management of monogeneans in *Seriola* aquaculture. Biocontrols are also being explored as an option to reduce monogenean egg fouling on net pens using shrimp and other crustaceans.[50–53] Recently, Skilton et al.[2] proposed synchronously timed deployment of light traps could be used to exploit positive phototaxis and hatching rhythms of *N. girellae* oncomiracidia. Indeed, shaded cages lowered *N. girellae* infections on fish, showing that light manipulation of parasites may be achieved in multiple ways.[54,55] Trujillo-González et al.[36] observed that newly recruited *N. girellae* can bury beneath the host fish scales, where they may be protected from bathing treatments. If this was experimentally demonstrated to provide them adequate protection from treatments, it would be prudent to amend the BeNeZe lower treatment limit equation to include the number of days larvae typically bury beneath scales.

7 | ACCOUNTING FOR HOST AND PARASITE IDENTIFICATION

Accurate identification of fish and parasite taxa is essential to determine the most appropriate management measures in aquaculture. For example, misidentification of morphologically similar species, such as *B. seriolae* and *N. girellae*, could lead to inappropriate use of BeNeZe and treatments not being applied at appropriate times. The taxonomic status of the taxa examined in this study is considerably complex and in a state of flux which can make identification challenging. BeNeZe was developed from the consolidation of multiple data sources and is reliant on accurate identification. While it is plausible that cryptic parasite species and/or varied host associations could result in differences in life history trait response to temperature, life cycle parameters may also be conserved within a species and comparative to other species of the same genus. Further investigations of parasite life cycle parameters to validate the application of BeNeZe or heighten precision of the tool should carefully document host–parasite associations and locality records and aim to deposit representative molecular and morphological samples in curated collections for identification and future verification.

Benedenia seriolae (Yamaguti, 1934) Meserve, 1938 was first described from *Seriola aureovittata* [= *S. lalandi*] in Japanese waters (as *Epibdella seriolae* Yamaguti 1934). Whittington et al.[56] proposed *B. seriolae* also infected *Seriola quinqueradiata* and *S. dumerili* in Japan based on 28S rDNA and species morphology. Perkins et al.[57] published the complete mitochondrial genome for *B. seriolae* collected from *S. hippos* in Australia. Following, Sepúlveda and González[58] suggested *B. seriolae* represents a species complex with at least three morphologically similar species each restricted to distinct geographic regions (i.e., Chile, Japan and Australia) and that substantial molecular divergence between *B. seriolae* specimens of Australian and Japanese origin may warrant recognition of separate species. Subsequently, Baeza et al.[59] proposed a new species, *B. bumboldti* (synonymous with *B. seriolae* of Sepúlveda and González[58] off Chile), based on molecular and minor morphological differences. Recently,

FIGURE 6 Screen shot of the BeNeZe app showing parasite and temperature selection options, timing of key life stages for the selected temperature and the recommended treatment period for the second treatment following the initial treatment

Kawato et al.[60] sequenced the complete mitochondrial genome of *B. seriolae* from Japan which shared 85% identity with the Australian specimen[57] and exhibited slight differences in the gene arrangement. A formal proposal to separate Japanese and Australian *B. seriolae* has not been made to date.

Neobenedenia girellae is a cosmopolitan species with a large diversity of susceptible host species.[22] *Neobenedenia* spp. have been recorded from *Seriola* hosts from numerous localities but are not yet known from the Mediterranean Sea or the Southeast Pacific off New Zealand (Table 1). Ogawa et al.[61] indicated that unregulated importation of *S. dumerili* fry to Japan may have been the source of *N. girellae* infection in Japanese fishes. Indeed, *N. girellae* has likely dispersed through the live ornamental aquarium trade.[62,63] The delineation of two species, *N. girellae* and *N. melleni*, has been a source of controversy and confusion for decades, but recent molecular profiling demonstrated that a large proportion of previous identifications made as *N. melleni* are erroneous.[22] Given difficulties to morphologically distinguish species and that morphological variation may be exhibited within *Neobenedenia* species,[64] authors occasionally attribute species as '*Neobenedenia* sp.' (see Table 1). *Neobenedenia girellae* is also challenging to distinguish from *B. seriolae*, but egg morphology and minor features of adult parasites may be used on fish farms to aid preliminary identification using microscopy in the absence of molecular tools.[65,66] Morphological differences of these two species are also highlighted in the BeNeZe website and manual (https://beneze.cawthron.org.nz/; Appendix S1).

Zeuxapta seriolae (Meserve, 1938) Price, 1962 was first described from *Seriola quinqueradiata* Temminck & Schlegel in Japan. It has been formally redescribed on several occasions[67–70] and

is known to occur in the Pacific, Atlantic, Indian and Southern Oceans, including the Mediterranean Sea (Table 1). While most records are from *Seriola* species, it is also known from the carangid *Caranx hippos*[70,71]; note uncertainty around host identification. According to the World Register for Marine Organisms, there are four recognised synonyms including *Heteraxine meservei* Sproston, 1946, *Microcotyle seriolae* Yamaguti, 1940, *Zeuxapta japonica* Yamaguti, 1961, and *Zeuxapta zyxivaginata* Unnithan, 1957 as well as one superseded combination *Axine seriolae* Meserve, 1938. Some authors publish under the synonym *Z. japonica* [8] and future molecular work may confirm or refute whether *Z. japonica* should be reinstated. There is evidence of geographical genetic variation of *Z. seriolae* between regions in Chile.[72] Observed differences in biological traits between regions were confounded by temperature at the time of sampling[72] and require further investigation given the strong influence of temperature on fecundity and size of other monogeneans.[15]

The taxonomy of *Seriola lalandi* is a topic of considerable scientific discussion. Martinez-Takeshita et al.[73] suggested three cryptic species bear the name *Seriola lalandi* and proposed to reinstate junior synonyms *Seriola aureovittata* Temminck and Schlegel for the northwest Pacific (type locality, Japan), and the northeast Pacific species to *Seriola dorsalis* (type locality Mexico) and *Seriola lalandi* Valenciennes, 1833 (type locality Brazil) to the southern hemisphere. Later in the same year, Purcell et al.[74] showed evidence for four significantly differentiated populations corresponding to the northeast Pacific, northwest Pacific, south Pacific and south Atlantic and suggested there may be at least three cryptic species of *S. lalandi*. Premachandra et al.[75] agreed that there are three different *S. lalandi* populations, but they suggested that the reinstatement of species by Martinez-Takeshita et al.[73] may be premature, and that low genetic divergence supports the more traditional view that *S. lalandi* in the Pacific comprises three distinct populations rather than species subdivisions. Recently, Kerwath et al.[76] showed that remote shallow seamounts can also contribute to genetic and phenotypic distinctions in *S. lalandi*. The taxonomy of *Seriola* spp. may be further complicated by the deliberate movement of animals for aquaculture and the potential genetic introgression of aquaculture escapees into wild fish populations.[77]

8 | FUTURE DATA GATHERING AND CONSOLIDATION

The BeNeZe decision support tool presents a base for consolidation of data to inform integrated parasite management in aquaculture. Fish health professionals and researchers are encouraged to validate the tool or, alternatively, create a tailored database for their specific scenario. This should begin with accurate species identification while acknowledging complexity in both *Seriola* spp. and monogenean identification and taxonomy.[65,78] Local physicochemical factors should also be considered. Additional water quality parameters (e.g., pH, ammonia, turbidity and contaminants) may influence monogenean infection dynamics to the extent that they are considerably different from expected patterns (see ref. 79 for review).

Data collection should be precise to limit discrepancies in life cycle parameters due to differences in method of egg incubation including the time of initial egg collection and lighting regimes.[44] Egg incubation is typically conducted in static dishes with daily water renewal; however, aeration of the solution may be more representative of the farm environment and could yield higher hatching success. Contamination of egg cultures can also be avoided by cleaning the eggs.[44] Monogeneans typically exhibit egg-hatching rhythms and egg-laying rhythms,[80,81] consequently, the time of day when experimental observations are made influences whether time to first and last hatch or sexual maturity are observed. Development of more complex epidemiological models to predict infection pressure through time should account for the fact that fecundity and the duration of oviposition are temperature and age dependent[15,81] and that hatching success is influenced by temperature and salinity (Figure 3).

Data on oncomiracidia infectivity would be particularly valuable for a revised model. BeNeZe used a proxy for infectivity based on oncomiracidia longevity; however, it is unclear what proportion of their lifespan that larva remains infective. Furthermore, oncomiracidia longevity is often assessed in confined laboratory vessels to enable monitoring and may not be representative of aquaculture environments. More applicable data should be obtained on oncomiracida infectivity by determining infection success on fish in tanks through time.[36] This information would be particularly valuable for *B. seriolae* where there are no data available. Further information for *N. girellae* oncomiracidia longevity/infectivity at lower temperatures would also be valuable considering eggs laid in cooler temperatures are larger and may provide more energy reserves.[15] There is no evidence that salinity influences development rates in *B. seriolae*, *N. girellae* and *Z. seriolae* and it was not included in the BeNeZe tool. However, Villar-Torres, Montero[82] observed that egg development tended to slow towards hypersaline and hyposaline salinities in the monogenean *Sparicotyle chrysophrii*; thus, salinity may need to be considered in the development of equivalent tools for other parasite species.

Egg viability should also be considered as it is highly applicable for more complex parasite epidemiology and modelling for health managers to estimate parasite recruitment following treatment. In future, BeNeZe could be modified to support the addition of other ectoparasites in *Seriola* aquaculture such as sea-lice. Endoparasites such as blood flukes could also be incorporated with recommendations on the frequency of biofouling management to remove susceptible intermediate polychaete hosts.[83,84]

9 | CONCLUDING REMARKS

Parasite populations may evolve in response to selective parasite management (see ref. 85 for review); thus, it is important to apply multiple tools as part of an integrated management strategy.

BeNeZe should complement farm biosecurity, prevention measures and integration of other management measures where possible (e.g., filter or net cleaning, net changes). Indeed, the tool will be most useful to farmers that engage in parasite surveillance to monitor parasite burdens because immersion treatments are more effective when parasite infection intensities are low. If fish stocks are severely compromised from anaemia or secondary bacterial infection, they may not survive stressors associated with immersion treatments, particularly during summer. Farmers that monitor infection burdens (while acknowledging potential sampling bias)[86,87] and parasite development and maturation will be able to identify infection burdens or 'trigger points' to commence the initial treatment. Monitoring the efficacy of treatments baths will help avoid the development of resistance in parasites.[11] The application of BeNeZe as part of an integrated parasite management plan can help improve farm operational efficiency and extend treatment intervals.

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTION

Kate Suzanne Hutson: Conceptualization; Data curation; Funding acquisition; Investigation; Methodology; Project administration; Resources; Writing—original draft; Writing—review & editing. **Allan James Mooney:** Data curation; Investigation; Methodology; Writing—review & editing. **Ingo Ernst:** Conceptualization; Data curation; Investigation; Methodology; Writing—review & editing. **Alexander Karlis Brazenor:** Data curation; Investigation; Methodology; Writing—review & editing. **Max Scheel:** Software; Validation; Visualization. **Javier Atalah:** Conceptualization; Data curation; Formal analysis; Methodology; Validation; Writing—review & editing.

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Not applicable.

PATIENT CONSENT STATEMENT

Not applicable.

PERMISSION TO REPRODUCE MATERIAL FROM OTHER SOURCES

Review was generated from publicly available and author data.

CLINICAL TRIAL REGISTRATION

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DATA AVAILABILITY STATEMENT

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ORCID

Kate Suzanne Hutson https://orcid.org/0000-0003-2408-3990
Javier Atalah https://orcid.org/0000-0003-0625-3431

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