MATHEMATICAL MODELS FOR THE CONTROL OF *ARGULUS FOLIACEUS* IN UK STILLWATER TROUT FISHERIES

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Dedicated to my Nana

1936 - 2013

DECLARATION

I hereby declare that this work has not been submitted for any other degree at this University or any other institution and that, except where reference is made to the work of other authors, the material presented is original.

Stirling, 2013

Nicola Jane McPherson

ABSTRACT

Species of *Argulus* are macro-, ecto-parasites known to infect a wide variety of fish, but in the UK mainly cause problems in rainbow (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*). *Argulus foliaceus* is estimated to have caused problems in over 25% of stillwater trout fisheries in the UK.

While *A. foliaceus* does not usually cause high levels of mortality, the parasite affects fish welfare, and also makes fish harder to catch due to morbidity and reduced appetite. This can cause severe economic problems for the fishery, resulting in reduced angler attendance due to poor capture rates and the reduced aesthetic appearance of fish; in the worst-case scenario this can result in the closure of the fishery. Current methods of control include chemical treatment with chemotherapeutant emamectin benzoate (Slice), physical intervention with egg-laying boards which are removed periodically and cleaned in order to reduce the number of parasites hatching into the environment, and the complete draining and liming of the lake to remove all free-living and egg stages of the parasite. While these treatments have all been shown to reduce parasite numbers, none are known to have resulted in permament eradication of the parasite. There is evidence to suggest that *A. foliaceus* will eventually develop resistance to Slice - the only currently available chemical treatment against the infection - and egg-laying boards and the draining and liming of the lake are both time- and labour-intensive.

Previous studies have shown that slow fish turnover is a risk factor with respect to *A. foliaceus* infections, and with a wide variety of stocking practices occurring in the UK one of the first aims of this project was to determine their impact on the host-parasite dynamics. Mathematical models provide a cost-effective way of examining the impact of such practices, and after a literature review (chapter one), in chapter two a three-compartment mathematical model was adapted for use in the *A. foliaceus*-trout system. Four generalised stocking methods were then incorporated and analysed, and a minimum threshold host density was found to

be necessary to sustain the parasite. Including a function which reduced the capture rate as the parasite burden increased allowed the parasite to survive at a lower host density, as susceptible fish were removed from the water at a slower rate, and attached parasites also remained in the water for longer. This resulted in hysteresis in the model, as the invasion threshold for the parasite remained the same, but once established the parasite became harder to eradicate, requiring significant reductions in the host density.

In chapter three the model was further developed in order to improve its biological realism. Several features were added and these included: natural host mortalities, a separate compartment for the parasite egg population, and parasite survival after the natural or parasite-induced mortality of its host. In chapter four seasonality was added by incorporating temperature-dependent egg-laying rates and an over-wintering period during which the parasite was unable to reproduce. The model was then fit to the available data, and estimates for the rate of parasite-induced host mortalities and the parasite's rate of attachment to a host were found.

In chapter five we returned to stocking methods, this time looking at the frequency and timing of stocking events and the impact of imposing a rod limit (whereby anglers are only permitted to capture four fish per visit); it was concluded that while current guidelines suggest that very frequent trickle stocking is recommended when dealing with *Argulus* spp. infections, monthly stocking does not appear to worsen the infection, and if the fish capture rate is high then less-frequent stocking may also be permissable - particularly if stocking occurs towards the end of the year when the parasite is no longer active. This practice may, however, be detrimental to the fishery due to low fish densities in the summer months.

In chapter six treatment with Slice was included in the model, and it was demonstrated that with constant treatment, and in the absence of reservoir hosts and a withdrawal period from the drug prior to stocking treated fish into the fishery, the parasite was eradicated. Under current veterinary cascade guidelines, however, trout are required to undergo a withdrawal period of 500 degree days prior to being made available for human consumption. When this was included in the model the drug still decreased parasite abundance, but did not eradicate it - this is in agreement with results reported by communications with fishery managers currently treating fish with Slice. A reduction in the withdrawal period of 25% was shown to further decrease parasite abundance, but still did not result in parasite extinction.

As constant treatment with Slice is not advisable due to the potential for resistance build-up, we then sought to find time at which to apply a single treatment of Slice, and found that this was in August when the temperature was highest and the parasite was reproducing and attaching to hosts quickly. Egg-laying boards were also incorporated into the model and similarly to findings by Fenton et al. [11] the success of this treatment was mostly dependent on the proportion of eggs being laid on the boards (as opposed to natural substrates). In contrast with the *A. coregoni* system, however, the boards would have to be cleaned and replaced more frequently that once per year, as several cohorts of *A. foliaceus* emerge during a single year.

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CHAPTER 1: LITERATURE REVIEW

1.1 INTRODUCTION

1.1.1 *History and distribution of* Argulus *species*

Species of the macro-parasite *Argulus* (Crustacea: Branchiura) have been reported as a problem in over 25% of the UK's stillwater trout fisheries [50]. An outbreak of *Argulus* spp. in a fishery harms fish welfare as well as the reputation of the fishery, and in some cases can lead to its closure [35, 12]. *Argulus* spp. attach to their hosts using hooks or suckers formed from modified first maxillae [49]. They feed through a mouth tube, and it is thought that the separate pre-oral spine injects an anticoagulant into the fish, making them easier to feed from [45].

Branchiura are parasitic crustaceans, comprised of around 170 distinct species split across 6 genera, the largest of which is *Argulus* spp. Until recently *Argulus* spp. had an uncertain position in the class Maxillopoda (classification presented in table 1.1), however recent phylogenetic anaylsis by Regier et al. [39] suggests the position illustrated in figure 1.2. Three freshwater species are present in UK waters and all three have been the subject of comprehensive research across the world; these are *Argulus japonicus* Thiele, 1900, *Argulus coregoni* Thorell, 1864 and *Argulus foliaceus* Linnaeus, 1758.

The majority of the 134 *Argulus* species are ecto-, macro-parasites of fish, although *Argulus americanus* has been known to parasitise tadpoles of the frog *Rana heckscheri* (eg. Goin and Ogren [13]). Hargis [19] also reported one case of attachment of *Argulus laticauda* Smith, 1874 to a human eyeball.

Table 1.1: Classification of *Argulus* spp.

Kingdom	Animalia
Phylum	Arthropoda
Subphylum	Crustacea
Class	Maxillopoda
Subclass	Branchiura Thorell, 1864
Order	Arguloida Yamaguti, 1963
Family	Argulidae Leach, 1819

Species of *Argulus* (pictured in Figure 1.1) have direct life cycles, as they are able to survive on a single host species, and are often referred to as fish lice - as opposed to sea lice - as most live in freshwater. Some marine species also exist, for example *Argulus arcassonensis* Cuènot, 1912 has been found in UK coastal waters [23].

Argulus japonicus was first described in China, and through movement of fish stocks has since been discovered in Europe, North America, Australasia and Africa. *A. coregoni* was first described in Japan, but has since been found throughout Europe. *Argulus foliaceus* is the most prevalent species in the UK, is common throughout freshwater lakes in Europe [53], and is known to cause severe damage to trout stocks [29]. In the UK *A. foliaceus* is known to cause problems in trout fisheries [50].

The aim of the current research is to determine, using mathematical models, how different interventions against *A. foliaceus* affect the host-parasite dynamics in UK stillwater trout fisheries. In order to create an informative model, it is first necessary to have a firm understanding of the dynamics between the parasites and their hosts within fisheries. The purpose of this

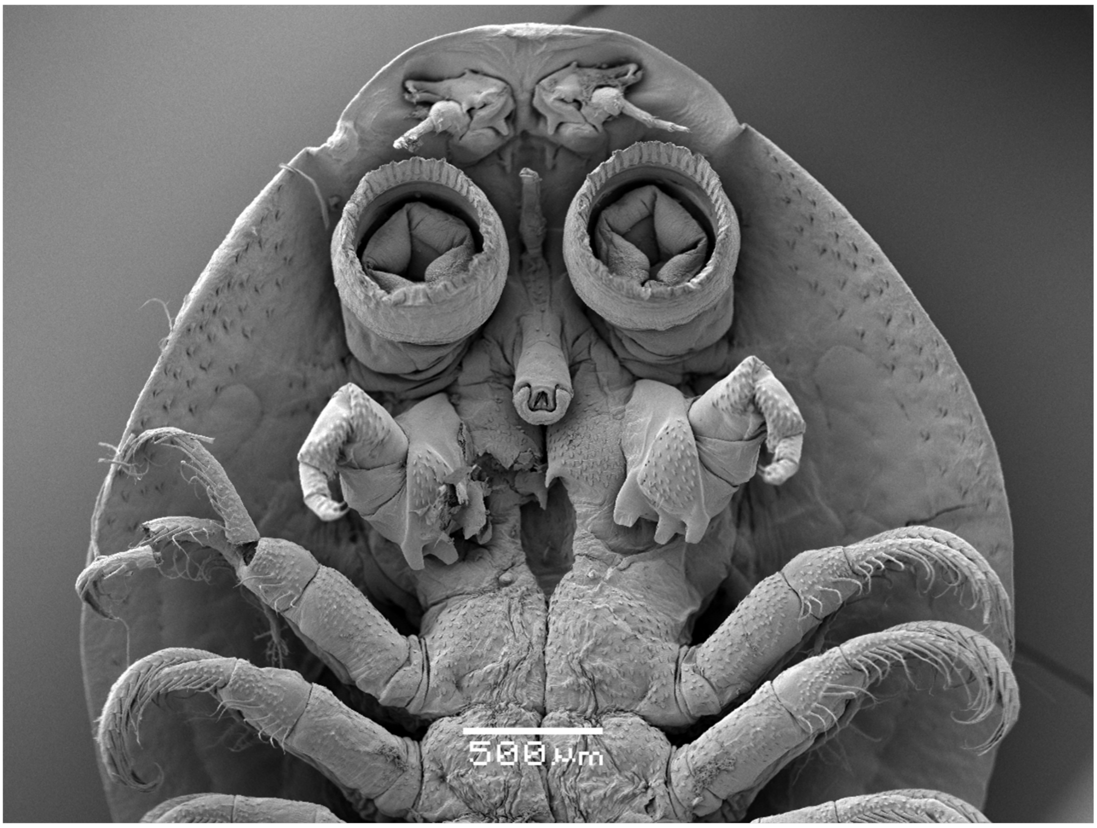

Figure 1.1: SEM image of an argulid courtesy of Andrew Shinn, Institute of Aquaculture

chapter is therefore to describe the key mechanisms driving *Argulus* spp. infections, and present the information required to parameterise such a model.

The simplest *Argulus* spp. management strategy would involve straightforward but effective changes in the management of the fishery, and it is hoped that significant improvements will be made possible by altering the method, frequency and timing of stocking. Intervention with currently available treatments such as egg-laying boards and chemical treatment with Slice® (emamectin benzoate, Schering-Plough Animal Health) will also be examined.

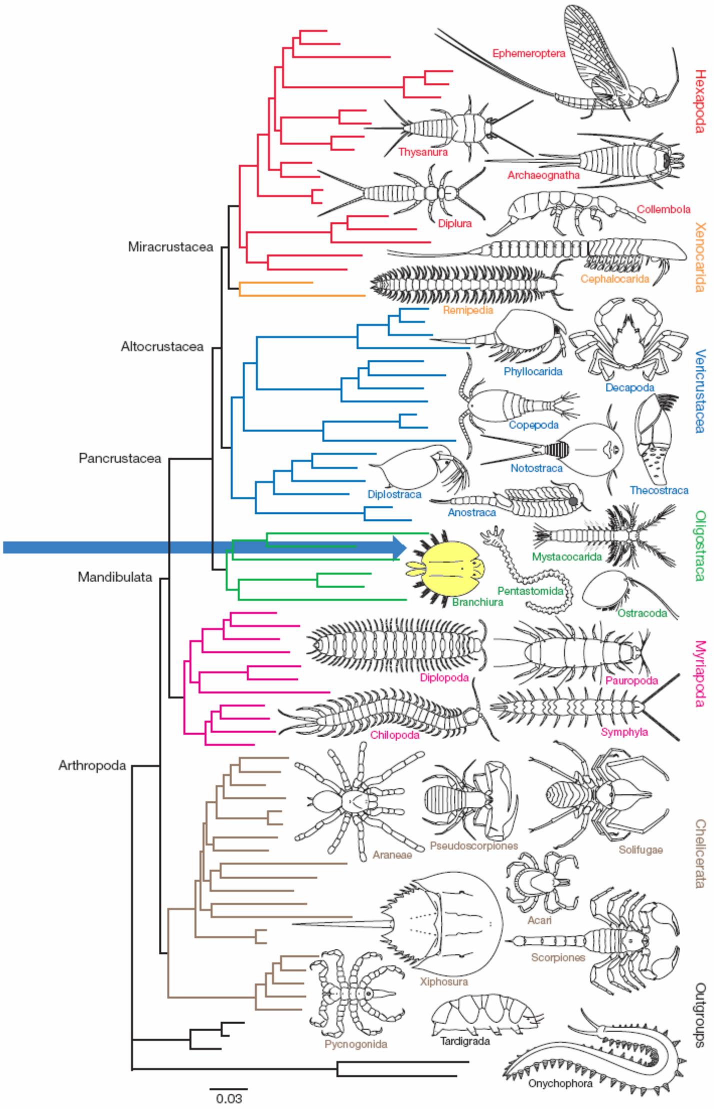

Figure 2 | Phylogram of relationships for 75 arthropod and five outgroup species. Based on likelihood analyses of 62 nuclear protein-coding genes. Branch lengths are proportional to the amount of inferred sequence change, with the topology and analytical conditions identical to the degen1 analysis in Fig. 1. Line drawings of representatives of the major taxonomic groups show the morphological disparity across Arthropoda. Scale bar, nucleotide changes per site.

Figure 1.2: Phylogram from Regier et al. [39] illustrating the phylogenetic position of *Argulus* spp. (highlighted)

Angling is widely recognised as the most popular outdoor participation sport in the UK. While the UK's Agriculture and Fishing industry employed 250,943 people in 2008, no accurate figures concerning the number of people employed in the angling industry appear to be available. Estimates in grey literature suggest the equivalent of anywhere between 5000 and 20000 full time positions are occupied by those involved in the running of fisheries and the production and sale of tackle and angling magazines. Angling has also been acknowledged as making significant contributions to employment and the rural economy by the Commission for Rural Communities (State of the Countryside Report, 2008).

Angling in the UK is continuing to grow in popularity, and in 2009 the Environment Agency sold 1.357 million rod licences - a 27% rise from 2000. Licence income generates £24 million each year, and funds most of the Environment Agency's Fisheries service [34]. Growing demand for angling waters means that many lakes are now stocked to high densities, increasing the likelihood of disease and parasitic infections, both of which thrive in densely populated environments. Knight [25] points out that the standard of fish expected by anglers has also increased; a fishery suffering an infection like *Argulus* spp. which impacts the weight, condition and appearance of stock can therefore rapidly lose their reputation, and will likely suffer from reduced angler numbers, potentially causing job losses and risking the closure of the fishery.

1.2.1 *Stillwater trout fisheries*

Trout fisheries in the UK can be riverine or stillwater and are often stocked with brown (*Salmo trutta*) and rainbow (*Oncorhynchus mykiss*) trout, although some fisheries relying on natural recruitment do exist. This thesis will focus on stillwater trout fisheries as this is where the majority of problem *Argulus* spp. infections occur in the UK. An example of a typical production cycle of *O. mykiss* is presented in figure 1.3.

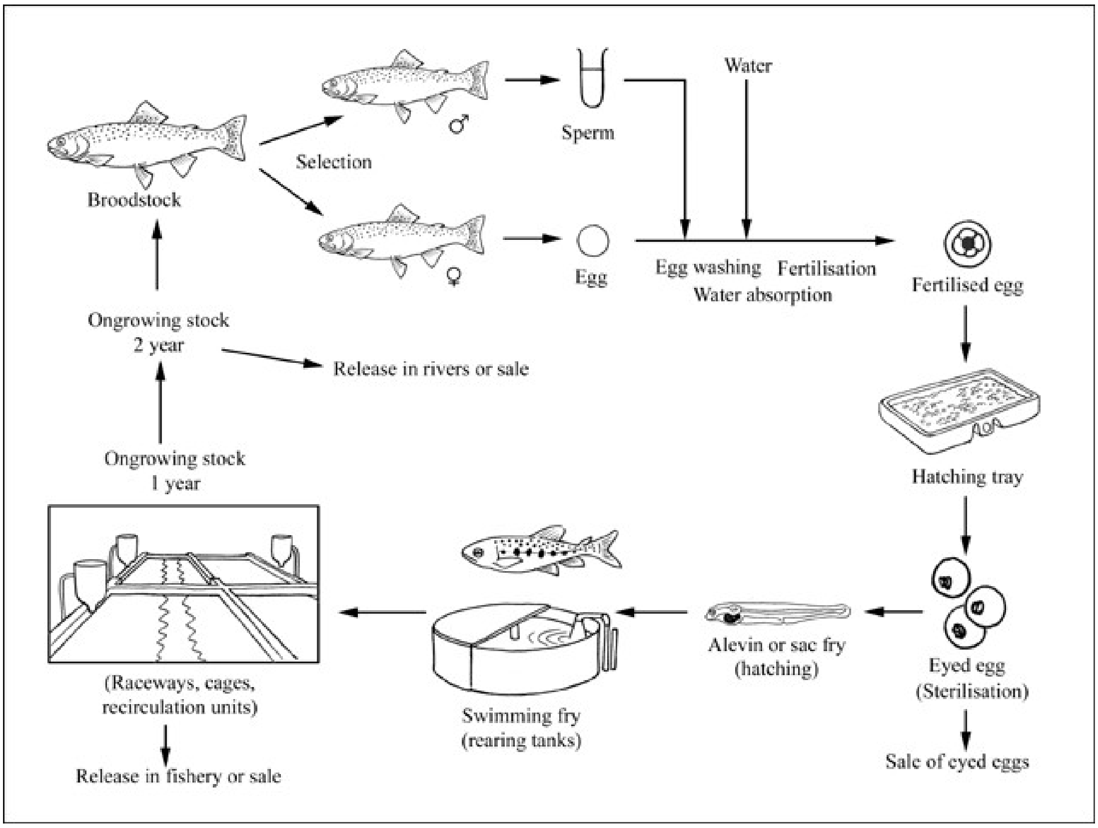

Figure 1.3: Production cycle of *O. mykiss* (Image from `http://www.fao.org/fishery/culturedspecies/Oncorhynchus_mykiss/en`)

Currently, very little published data is available on the management practices of fisheries in the UK. The remainder of this section is designed to give an idea of how fisheries are run, and has been informed by personal communications with relevant stakeholders.

As previously stated, UK stillwater fisheries often stock with brown and rainbow trout, but many also have natural populations of other species, such as carp *Cyprinus cario* and stickleback *Gasterosteus aculeatus*. Rainbow trout are particularly popular with anglers, but are also expensive to farm and buy, as they do not breed naturally in fisheries. Although the production cycle is well-designed, it takes around two to three years and a great deal of effort to grow fish to the size required for stocking. While the production cycles of rainbow and brown trout are similar, rainbow trout are farmed heavily for food and mostly sold for consumption directly from the farm, whereas brown trout are primarily farmed for restocking [9]. Fish typically arrive at the fishery about 9-20 months old [10], having been carefully checked for signs of disease and infection. While most fisheries buy fish from fish farms, some may be bought young and "grown on" in raceways or cages on site. Eggs are generally obtained from farmed broodstock. Fertilised eggs then hatch in tanks to eyed eggs, and again through alevin to fry, before being transferred to rearing tanks and raceways, where they are grown to marketable size over a period of 9-20 months. At this stage stock is sold to fisheries - while some broodstock may be retained in order to continue the production cycle.

Stocking habits can vary considerably between fisheries; some buy fully grown fish and stock them immediately into the water for anglers. Others may buy younger fish and grow them on in raceways or cages prior to stocking. Some fisheries are able to “trickle” stock regularly with small numbers of fish - adding roughly the same amount of fish that have been caught in the previous day or week, while others may receive deliveries of fish monthly, quarterly or even yearly.

Typically fisheries sell tickets to anglers, which allow them to catch a certain number of fish which they then take home. Some fisheries permit the catch and release of fish, while others prohibit this as it stresses fish and may increase mortality. The quality of fish can also differ between sites - at one end of the spectrum fisheries stock trout up to 14lbs in weight and stock to high densities to guarantee a catch, but charge a premium for this; while others stock to lower levels with smaller fish to provide a challenge for enthusiasts. Angler numbers also vary across sites and throughout the year; some fisheries being closed altogether in winter, and others remaining busy throughout the year. Although there was not enough data to justify the inclusion of seasonal capture rates in this thesis, real capture data from a fishery in England is used for parameter optimisation in chapter four.

1.3 PARASITE LIFE CYCLE AND DEVELOPMENT

The life cycles of *Argulus* spp. relevant to the UK are already well-documented [14, 37, 48, 54, 49]; however the specific parameters required for an accurate model of *A. foliaceus* have been published across many different papers. The aim of this section is to give an overview of the parasite's life cycle, and to collate the associated quantitative information available from the literature that is necessary to parameterise the *A. foliaceus* models presented in this thesis.

1.3.1 *Seasonality and hatching*

Overwintered eggs of *Argulus* spp. begin to hatch in spring when the water temperature reaches around 8-10 °C [46, 43]. For *A. foliaceus*, *A. coregoni*, and *A. japonicus*, the first two stages have been described as being so similar that it is very difficult to distinguish between them [40]. All three species hatch at a fairly advanced stage known as a metanauplius, with mouth tube and pre-oral spine present. Rushton-Mellor and Boxshall [40] describe 11 developmental stages of *A. foliaceus*, while *A. coregoni* has a total of nine [44].

Due to a shared minimum hatching temperature of between 8 and 10 °C, the seasonal life cycles of these three *Argulus* species vary across the world according to the temperature and length of the dormant period. It is thought that in Finland, where water temperatures are typically lower than in the UK, *A. coregoni* have only one true generation per year which hatches entirely from over-wintered eggs, and that the hatching period is extended throughout the year regardless of when the eggs were laid [15, 16]. Six overlapping cohorts and almost two full generations of *A. foliaceus* were observed over a 12-month period in five stillwater fisheries in England [51].

Of the six *A. foliaceus* cohorts described by Taylor et al. [51], three overwinter - two as eggs which hatch the following spring, and one hatched stage - although abundance is typically very low over the winter months [37, 51]. Taylor's data suggests that even overwintered eggs of *A. foliaceus* emerge at a time dictated by the time of egg-laying.

Bower-Shore [7] stated that eggs take 30-35 days to hatch, but did not specify the temperature, while Pasternak et al. [37] described hatching times of between 25 and 51 days in summer in a Finnish lake. Taylor et al. [51] estimated between 30-42 days from egg-laying to hatching at temperatures *ca.* 18 °C, and between 164-178 days at an average temperature of *ca.* 7 °C, although it should be noted that the last figure includes an overwintering period where eggs were unable to develop. Pasternak et al. [37] found *A. foliaceus* eggs which had been maintained at 5°C for 5 months began to hatch 24 days after they had been transferred to a temperature of 20 °C and continued to hatch for a further 4.5 months. The same authors reported that hatching success was reduced from 76% to 66% in this instance, relative to parasites which had been kept at a constant temperature.

Pasternak et al. [37] noted that the hatching period was significantly longer in a lake with low host density than a fish farm with a high concentration of hosts and suggested that this was a mechanism to ensure survival in periods when hosts are scarce. Hakalahti et al. [16] hypothesised that a significant proportion of *A. coregoni* eggs in Finland entered into an egg bank, similar to a plant's seed bank, hatching over an extended period in order to survive periods of low host availability; this implies that for *A. coregoni* the time at which eggs hatch is only weakly related to the time the eggs were laid. The use of length-frequency data by Taylor et al. [51], however, suggests that two overlapping cohorts of *A. foliaceus* overwinter as eggs, and these remain distinct throughout the hatching process, conserving the fixed hatching times.

1.3.2 *Attachment, distribution and host preference*

A key parameter in modelling host-parasite relationships is the transmission coefficient β, which is used to quantify the number of successful infections which occur per host per parasite in a given time period in a fixed geographical area or volume of water. For macroparasite models this is the product of the contact rate between hosts and free-living parasites and the proportion of contacts which result in successful infection, but is usually estimated without explicit calculation of the two factors. The transmission coefficient was estimated to be $0.001\text{m}^{-3}\text{day}^{-1}$ for *A. coregoni* in rainbow trout Pasternak et al. [36], Fenton et al. [11]. Most of the data required to calculate this for *A. foliaceus* on rainbow trout was given in Pasternak et al. [37], but the size of buckets used during the experiments was not provided so an accurate estimate cannot be found. With data provided in Mikheev and Pasternak [31] β was estimated as 0.0384 m^{-3} day $^{-1}$ (see Appendix A):

Aggregated parasite populations can be generated by heterogeneity within the host population; for example some colours of fish may be more easily seen and therefore more likely to become infected; however, Bandilla et al. [4] found that there was little or no difference in innate susceptibility of rainbow trout to *A. coregoni* and instead found that exposure time was crucial in determining the amount of lice attached to a fish. This is supported by communications with fishery managers (unpublished data) who believe that older fish which spent more time in the fishery tend to have higher burdens than the rest of the population. In addition, infected fish become stressed and suffer from reduced levels of activity, this in turn could make them likely candidates for repeated infection [4, 30].

A. foliaceus were shown to follow a negative binomial distribution on a number of different hosts [54], and different species of *Argulus* have often been described as aggregated on their hosts, such as *A. coregoni* on rainbow trout [4] and *A. foliaceus* on the stickleback *Gasterosteus aculeatus* [54]; indicating that a small minority of the host population harbour the majority of the parasites. Walker [54] also suggests that larval lice tend to be more aggregated than other stages, and become more dispersed as they mature. There is no evidence to suggest that trout acquire resistance to *Argulus* spp. following recovery from infection [14]; indeed Bandilla et al. [4] observed that *A. coregoni* had increased infection success with rainbow trout who had previously been infected compared to naive fish - the authors suggest that the stress caused by the first exposure may leave them more susceptible.

A common measure of a parasite's degree of aggregation is the parameter k' from the negative binomial distribution; small values of k' indicate that the level of aggregation is high, with a small number of hosts harbouring the majority of the parasite burden, while most hosts have few or no parasites. This parameter is used to calculate the probability that a fish harbours i parasites, which is given by:

$$\binom{i+k-1}{i}\left(\frac{k}{\mu+k}\right)^{k}\left(1-\frac{k}{\mu+k}\right)^{i} \tag{1.1}$$

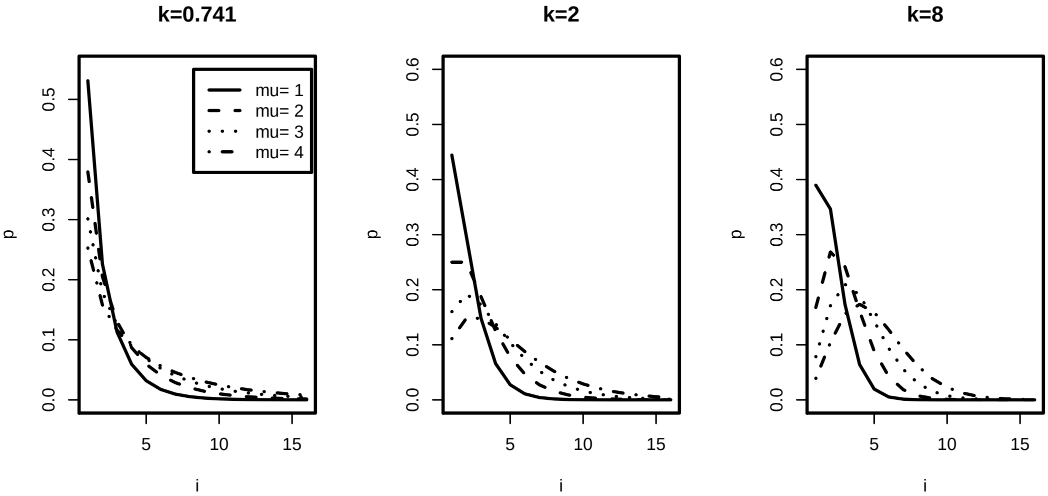

Figure 1.4: Probability density function for the negative binomial distribution

where μ is the mean number of parasites per host across the whole fish population. Figure 1.4 shows the probability density function for the negative binomial distribution, with i, the parasite burden, on the horizontal axis, and p, the probability that a given host harbours i parasites, on the vertical axis. The aggregation parameter, k', was estimated as 0.741 for *A. coregoni* on rainbow trout by Bandilla et al. [4], and in the absence of more appropriate data, is assumed to be similar for *Argulus foliaceus*.

Host specificity

As a generalist species, *A. foliaceus* is often found on species other than trout, although in the UK infections of trout cause more concern, since these represent the greatest economic loss. Walker [54] found that *A. coregoni* changed its host preference during its life cycle; larval and juvenile lice were more abundant on sticklebacks while carp and gudgeon *Gobio gobio* proved more popular with adult lice. A similar case has been recorded in the UK, where a large number of adult lice appeared on trout where there had previously been few sightings of juveniles. Since *Argulus* spp. could not reach adulthood without attaching to a host, it is most likely that the younger stages infected sticklebacks and other fish species resident in the lake (N. Taylor, personal communication).

1.3.3 *Development*

Once hatched, argulids have a short life expectancy unless they manage to attach to a suitable host; the maximum survival period varies considerably according to temperature, species, and developmental stage (see table 1.2).

Table 1.2: Maximum off-host survival times collected from the literature

Maximum off host survival time (days)				
Species	Stage	Days	Temperature (°C)	Source
A. foliaceus	Larval	5	15	Walker [54]
	Juvenile	7	15	
	Adult	14	9	
A. japonicus	Larval	9	22	Walker [54]
	Juvenile	9	22	
	Adult	13	15	
A. coregoni	Larval	7.25	16.5	Hakalahti [14]

Mikheev et al. [32] and Walker [54] found that newly-hatched *A. foliaceus* could survive a maximum of 5 days at 15 °C, and an average of around 2.10-3.26 days, while Shafir and Oldewage [42] and [54] found that *A. japonicus* survived a maximum of 9 days at 22 °C and an average of 2.39 to 5.17 days. Hakalahti [14] found *A. coregoni* survived a maximum of 7.25 days at 16.5 °C. Mean survival times for different life stages of all three species are given in table 1.3.

A. foliaceus reach maturity after 11 moults and unlike most copepods, continue to grow thereafter, these moults are detailed in Rushton-Mellor and Boxshall [40]. The parasites' rate of growth is related to temperature; Schluter [41] showed that this relationship is not linear and obtained the estimates in the second column of table 1.4. Taylor et al. [51] went

Table 1.3: Average off-host survival times collected from the literature

Mean off host survival time (days)			
Species	Stage	Days	Source
A. foliaceus	Larval	2.1-2.36	Mikheev et al. [32], Walker [54]
A. japonicus	Larval	2.39-5.17	Walker [54], Shafir and Oldewage [42]
	Adult	2.46-9.43	Walker [54]
A. coregoni	Juvenile	5.75	Hakalahti [14]

further and showed that development time in days, D from hatching to egg-laying can be estimated using the formula $D = 3900/G$, where the daily growth G in μm is given by $G = (0.434T + 0.361)^2$, T being the temperature (°C). These figures, and estimates from Kimura [24] for the maturation time of *A. japonicus* are given in table 1.4.

Table 1.4: Days from hatching to adulthood (reproduced from Taylor et al. [51])

Days from hatching to adulthood			
	A. foliaceus		*A. japonicus*
Temperature (°C)	Taylor et al. [51]	Schluter [41]	Kimura [24]
16	73	79	47
20	48	52	35
24	34	32	26

1.3.4 *Reproduction and egg laying*

A. foliaceus usually mate on the fish, but have been known to mate on stones or leaves [26]. *Argulus* spp. can mate multiple times, but it is thought that once is enough to fertilise all the eggs a female can produce.

It has also been shown that for *A. coregoni*, host switching of the male becomes significantly greater than the female when the parasites reach maturity, and this is further pronounced when there are no available mating partners on the same host [6].

Bower-Shore [7] found that, after mating, female *A. foliaceus* left their hosts to lay eggs on firm surfaces such as rocks in batches of around 100-150 eggs. Hakalahti et al. [18] found *A. coregoni* laid between 67 and 869 eggs in their study, with an average of 317, and found no correlation between the body length of the female and the number of eggs laid.

Kimura [24] found that *A. japonicus* only laid eggs in the dark under experimental conditions, while Harrison et al. [20] found that *A. foliaceus* laid their eggs throughout the day, but laid substantially more eggs during hours of daylight than hours of darkness.

Generally, mortality after egg-laying is high [7, 18], although Pasternak et al. [37] observed that female *A. foliaceus* returned to the host after the first egg laying; detaching again to lay a second batch within 2-4 days. For *A. coregoni* Hakalahti et al. [18] observed that 96% of females collected in July laid eggs only once, while in August 25% returned to the host and and laid another clutch within 1-9 days of the first laying. Despite this, no significant difference was found between the total number of eggs laid per female between the two months, or between females who laid once and twice. In Pasternak's study an average of 228 eggs were laid per female [37].

1.4.1 *The signs and impact of an* Argulus *spp. outbreak*

In summer months Walker [54] noted that an increase in the level of jumping exhibited by trout in a Norwegian fishery coincided with an increase in *Argulus* spp. abundance, and Bandilla et al. [5] noted that three rainbow trout infected with *A. coregoni* jumped out of their tanks during their study.

Unusual shoaling activities are often reported in the early stages of an infection, with fish swimming in tight circles, supposedly trying to rid themselves of the parasite [35, 38]. *Argulus* spp. induce fin damage, scale loss [35], and cause blood loss [48] in their hosts. Lesions caused by parasites leave fish susceptible to secondary infections, and it has been shown that *A. coregoni* significantly increases the likelihood of mortality in rainbow trout due to the bacterial infection *Flavobacterium columnare* [5].

As the parasite burden increases, fish become lethargic; suffering weight loss and becoming harder for anglers to catch as a consequence of reduced appetite and feeding. When fish are caught, there is usually a significant reduction in their aesthetic appeal, characterised by the presence of possibly hundreds of parasites, lesions, haemorrhaging, and general poor condition and weight [52]. Although mortality does occur in UK fisheries, the main problem associated with outbreaks of *Argulus* spp. is perceived to be the reduction in catch rates and loss of aesthetic appeal [50]. The decline in catch rates combined with some fish mortality means that *Argulus* spp. outbreaks not only have severe repercussions for fish welfare, but also for the affected fisheries and the trout fishing industry.

1.4.2 *Risk factors*

Taylor et al. [52] identified several risk factors such as low water clarity, slow stock turnover and high temperature as statistically significant in estimating parasite abundance, and suggested that an *Argulus* spp. infection may not be the sole cause of low catch rates. It is possible that high turbidity, temperature, or low turnover alone can prevent fish taking to bait, and when this occurs alongside an *Argulus* spp. infection, the reduction in catches caused by the parasite are exaggerated. Another possibility suggested by Taylor et al. [50] is that low water clarity is actually the result of fish rubbing themselves on the lake bed to dislodge the parasite. Since trout are visual feeders it is also possible that any predation by brown trout on unattached *A. foliaceus* [50] and *A. coregoni* [6] is decreased.

Bandilla et al. [4] found that fish who had been kept in captivity longer were more susceptible to infection, which supports a hypothesis that while fish may not have different innate susceptibility, they may become more vulnerable if not caught quickly - this would also partially explain why fisheries with lower stocking frequencies are more likely to suffer problem infections. Low stocking frequencies go hand in hand with lower catch rates, which means that infected fish and their parasites are less likely to be removed from the lake, further exacerbating the problem.

1.5 TACKLING *argulus* SPP. INFECTIONS

1.5.1 *Current methods*

One proposed solution to a severe *Argulus* spp. outbreak is to drain and lime the infected lake. A fallow period is also recommended, which involves the prolonged closure of the fishery and complete restocking before the fishery can open for business again - this means that any parasites surviving the draining of the lake would die due to the lack of hosts. This extreme measure is difficult and costly considering the low profit margins of most fisheries and the economic loss caused by the temporary closure. Draining and fallowing is also impossible for some large systems and does not guarantee that the problem will not return.

Slice (emamectin benzoate, Schering-Plough Animal Health) is a chemotherapeutant that can be delivered to fish in their feed before stocking, and has been shown to offer fish a finite period of protection against *Argulus* spp., paralysing and killing parasites that attach when the remaining dose is sufficiently high.

Slice is not licensed for use in rainbow trout, or against *Argulus* spp. in the UK, but can be administered under the veterinary cascade system. This states that fish must have 500 degree days withdrawal from the drug before they are stocked into the fishery and made available for consumption (Veterinary Medicines Directorate, Guidance on the use of the Cascade). The efficacy of the drug declines exponentially over time, so it is likely to be much reduced by the time fish come into contact with the parasites; there is therefore a great deal of concern that *Argulus* spp. will develop resistance to the treatment if it is not used responsibly, since a trace of the drug may remain for a significant time after the dose has dropped so far as to be ineffective. If the drug is to be used effectively in the UK, it is essential that it is used in a responsible and targeted manner to prevent, or delay, resistance development.

Fenton et al. [11] proposed that the proportion of *Argulus coregoni* eggs entering an "egg bank" had a significant effect on the outcome of treatment with Emamectin benzoate, and demonstrated that while high doses of treatment could sustain a lower abundance five years after treatment, this was reliant on only a small proportion of eggs entering the bank.

Gault et al. [12] showed that egg-laying boards suspended in the lake, cleaned, and replaced at regular intervals (thus removing a proportion of eggs laid) could be used to reduce parasite abundance. This method is costly, and may have a negative impact on the appearance of the lake. Work by Fenton et al. [11] found that while there was a linear relationship between the proportion of eggs removed by boards and the growth rate of the parasite population, and that egg-laying boards had a lasting effect five years later, this was also dependent on low levels of egg-banking. Hakalahti et al. [16] also noted that female *A. coregoni* had a preference for stones near the egg-laying boards, rather than the boards themselves, and suggested that for such apparatus to be effective, “ponds should not contain stones or any other hard substrata attracting female lice". Nevertheless, around 1.5 million eggs were destroyed during the same study, which would presumably have reduced the abundance of the following parasite generation.

1.5.2 *Study Aims*

Given the problems inherent in the current control methods, the first aim of this thesis will be to determine, using mathematical models, the impact of different fishery management strategies on the host-parasite dynamics, and to see whether these can be optimised to reduce the severity of an *Argulus* spp. outbreak. Such management strategies may involve increasing stock turnover and altering stocking patterns, since this has been shown to have a significant effect on parasite abundance by removing high numbers of juvenile *Argulus* spp. [52]. The optimised use of Slice and egg-laying boards will also be considered.

1.5.3 *Using mathematical models to find a solution to* Argulus *spp. infections*

Mathematical models have their origins in work by Malthus, for whom the malthusian growth model was named, after proposing that populations grow in a geometric, rather than linear, fashion [27]. In 1838 Verhulst named and published the logistic growth function, which sees population growth bounded by a carrying capacity dependent on some limiting factor, such as space or resources. Since then mathematical models have been further developed to capture the spread of disease within and between populations, and increasingly complex dynamics between species, such as predators and prey, parasites and their hosts.

While many models have been developed for use in terrestrial environments, aquatic systems have received relatively little interest.

1.5.4 *Macroparasite Modelling*

Microparasitic disease models can take many different forms, but the most popular have equations which model the rate of change of susceptible, infected, recovered or immune subclasses of a larger population, and are based on the assumption that disease is passed directly from host to host. Macroparasite models differ in that the parasite burden per host is generally a good measure of how ill the host is, and how likely they are to die as a result of the infection. Because of this it is necessary to distinguish not only between infected and susceptible hosts, but the distribution of parasites across their hosts.

The methods of infection are also different; while microparasitic infection almost always passes from host to host through contact with infected hosts or by birth, macroparasitic infections are often spread through contact with free-living, unattached stages of the parasite, so it is more appropriate to model this population explicitly with interaction between the host and free-living populations causing the bulk of infection, rather than contact with infected hosts.

A three-equation model describing hosts (H), attached parasites (P) and free-living stages (W), described in the equations below, was introduced by Anderson and May in 1978, and this will be used as a basis for the models in this research. Hosts reproduce at rate a, and die at rate b, while parasites reproduce at rate λ, die at rate d and attach to hosts at rate β, where they experience a lower rate of mortality, μ. A description of these parameters are given in table 1.5.

$$
\begin{aligned}
\frac{dH}{dt} &= (a-b)H - \alpha P \\
\frac{dP}{dt} &= \beta HW - (\mu+\alpha+b)P - \alpha k P^2/H \\
\frac{dW}{dt} &= \lambda P - dW - \beta HW
\end{aligned}
$$

The expected value, $E(i)$, of parasites per host is given by the mean - i.e. the total number of parasites divided by the total number of hosts; thus, the rate at which parasite-induced host mortalities occur is given by:

$$\alpha HE(i) = \alpha H\mu = \alpha H\frac{P}{H} = \alpha P \tag{1.2}$$

so that α gives the rate at which a single parasite kills a single host. The model carries the assumption that when a host dies, any parasites attached to it also die (in chapter three this is altered so that these parasites merely detach from the host). The expected number of parasites

Table 1.5: Definitions of parameters used in the *Argulus* spp. macroparasite model. Note that $k = (k' + 1)/k'$.

Parameter and variable fefinitions	
H	host density
P	attached parasite density
W	unattached parasite density
a	host reproductive rate
b	host mortality rate
α	increased host mortality due to infection
β	rate of attachment
μ	mortality of attached stages
d	mortality of free-living stages
k'	inverse aggregation coefficient
λ	parasite birth rate

on a host killed by the parasite is given by $E(i^2)$, which, for parasites following a negative binomial distribution, is given by:

$$
\begin{aligned}
E(i^2) &= \mu + \left(\frac{k'+1}{k'}\right)\mu^2 && (1.3)\\
&= \frac{P}{H} + \left(\frac{k'+1}{k'}\right)\frac{P^2}{H^2} && (1.4)
\end{aligned}
$$

When this is multiplied through by αH, the result is $\alpha P + \alpha k P^2/H$, as shown in the model (note that $k = (k'+1)/k'$).

When $a > b$, the host population grows exponentially in the absence of parasitic infection. Analysis of the model shows that if the rate of reproduction of the parasite is sufficiently high relative to its loss rates, then the parasite regulates the host population to an equilibrium value. If $a < b$ then both populations go extinct.

Many macroparasite models have been based on this model; Fenton et al. [11] developed models which were modified to account for the effects of "egg-banking" by *A. coregoni* in Finnish fish farms. They assumed a constant host population and highlighted the effects of variability in hatching rates and the presence of a parasite egg bank on control methods such as egg-laying boards and treatment with Slice.

Models developed here will be tailored specifically for *A. foliaceus* in UK stillwater fisheries. While it is hoped that the models could potentially be applied to other situations across the world, one factor which distances the work here from Fenton's is the extended hatching period suggested by Hakalahti et al. [16], (see section 1.3.1). *A. coregoni* in Finland only have one reproducing generation each year, while *A. foliaceus* have almost two full generations, and *A. foliaceus* hatch throughout the year in a fairly coordinated manner related to the time they were laid. This means well-timed treatment is more likely to be successful here in the long term, since egg-banking is not a concern for this species.

The models will be adapted to allow for different stocking rates and frequencies. Different harvesting rates which vary with temporal conditions such as host density and parasite burden will also be examined.

The parameters likely to be required in constructing the model are given and described in Appendix A. Some of these are readily available in the literature while in some cases figures for *A. coregoni* are given where estimates for *A. foliaceus* have not been found. In chapter four stocking data from one of the five sites studied by Taylor et al. [52] is incorporated into the model and used to optimise some of the remaining parameters.

1.6 THESIS OUTLINE

Chapter one provides a review of the literature available on *Argulus* spp. which is relevant to the modelling aims. In chapter two, Anderson and May's model is adapted to examine the impact of different stocking regimes on the survival of the parasite, and the consequences of this on fish mortalities and rod capture are also investigated. Additionally the impact of a parasite-induced reduction in fish capture is analysed.

In chapter three further adaptations are made to the model to improve its biological realism and facilitate analysis in subsequent chapters of this thesis. Similarly, in chapter four seasonality is added to the model to reflect the highly seasonal life cycle of *Argulus* spp., and the available data is used to optimise several of the model parameters.

In chapter five the impact of stocking on the parasite is again addressed, this time specifically the timing of stocking events, and the differences that might be expected when fish are stocked less frequently (models prior to this assume continuous stocking throughout the year). In chapter six chemical intervention with emamectin benzoate is modelled, and the potential impact of a reduction in the withdrawal period required before fish are stocked into the fishery for capture is examined. The potential efficacy of egg-laying boards, and the impact of their removal rate is also addressed.

2

STOCKING METHODS AND PARASITE-INDUCED REDUCTIONS IN CAPTURE

The following work has been published under the title "Stocking methods and parasite-induced reductions in capture: modelling Argulus foliaceus *in trout fisheries" in the Journal of Theoretical Biology (N.J. McPherson, R.A. Norman, A.S. Hoyle & N.G.H. Taylor, 2012). The following chapter is largely a reproduction of the paper, though some points have been expanded upon for inclusion in this thesis.*

The aim of this chapter is to determine the impact of four commonly used fish stocking methods both on the parasite dynamics, and on fisheries' yields. The wider consequences of the resultant reduction in host feeding are also of interest. To this end four different stocking methods were incorporated into Anderson and May's macroparasite model [28], which comprises three differential equations representing the host, attached parasite and free-living parasite populations. To each of these, a reduction in the fish capture rate, inversely linked to the mean parasite burden is added and the effects interpreted. Results show that 1) the common practice of increasing the stocking rate as catches drop may be counterproductive; 2) in the absence of any wild population of reservoir hosts, the parasite will be unable to survive if the stocking rate does not exceed the rate of capture; 3) compensatory stocking to account for fish mortalities can have disastrous consequences on yield; and 4) the parasite can, under certain circumstances, maintain the host population by preventing their capture.

INTRODUCTION

Species of *Argulus* are ectoparasites, which are able to infect a wide variety of fish, but in the UK have a significant impact on rainbow (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*).

While infections are generally of little concern in natural environments, in stocked fisheries - and under some circumstances in fish farms - the consequences can be more severe [50, 35].

In the UK *Argulus* spp. have been estimated to cause problems in over 25% of managed recreational trout fisheries [50]. Three species are known to be present in the UK: *Argulus foliaceus*, *A. coregoni* and *A. japonicus*, but *A. foliaceus* is the most prevalent. Although mortality due to infection can occur, the biggest perceived threat is economic, caused by decreased angler attendance, attributed to reduced aesthetic appearance of fish and difficulties in catching them, due to reduced feeding suggested to be a consequence of parasitism [50]. Infections by *Argulus* spp. cause damage to the host skin, leaving fish more vulnerable to secondary infections [5]. The parasite can also induce considerable stress - in the early stages of infection this results in increased shoaling and flashing, but eventually leads to morbidity, loss of appetite, and in severe cases, death (e.g. [35]).

Currently, attempts to reduce *Argulus* spp. infections in trout fisheries centre on the use of: 1) an in-feed chemotherapeutant, emamectin benzoate (Slice Schering-Plough Animal Health) fed to fish prior to stocking that subsequently provides a finite period of protection from infection [16], 2) the use of substrates suspended in the water column or on the surface that allow parasite eggs to be collected and removed [12], and 3) in the most extreme cases, draining, drying the fishery and applying lime to kill all eggs prior to refilling and stocking with uninfected fish. All of these measures can be logistically difficult, labour intensive and highly variable in their effectiveness. Emamectin benzoate potentially offers the most effective method of control at present, however, with only this chemotherapeutant available, there are concerns that resistance will develop. Additionally, the logistics and costs of administering this treatment effectively may be prohibitive for some. While research has shown that removable egg-laying substrates may reduce the level of infection, the long term efficacy of this has yet to be proven in a fishery context. Additionally, the number of these structures, and the labour required to remove and replace them regularly enough to destroy sufficient eggs to break the parasites life-cycle is high, and may affect the aesthetics of the fishery. Their efficacy may also be compromised by the presence of abundant natural egg-laying surfaces such as rocks and sunken logs. Draining, drying and liming a fishery is extremely labour intensive, and impossible for many sites; although fishery owners report it to successfully reduce *Argulus* spp. burdens for several years, in the long term, high infection levels often return.

Given the problems associated with each of these treatments, altering fishery management practices may provide a more effective and sustainable way of reducing the impact of *Argulus* spp. infections. Low water clarity and slow stock turnover rates (the time taken to remove and replace the standing stock of fish) are associated with problem infections [50, 52]. Although altering water clarity may be difficult for a fishery owner, stocking practices are subject to their direct control. At present, the effects of different stocking regimes on *A. foliaceus* dynamics in fisheries is unknown, but could be key in minimising the impact of such infections [50].

All fisheries are different in the way they are managed, however stocking practices can be divided into two broad categories: batch stocking, where several large batches of fish are stocked in a year, and trickle stocking, where relatively small numbers of fish are stocked frequently, on a daily, weekly or monthly basis. In this study, the focus is on the latter, which is commonly used in smaller fisheries, which in turn are most commonly affected by *Argulus* spp. infections.

The aims of this study were to develop mathematical models which describe the host-pathogen dynamics of *Argulus* spp. and trout in fisheries, under different stocking regimes and levels of fishing pressure, and to determine the effects of parasite-induced reductions in catch rates on these dynamics. To this end, the following (generalised) trickle stocking practices that a fishery owner may adopt in the presence of, or response to, an *Argulus* spp. infection were investigated: 1) Constant - an equal number of fish are stocked at each time point regardless of capture or mortality rates; 2) Replacement - all fish caught are replaced, but no adjustment for mortality is made; 3) Compensatory - all fish caught are replaced, and additional fish are also added to compensate for mortality, and finally, 4) Reactionary - where a fishery owner stocks at a level required to maintain a specific capture rate, rather than to replace dead or captured fish. Each model was analysed with and without a parasite-induced reduction in catch rate, to identify the influence this might have on the resulting dynamics.

These models are based on those developed by Anderson and May ([1], [28]), which have also been used to model the influence of egg-banking by *Argulus coregoni* on population dynamics in Finland [11].

Introduction to the model

Throughout this chapter the following model is modified to include different fish capture rates and stocking methods. The equations below represent the rates of change of the fish, attached parasite and free-living juvenile parasite population densities which are given by H, P, and W respectively. The free-living parasites are modelled separately as *Argulus* spp. lay their eggs off the host, and the survival rates of unattached parasites are significantly lower than those attached to a host.

$$\begin{aligned}\frac{dH}{dt} &= s(H) - Hc(H,P) - \alpha P\\ \frac{dP}{dt} &= \beta HW - P(\mu + c(H,P) + \alpha) - \alpha k\frac{P^2}{H}\\ \frac{dW}{dt} &= \lambda P - dW - \beta HW\end{aligned}$$

The increased rate of host mortality per parasite per host is given by α, and therefore $\alpha H\frac{P}{H} = \alpha P$ determines the mean rate at which hosts die due to infection. The parameter β is the rate at which free-living parasite stages attach to the fish; μ is the attached parasite's mortality rate, and λ and d are the birth and mortality rates of the free living stages respectively. The derivation of the $\alpha P(1 + k\frac{P}{H})$ term is fully explained in May and Anderson [28] (and reiterated in chapter one of this thesis), and is the rate at which attached, overdispersed parasites die due to the increased mortality they inflict upon their hosts. The parameter k is shorthand for $(k' + 1)/k'$, where k' is an inverse measure of aggregation of the parasites across their hosts used to parameterise the negative binomial distribution (analysis by the authors of unpublished data from [51] shows that *A. foliaceus* are aggregated on their hosts, and Bandilla et al. [4] provided an estimate of k' for *A. coregoni*).

Table 2.1: Definitions of parameters used in the *Argulus* spp. macroparasite model. Note that $k = (k' + 1)/k'$.

Parameter Estimates and Definitions	
Parameter	
s	host stocking rate
c	(optimum) capture rate
α	increased host mortality due to infection
β	rate of attachment
μ	mortality of attached stages
d	mortality of free-living stages
k'	inverse aggregation coefficient
λ	parasite birth rate

Descriptions of the parameters are summarised in table 2.1, and a schematic representation of the model is given in figure 2.1.

The stocking rate, $s(H)$, was altered in each model. The capture rate was given by $c(H, P) = c$ initially, and was multiplied by $e^{-\theta P/H}$ to express the parasite-induced reduction in capture rate, giving $c(H, P) = ce^{-\theta P/H}$, to reflect the fact that the catch rate is a maximum of c with no infection, and tends to zero when the mean parasite burden is very high.

Throughout this paper the steady states of the models are calculated by setting the right-hand side of each model equation equal to zero. The steady states are found by solving these to give expressions for the host, attached parasite, and free-living parasite population sizes in terms of the other parameters. The stability of these equilibria was then determined using standard methods of analysis (e.g. [33]).

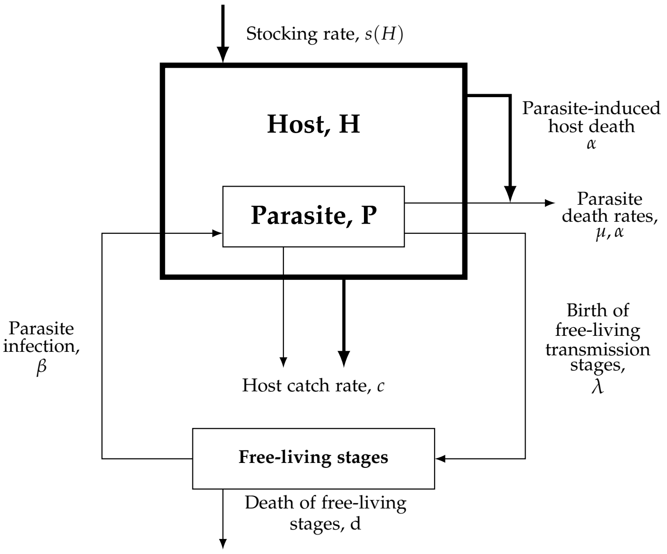

Figure 2.1: Schematic representation of the *Argulus* spp. macroparasite model: hosts (fish), are added at rate s(H), and removed only by capture or parasite-induced mortality; parasites hatch from eggs into the free-living compartment, and attach to hosts at rate β. As well as being removed by natural and self-induced mortality (since parasites die when their hosts die), parasites are also removed when their host is caught.

2.1 BASELINE MODEL

The case where $s(H) = aH$ and $c(H,P) = c$ was fully analysed in May and Anderson [28]. While this model is not appropriate for investigating stocked fish populations, as the host growth rate increases with the host density, it has clear applications to other fish that *Argulus* spp. can infect, such as brown trout and sticklebacks, natural populations of which are often present in the same fisheries as *O. mykiss*, and may provide a reservoir for *Argulus* spp. infection even when no fish are stocked. This model is included here to show the impact of the reduction in capture on a well-known model, and also to provide a point of departure for the other models presented in this paper.

Anderson and May's convention of using a as the host reproduction rate is retained here - other parameters will be used in later models to denote artificial stocking. For this paper, the host mortality rate is replaced with a capture rate, c - natural fish mortalities are neglected since they are often low in fisheries, and are not a primary concern of this research.

Constant catch rate

The model and results, (as analysed in May and Anderson [28]) are

$$\begin{aligned}
\frac{dH}{dt} &= aH - cH - \alpha P \\
\frac{dP}{dt} &= \beta HW - P(\mu + \alpha + c) - \alpha k \frac{P^2}{H} \\
\frac{dW}{dt} &= \lambda P - dW - \beta HW.
\end{aligned}$$

The system has equilibrium

$$H^* = \frac{d\gamma}{\beta(\lambda - \gamma)} \tag{2.1}$$

$$P^* = \frac{H^*}{\alpha}(a - c) \tag{2.2}$$

$$W^* = \frac{\gamma}{\beta}(a - c), \tag{2.3}$$

with $\gamma = k(a - c) + \mu + \alpha + c$. The birth rate, a, must exceed the catch rate, c, in order for the host to survive; if this condition is violated then both host and parasite die out. If $a > c$ and the hatching rate of the parasite exceeds the sum of attached parasite losses at the coexistence equilibrium ($\lambda > \gamma$), then the parasite is able to establish itself and regulate the host population to the equilibrium above, otherwise the host population grows exponentially.

2.1.1 *Parasite-induced reduced catch rate*

Taking into account the parasite-induced reduction in capture, the model becomes:

$$\begin{aligned}
\frac{dH}{dt} &= aH - ce^{-\theta P/H}H - \alpha P \\
\frac{dP}{dt} &= \beta HW - P(\mu + \alpha + ce^{-\theta P/H}) - \alpha k \frac{P^2}{H} \\
\frac{dW}{dt} &= \lambda P - dW - \beta HW.
\end{aligned}$$

The severity of catch rate reduction per parasite per host is given by θ, and the model is equivalent to the baseline model when $\theta = 0$. The exponential term makes it possible to express the equilibrium values only by using a manipulation of the Lambert W function (for an overview and history of this function see [8]). The first equation is set equal to zero and rearranged so that:

$$e^{-\theta \frac{P^*}{H^*}} = \frac{a}{c} - \frac{\alpha}{c} P^*/H^*. \tag{2.4}$$

Although this is analytically intractable, by noting that the solution of $e^{Ax+B} = Cx + D$ can be expressed as

$$x = -\frac{\omega\left[-\frac{A}{C} e^{B - \frac{AD}{C}}\right]}{A} - \frac{D}{C}, \tag{2.5}$$

where ω represents the Lambert W function, and by letting $x = \frac{P^*}{H^*}$, it can be deduced that for this model the mean parasite burden is given by

$$\frac{P^*}{H^*} = \omega\left[\frac{-c\theta e^{\frac{-a\theta}{\alpha}}}{\alpha}\right]/\theta + \frac{a}{\alpha}. \tag{2.6}$$

Letting $\nu = \omega[-\frac{c\theta}{\alpha} e^{-a\theta/\alpha}]/\theta + \frac{a}{\alpha}$ and $\gamma_\omega = \mu + \alpha + ce^{-\theta\nu} + \alpha k \nu$ the following equilibrium can be found:

$$H^* = \frac{d\gamma_\omega}{\beta(\lambda - \gamma_\omega)} \tag{2.7}$$

$$P^* = \frac{H^*}{\alpha(k-1)}\left[\frac{\beta H^* \lambda}{\beta H^* + d} - \mu - \alpha - a\right] \tag{2.8}$$

$$W^* = \frac{\lambda P^*}{\beta H^* + d}. \tag{2.9}$$

The necessary conditions for existence of a coexistence equilibrium are now $\lambda > \gamma_\omega$ and $a > \frac{\alpha}{\theta}(1 + \ln\frac{c\theta}{\alpha})$ (since $\omega[x]$ only has a real solution if $x > -1/e$). The characteristic equation $\Lambda^3 + a_1\Lambda^2 + a_2\Lambda + a_3 = 0$ of the Jacobian matrix evaluated at the (H^*, P^*, W^*) equilibrium has coefficients

$$a_1 = \beta H^* \lambda + \beta H^* + d + \alpha\frac{P^*}{H^*}(k-1) \tag{2.10}$$

$$a_2 = \beta H^*(\lambda - \mu - \alpha - a) - d(\mu + \alpha + a) \tag{2.11}$$

$$a_3 = d\beta W(\alpha - ce^{-\theta P/H}). \tag{2.12}$$

Trivially, $a_1 > 0$, and $a_2 > 0$ as long as the condition that the parasite's hatching rate must exceed its loss rates ($\lambda > \gamma_\omega$) is met. For a_3 to be greater than zero the parasite-induced death rate must exceed the effective equilibrium catch rate ($\alpha > ce^{-\theta\nu}$).

For this model, the hatching and birth rates must be sufficiently high for the coexistence equilibrium to be positive, eg. $\lambda > \gamma_\omega$ and $a > \frac{\alpha}{\theta}(1 + \ln \frac{c\theta}{\alpha})$. If the hatching rate is low then the parasite will die, and the host population will either grow exponentially if births exceed catches ($a > c$), or die out if $a < c$. If the hatching rate is sufficiently large, then coexistence will always occur if the birth rate exceeds the catch rate. Depending on the initial state of the system, coexistence may also be possible even when the host birth rate is lower than the maximum catch rate, if $a > \frac{\alpha}{\theta}(1 + \ln \frac{c\theta}{\alpha})$ and $\theta > \alpha/c$.

In order to illustrate the dynamics more clearly, a bifurcation diagram is presented in figure 2.2. For $a < \frac{\alpha}{\theta}(1 + \ln \frac{c\theta}{\alpha})$ the coexistence equilibrium value is complex and unstable; the real part of this solution is shown. A branching point occurs at $a = \frac{\alpha}{\theta}(1 + \ln \frac{c\theta}{\alpha})$, and if this point is positive (i.e. if $\theta > \alpha/c$), then between this point and $a = c$ the system exhibits hysteresis. Both the mean parasite burden and the range of values of a for which bistability occurs increase as θ increases. For $a > c$ only the coexistence equilibrium is stable (assuming the parasite reproduction rate is sufficiently high).

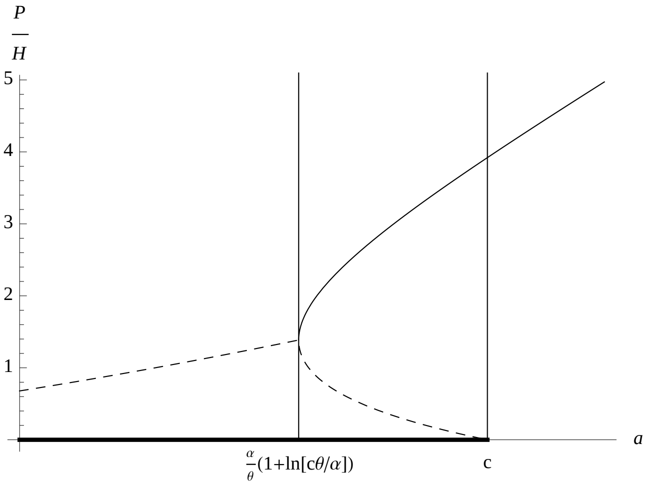

Figure 2.2: Bifurcation diagram of mean parasite burden plotted against host birth rate ($0 < a < 0.042$) for the baseline reduced capture model with $c = 0.04$, $\theta = 0.1$, and $\alpha = 0.001$: the solid lines represent the stable equilibria, while the dotted lines represent the unstable equilibria (below $a = \frac{\alpha}{\theta}(1 + \ln(c\theta/\alpha))$ the solution is complex, the real part is shown). Note that the host-only equilibrium, represented by the thick line along the horizontal axis, is stable for $a < c$.

In essence, this shows that the invasion threshold for the parasite is higher than the exclusion threshold; while it may be sufficient to keep $a < c$ to avoid an outbreak, once the parasite is established, stronger control measures will be needed in order to eradicate it.

In the baseline model, $a > c$ was a necessary condition for the survival of the host. With the inclusion of the reduced catch rate this is no longer the case since the parasite provides protection from capture for its host (and itself) by making the fish more difficult to catch. This result is somewhat counterintuitive - in general parasites reduce their hosts' ability to survive, but in this model the host is able to survive under conditions which would usually bring about its extinction, as a direct result of the infection.

2.2 CONSTANT STOCKING

The baseline model had a growth rate proportional to the population size, which is useful for wild populations, but not appropriate to describe a system in which fish are stocked artificially and do not actually reproduce, such as a stillwater rainbow trout fishery. A constant stocking rate is considered in this model, with $s(H) = s$; which is equivalent to fishery managers stocking the same number of fish per unit time regardless of how many are being caught.

Constant catch rate

The model becomes:

$$\frac{dH}{dt} = s - cH - \alpha P$$
$$\frac{dP}{dt} = \beta HW - P(\mu + \alpha + c) - \alpha k \frac{P^2}{H}$$
$$\frac{dW}{dt} = \lambda P - dW - \beta HW$$

Two equilibria are present: $(H^*, P^*, W^*) = (s/c, 0, 0)$, which is stable when

$$s < \frac{cd(\mu + \alpha + c)}{\beta(\lambda - \mu - \alpha - c)}, \tag{2.13}$$

and

$$\begin{aligned}
H^* &= \frac{1}{2}\left[\frac{d\gamma + \beta sk}{\beta(\lambda-\gamma)} \pm \sqrt{\left(\frac{d\gamma + \beta sk}{\beta(\lambda-\gamma)}\right)^2 + 4\frac{dsk}{\beta(\lambda-\gamma)}}\right] \\
P^* &= \frac{H^*}{\alpha k}\left[\frac{\beta H^* \lambda}{\beta H^* + d} - \mu - \alpha - c\right] \\
W^* &= \frac{\lambda P^*}{\beta H^* + d},
\end{aligned}$$

where $\gamma = \mu + \alpha - c(k-1)$. There is always a unique positive solution for the H^* expression, since the first fraction inside the brackets will always be smaller than the square rooted term. For P^* to be positive, the hatching rate of the parasite must be higher than its combined loss rates at the host-only equilibrium ($\lambda > \mu + \alpha + c$), and the host density must exceed the quantity

$$H_{crit} = \frac{d(\mu + \alpha + c)}{\beta(\lambda - \mu - \alpha - c)}, \tag{2.14}$$

Combining the two gives:

$$s > \frac{cd(\mu + \alpha + c)}{\beta(\lambda - \mu - \alpha - c)}. \tag{2.15}$$

Thus $(s/c, 0, 0)$ is stable when condition 2.13 is met, and the coexistence equilibrium exists when it is not. It can be shown, using linear stability analysis, that the (H^*, P^*, W^*) equilibrium is always locally stable for positive equilibrium values. The mean parasite burden at equilibrium can be expressed as

$$\frac{P^*}{H^*} = \frac{1}{\alpha k}\left(\frac{\beta H^* \lambda}{\beta H^* + d} - \mu - \alpha - c\right), \tag{2.16}$$

and this demonstrates that the mean parasite burden grows as the host population grows (although the mean parasite burden has a limit of $(\lambda - \mu - \alpha - c)/\alpha k$ as $H \to \infty$). A high stocking rate, s, is a prerequisite for infection (since the stocking level must be sufficiently high for the coexistence equilibrium to be stable), and further increases of the stocking rate beyond this point will increase the density of the host population as well as the mean parasite burden.

2.2.1 *Parasite-induced reduced catch rate*

The model was then altered so that $c(H,P) = ce^{-\theta P/H}$; the parasite-free equilibrium remains unchanged, and the condition for its stability remains unchanged. Now for the coexistence equilibrium

$$\frac{P^*}{H^*} = \frac{1}{\alpha(k-1)}\left[\frac{\beta H^* \lambda}{\beta H^* + d} - \mu - \alpha - \frac{s}{H^*}\right], \tag{2.17}$$

and

$$ce^{-\theta\frac{P}{H}} = \frac{s}{H} - \alpha\frac{P}{H}. \tag{2.18}$$

An exact analytic solution could not be found for H^*, however, upper and lower bounds can be found by letting $e^{-\theta P/H} = 0$ and $e^{-\theta P/H} = e^{-\theta\frac{(\lambda-\mu-\alpha)}{\alpha(1-k)}}$ (since P^* saturates at $\frac{(\lambda-\mu-\alpha)}{\alpha(k-1)}$ as $H^* \to \infty$) as follows:

$$H^* > \frac{\frac{\beta sk+d\gamma_1}{\beta(\lambda-\gamma_1)} + \sqrt{\left(\frac{\beta sk+d\gamma_1}{\beta(\lambda-\gamma_1)}\right)^2 + \frac{4dsk}{\beta(\lambda-\gamma_1)}}}{2}$$
$$H^* < \frac{\frac{\beta sk+d\gamma_2}{\beta(\lambda-\gamma_2)} + \sqrt{\left(\frac{\beta sk+d\gamma_2}{\beta(\lambda-\gamma_2)}\right)^2 + \frac{4dsk}{\beta(\lambda-\gamma_2)}}}{2},$$

where $\gamma_1 = \mu + \alpha - ce^{-\theta\frac{(\lambda-\mu-\alpha)}{\alpha(k-1)}}(k-1)$ and $\gamma_2 = \mu + \alpha - c(k-1)$. The condition for existence of a positive P^* is now:

$$H^* > \frac{1}{2}\left[\frac{\beta s + d(\mu+\alpha)}{\beta(\lambda-\mu-\alpha)} + \sqrt{\left[\frac{\beta s + d(\mu+\alpha)}{\beta(\lambda-\mu-\alpha)}\right]^2 + \frac{4ds}{\beta(\lambda-\mu-\alpha)}}\right]. \tag{2.19}$$

As in the previous model, if $s > \frac{cd(\mu+\alpha+c)}{b(\lambda-\mu-\alpha-c)}$, only the coexistence equilibrium is stable. Now, however, it is also possible for the parasite to persist if the stocking level is slightly lower than this threshold. Simulations for a range of parameters show that, providing that (2.18) has a real, positive solution, hysteresis occurs for a set of values of s such that $s < \frac{cd(\mu+\alpha+c)}{b(\lambda-\mu-\alpha-c)}$, and either the host-only or coexistence equilibrium can be reached depending on the initial conditions. In addition, if θ is high relative to α the reduction in capture may mean that the coexistence host density is higher than it is in the absence of the parasite. Biologically this is explained by the level of capture reduction exceeding the increased rate of host mortality.

To model replacement stocking, where the number of fish caught are replaced exactly, the stocking rate is set equal to the catch rate.

Constant catch rate

The constant catch rate model is given by:

$$\frac{dH}{dt} = -\alpha P$$
$$\frac{dP}{dt} = \beta HW - P(\mu + \alpha + c) - \alpha k \frac{P^2}{H}$$
$$\frac{dW}{dt} = \lambda P - dW - \beta HW.$$

From the first equation it is clear that the only possible equilibrium value for the parasite population is $P^* = 0$, and it follows that $W^* = 0$. While the parasite is present, it will reduce the number of fish until there are eventually too few fish to maintain an infection.

The host population stabilises at a level determined by the initial population sizes when the parasite population reaches zero. The size of the resultant reduction in the host population size will also depend on the difference between the parasite's gain and loss rates - if λ is large relative to the other rates then the infection will be more prolonged and will result in more host mortalities. Increasing the stock turnover (c) reduces the damage done to the host population.

2.3.1 *Parasite-induced reduced catch rate*

Since the stocking rate is equal to the catch rate, the host equation remains unchanged when the catch rate is reduced. Reducing the catch rate in this case simply increases the survival time of the parasite. The host population stabilises when the parasite dies out, however, extinction of the parasite takes longer, and the host population suffers more as a result.

In this model, all fish that are caught are replaced, so that the cH term is eliminated from the model (as in the replacement model), and mortalities are also compensated for according to the equation:

$$dH/dt = \alpha P(q-1). \tag{2.20}$$

When the proportion of host mortalities replaced, q, is zero, the model is equivalent to the replacement model; when $0 < q < 1$, $100q\%$ of mortalities are replaced with “fresh" fish, and when $q = 1$ fish mortalities are compensated for precisely. If $q > 1$ then mortalities are over-compensated for.

The case where $q = 0$ has already been dealt with in the replacement model, and when $q < 1$ the analysis is quite similar - the parasite population will still die out, as the host population will become too small to sustain it, however the parasite may persist longer than when $q = 0$ due to the increased availability of hosts.

The stability of the $(H^*, 0, 0)$ equilibrium can be analysed to a certain extent. If $q = 1$ then $H^* = H[0]$ (the host population size does not change), and the survival of the parasite is dependent on the condition $\lambda > \gamma$ (where $\gamma = \mu + \alpha + c$), and whether the initial host population is large enough to sustain the parasite. To determine this threshold host population, the characteristic equation of the system, with H^* as an unknown and $P^* = W^* = 0$ is given by:

$$\Lambda[\Lambda^2 + \Lambda(\beta H^* + d + \gamma) + \gamma(\beta H^* + d) - \beta H^* \lambda] = 0. \tag{2.21}$$

The eigenvalues are negative providing the condition

$$H^* < H_{crit} = \frac{\gamma d}{\beta(\lambda - \gamma)} \tag{2.22}$$

is met. Thus, if mortalities are known and compensated for exactly, and the number of fish present is known, it is possible to determine whether or not an influx of parasites is likely to result in an on-going infection by comparing the fish density to the quantity H_{crit}. If the fish density exceeds H_{crit} then the parasite populations are given by:

$$P^* = \frac{H[0]}{\alpha k}\left[\frac{\beta H[0]\lambda}{\beta H[0] + d} - \mu - \alpha - c\right] \tag{2.23}$$

$$W^* = \frac{\beta H[0]\lambda}{\beta H[0] + d}. \tag{2.24}$$

If $q > 1$ and $H[0] > H_{crit}$ then the host and parasite populations will grow unboundedly. If $q > 1$ and $H[0] < H_{crit}$ then the outcome depends on which of two processes happens first - either the parasite population going extinct, or the host population reaching its critical value. Since the rate of growth of the host population depends on the parameter q, the larger q is, the more likely that the parasite will persist. This scenario results in the parasite and host populations growing exponentially, but this is a highly unlikely outcome. Numerical simulations show that if the host density were below its critical value before the infection began, then the influx of parasites would have to be extremely large in order to effect a substantial increase in the host density and allow the parasite to persist. Secondly, if the host population is initially low, then the managers of such a fishery would presumably be less likely than most to adopt an over-compensatory approach to stocking.

2.4.1 *Parasite-induced reduced catch rate*

In the baseline model with a parasite-induced reduction in catch rate, the mean parasite burden was estimated by a manipulation of the Lambert W function. The same technique is used in this model, so that, when $q = 1$:

$$H^* = H[0] \tag{2.25}$$

$$P^* = H[0]\left[\omega\left[\frac{-c\theta}{\alpha k}e^{-\theta\eta}\right]/\theta + \eta\right] \tag{2.26}$$

$$W^* = \frac{\beta H[0]\lambda P^*}{\beta H[0] + d}, \tag{2.27}$$

with $\eta = \frac{1}{\alpha k}\left[\frac{\beta H[0]\lambda}{\beta H[0]+d} - \mu - \alpha\right]$.

By noting that $\omega[x]$ has real solutions only if $x > -e^{-1}$, a critical value of H^* for the reduced system can be found:

$$H_{crit_2} = \frac{d\psi}{\beta(\lambda - \psi)}, \tag{2.28}$$

with $\psi = \frac{\alpha k}{\theta}(1 + \ln[\frac{c\theta}{\alpha k}]) + \mu + \alpha$.

For this model $\alpha k > ce^{-\theta P/H}$ is needed for stability of the coexistence equilibrium, and hysteresis occurs when $\theta > \frac{\alpha k}{c}$. Since $H_{crit} \geq H_{crit_2}$ always, the parasite is able to survive at a lower host density when the reduced catch rate is taken into account, depending on the initial conditions. Biologically, this is because parasites are being removed at a slower rate, and also have more time to infect fish which are being turned over at a slower rate.

2.5 REACTIONARY STOCKING

Some fisheries in the UK are stocked on a “reactionary" basis in order to maintain a desirable “rod average" (mean number of fish caught per visiting angler); in practice this means that a fishery manager will stock more fish as a reaction to low catch rates, and fewer if too many fish are being caught.

Constant catch rate

Under the assumption of a constant catch rate, the reactionary stocking rate is given by:

$$s(H) = \frac{\bar{c}(\bar{c}+1)}{cH+1}, \tag{2.29}$$

where $\bar{c}$ is the fishery’s “desired" catch rate of fish per day. This allows the stocking rate to become high when few fish are being caught, and low when too many fish are being caught. When the desired catch rate is met, $cH = \bar{c}$ (note that the parameter c is fish caught *per fish per* *day*, while $\bar{c}$ has units of fish *per day*) and the catch and stocking rates are equal. The model is now:

$$\frac{dH}{dt} = \frac{\bar{c}(\bar{c}+1)}{cH+1} - cH - \alpha P \tag{2.30}$$

$$\frac{dP}{dt} = \beta HW - P(\mu+\alpha+c) - \alpha k\frac{P^2}{H} \tag{2.31}$$

$$\frac{dW}{dt} = \lambda P - dW - \beta HW. \tag{2.32}$$

The simple, host only equilibrium is now $(\frac{\sqrt{1+4\sigma}-1}{2c}, 0, 0)$, $(\sigma = \bar{c}(\bar{c}+1))$. The characteristic equation for this equilibrium is:

$$\left(\Lambda + c + \frac{c\sigma}{(cH+1)^2}\right)(\Lambda^2 + \Lambda(\gamma+d+\beta H) + \gamma(d+\beta H) - \beta H\lambda), \tag{2.33}$$

with $\gamma = \mu+\alpha+c$. The first term in brackets shows that the first eigenvalue is always negative. For the remaining two eigenvalues to be negative the following condition is necessary:

$$\bar{c} < \frac{cd\gamma}{\beta(\lambda-\gamma)}. \tag{2.34}$$

As demonstrated in previous models, a high value of c, relative to the other parameters, will result in extinction of the parasite. Furthermore, if $\lambda > \gamma$, then the desired capture rate must be smaller than cH_{crit} (where $H_{crit} = \frac{d\gamma}{\beta(\lambda-\gamma)}$, the minimum value of H required to sustain the parasite population), i.e. the capture rate at the threshold H_{crit}, in order to eradicate the parasite. The higher stocking rate required to maintain a high capture rate may therefore provide an environment beneficial to a parasite like *Argulus* spp..

For the coexistence equilibrium, there are 2 equations which give the equilibrium parasite population in terms of the host population:

$$P^* = \frac{1}{\alpha}\left[\frac{\bar{c}(\bar{c}+1)}{cH^*+1} - cH^*\right], \text{and} \tag{2.35}$$

$$P^* = \frac{H^*}{\alpha k}\left[\frac{\beta H^*\lambda}{\beta H^*+d} - \mu - \alpha - c\right] \tag{2.36}$$

As before, $\lambda > \mu+\alpha+c$ is required to have a viable parasite equilibrium. We now have the added constraint $\sigma > cH^*(cH^*+1)$. By combining the two formulae for P^*, H^* can be expressed as a solution of a cubic:

$$H^{*^3} + H^{*^2}\left[\frac{\beta(\lambda+ck-\gamma)+cd(ck-\gamma)}{c\beta(\lambda+ck-\gamma)}\right] + H^*\left[\frac{ck-\sigma\beta k-\gamma}{c\beta(\lambda+ck-\gamma)}\right] - \frac{\sigma dk}{c\beta(\lambda+ck-\gamma)} = 0 \tag{2.37}$$

where $\sigma = \bar{c}(\bar{c}+1)$ and $\gamma = \mu + \alpha + c$. Already, from 2.36, $\lambda > \gamma$ is required for positive P^*, so all the denominators in equation 2.37 are positive. Since it is known that the signs of the ${H^*}^0$ and ${H^*}^3$ terms are negative and positive respectively, it can be deduced, using Descartes' rule of signs, that there is a unique positive solution for H^*.

The coexistence equilibrium is only viable when H^* is lower than its host-only value (since otherwise, from 6.13, the parasite population will be negative). Similarly, from 2.36, H^* must be greater than $\frac{d\gamma}{\beta(\lambda-\gamma)}$. Combining the two gives $\frac{d\gamma}{\beta(\lambda-\gamma)} < H^* < \frac{\sqrt{1+4\sigma}-1}{2c}$, which in turn gives $\frac{d\gamma}{\beta(\lambda-\gamma)} < \frac{\sqrt{1+4\sigma}-1}{2c}$ as a condition for existence of the coexistence equilibrium. This is equivalent to $\lambda > \gamma\left[\frac{2cd}{\beta(\sqrt{1+4\sigma}-1)}+1\right]$.

By writing the characteristic equation in terms of H^*, it can be shown that this coexistence equilibrium is always locally stable for positive values of H^*, P^* and W^*. It follows that $\lambda > \gamma\left[\frac{2cd}{\beta(\sqrt{1+4\sigma}-1)}+1\right]$ is a necessary and sufficient condition for the existence of a positive coexistence equilibrium.

2.5.1 *Parasite-induced reduced catch rate*

When the parasite-induced reduction in capture is added to the reactionary stocking model, the disease free equilibrium remains $\frac{\sqrt{4\sigma-1}+1}{2c}$, and its condition for stability is still:

$$\bar{c} < \frac{cd\gamma}{\beta(\lambda-\gamma)}. \tag{2.38}$$

The parasite equilibrium density is given by:

$$P^* = \frac{H^*}{\alpha(k-1)}\left[\frac{\beta H^*\lambda}{\beta H^*+d} - \mu - \alpha - \frac{\bar{c}(\bar{c}+1)}{H^*(cH^*+1)}\right] \tag{2.39}$$

By comparing this with 2.36 and noting that $\bar{c} > cH^*$ is necessary for stability of this equilibrium, it is evident that the size of the parasite population is higher after inclusion of the parasite-induced reduction in capture. The parasite survival threshold also lowers as θ, the severity of the reduction, increases, depending on the starting state of the system (note: θ appears in H^*).

Figure 2.3 shows two bifurcation plots for different values of θ. As in the baseline and constant stocking models, the mean parasite burden and range of parameters for which hysteresis occurs increase with θ.

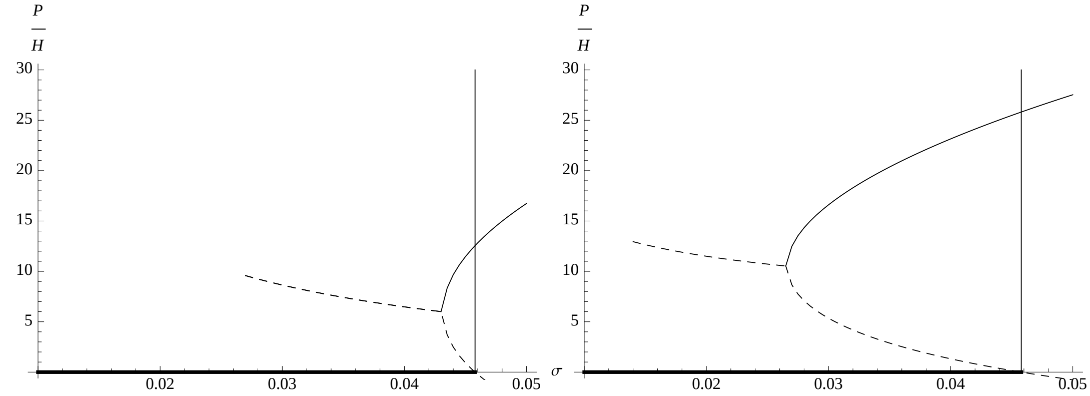

Figure 2.3: Bifurcation diagram of mean parasite burden plotted against σ for the reduced reactionary model, with $\theta = .05$ (left) and $\theta = .1$ (right): the solid lines represent the stable equilibria, while the dashed lines represent the unstable equilibria. The solid vertical lines represent $\bar{c} = \frac{cd\gamma}{\beta(\lambda-\gamma)}$ while the cut-off point on the left of each plot is the point at which $P*$ becomes negative. Note that the host-only equilibrium, represented by the thick line along the horizontal axis, is stable for $\bar{c} < \frac{cd\gamma}{\beta(\lambda-\gamma)}$, for parameters see Table 2.2.

2.6 COMPARISON OF MODELS

To illustrate the differences between the stocking methods covered in this paper, parameters were fixed to show how fisheries stocked according to the different models would react to the introduction of *A. foliaceus*. The model was parameterised using data from the literature, the details of which are summarised in table 2.2.

The model was initiated so that each "fishery" has 2 fish per m^3, and it was assumed that each is managed in such a manner that the number of fish caught is equal to the number stocked in each time period, in the absence of infection. For the constant capture model, this implies that $s = cH$, and for the compensatory model we let $q = 1$ to illustrate that even accurate compensation for mortalities can result in a persistent infection. For the reactionary model $\bar{c} = cH(= s)$. The stocking rate was set at $s = 0.08$, i.e. 0.08 fish are stocked per m^3 per day; c is thus 0.04, and $cH = .08$ - i.e. .08 fish are caught per m^3 per day. In the absence of infection, all fisheries continue to stock at the same rate, and the density of fish is constant at 2 per m^3. Under these conditions, however, the infected equilibrium is stable. If $W(0) = 10$, so that 10 parasites are present per m^3 of water, then the equilibrium solutions are as in figure 2.4. Note that attention here is restricted to low values of θ (less than 0.1), which allows for a significant reduction in capture (approximately halved for a mean parasite burden of 7).

Table 2.2: Definitions of terms in the Anderson and May model, and collected parameters for the *Argulus* spp. models. Values marked * were collected for *A. coregoni* since these have not yet been found for *Argulus foliaceus*. Note also that $k = (k' + 1)/k'$

Parameter Estimates and Definitions			
Parameter		Value	Source
s	host stocking rate	$0.0051\text{-}1.1\ \mathrm{m}^{-3}\mathrm{day}^{-1}$	10th and 90th percentiles, unpublished data
c	(optimum) capture rate	$0.0036\text{-}0.1404\ \mathrm{m}^{-3}\ \mathrm{day}^{-1}$	" "
α	increased host mortality due to infection	$0.001\ \mathrm{day}^{-1}$ [1]	
β	rate of attachment	$0.0384\mathrm{m}^{-3}\mathrm{day}^{-1}$	Mikheev and Pasternak [31]
μ	mortality of attached stages	$0.014\text{-}0.031\ \mathrm{day}^{-1}$	Taylor et al. [51]
d	mortality of free-living stages	$0.424\text{-}0.476\ \mathrm{day}^{-1}$	Walker [54]
h	hatching rate	$0.025\text{-}0.033\ \mathrm{day}^{-1}$	Taylor et al. [51]
n	average number of eggs laid by a female argulid	100-150	Bower-Shore [7]
k'	inverse degree of aggregation on the host	0.741*	Bandilla et al. [4]
i	parasite incubation period	37.67 days	Taylor et al. [51]
m	time from hatching to egg-laying	50 days	Taylor et al. [51], Schluter [41]
λ	rate of parasite births	$0.713 = (\frac{n}{2(i+m)})$	

When the models are parameterised equivalently and the desired catch rate is reasonably low, the constant and reactionary models are very similar in terms of all the metrics used in figure 2.4. Because these stocking methods do not react appropriately to the reduction in capture, as θ increases the host population densities become higher than even the parasite free

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[1] Practical limitations prevent the estimation of α in the field, and ethical constraints mean that there is little prospect of calculating it under laboratory conditions. For the purposes of comparing stocking methods and examining the impact of reduced capture rates, a value of $\alpha = 0.001$ (assuming fish can survive 20 days with a burden of 50 parasites) was chosen. The impact of choosing a different value of α is addressed at the end of this section.

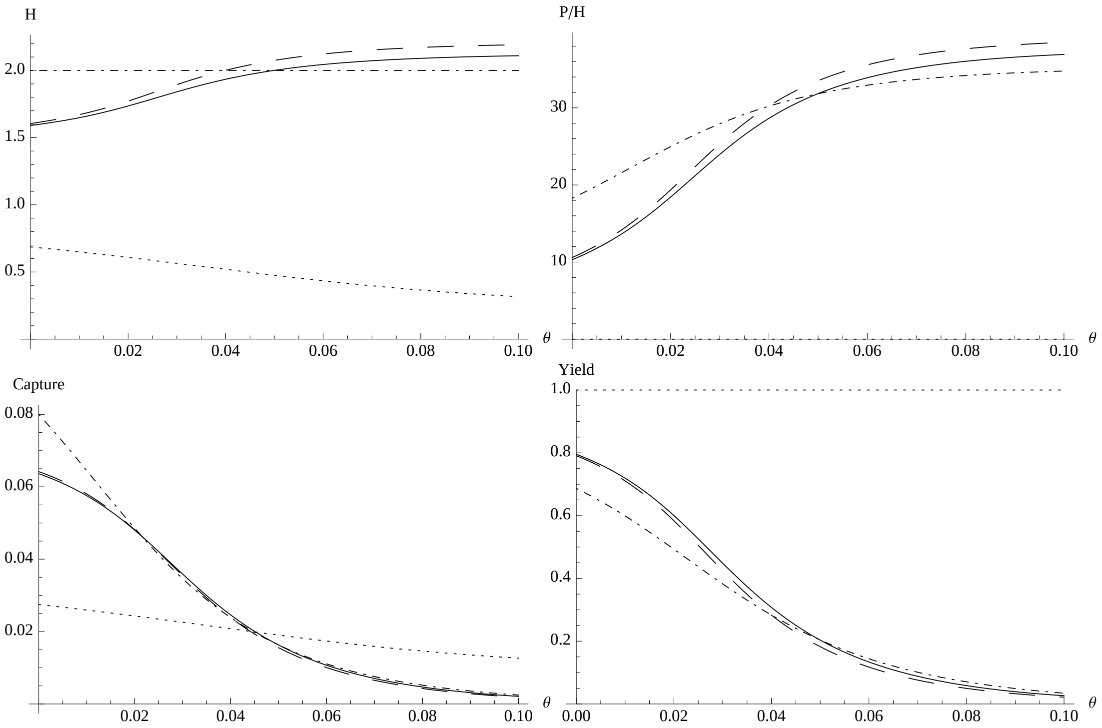


Figure 2.4: Equilibrium values of Population Density, Mean Parasite burden, Capture rate (cH^*) and Yield ($H^*c(H^*, P^*)/s(H^*)$) against θ for the constant (solid), replacement (dotted), compensatory (dot-dashed) and reactionary (dashed) models

equilibrium. In spite of the host population growth, capture and yield both decrease as the reduction in capture becomes stronger. For low values of θ, the compensatory model strongly favours parasite population growth.

It is clear that there is a trade-off between strategies, as by compensating for mortalities the catch rate is maintained, but the mean parasite burden is much higher. The question for fishery managers here is “quality or quantity" - anglers have the option of catching lots of parasitised fish under compensatory stocking, or a smaller number of healthy, parasite-free fish under replacement stocking. Notably, as the severity of capture reduction increases, the capture rate and yield drop at slower rates for the replacement and compensatory models than the constant and reactionary models. This can be explained by noting that the stocking rates for the replacement and compensatory models adapt in line with the capture rate.

The parasite inevitably dies out in the replacement model, but consequently the host density is permanently reduced to around 25% of its original value. This would be likely to have a severe impact on the economic viability of the fishery. Notably, the yield - given by fish caught divided by fish stocked at equilibrium - is unaffected, although high yield may easily be accompanied by very low capture rates. The clear benefit of the replacement stocking method is that the parasites die out completely after around 300 days, after which time the fishery could feasibly be restocked to its previous level - although it would be prudent to allow a parasite lifecycle to pass before restocking. It is worth noting that due to the overwintering capabilities of the parasite, this 300 days could extend beyond one calendar year, and during this period the capture rate would remain low.

The optimal stocking method depends on the severity of capture reduction, and also the aims of the fishery managers. For instance, if the reduction in capture is low, and the aim is to maintain a high capture rate, then the compensatory model would be best. If high yield and low parasite burden were considered the highest priority then replacement stocking would be the clear winner. The constant and reactionary models represent a compromise between the two (although this is dependant on the choice of a sensible value of $\bar{c}$; this is discussed in the next section).

With a more substantial reduction in capture, the replacement model becomes the optimal choice in terms of parasite burden, capture rate and yield, in spite of the fact that it results in a much lower host density. The second best choice is the compensatory model, which in spite of its flaws originally, is better placed to deal with the reduction in capture than either the constant or reactionary model, due to the fact that the stocking rate decreases along with the capture rate.

The implications of this are that fisheries with stocking rates which do not adapt appropriately to changes in capture are more susceptible to drops in yield which may accompany decreases in capture associated with a parasite like *Argulus* spp..

It should be noted that even a small increase of q beyond 1 will result in heavier parasite burdens and reduced yield in capture for the compensatory model. Also, for relatively high values of α, changes in θ have less impact as mortalities compensate for the reduction in capture. For example the same plots with $\alpha = 0.01$ are closer to straight lines for $\theta < 0.1$, and the compensatory model consistently performs the poorest in terms of mean parasite burden and yield. The result of this is that, for the models presented here, the reduction in capture is less significant in determining the optimal stocking method when the rate of parasite-induced mortalities is also high.

2.6.1 *A caveat to the reactionary model*

In the previous example, the constant and reactionary models were almost equivalent, since the models were set up to give as close a comparison as possible. Figure 2.5 shows that as θ increases, having a higher desired capture rate actually leads to fewer captures. Regardless of θ, the yield drops whenever $\bar{c}$ increases due to the subsequent increased level of parasitism and mortalities. Attempting to maintain a high catch rate by increasing stocking when the parasite in question reduces the capture rate may therefore be counterproductive.

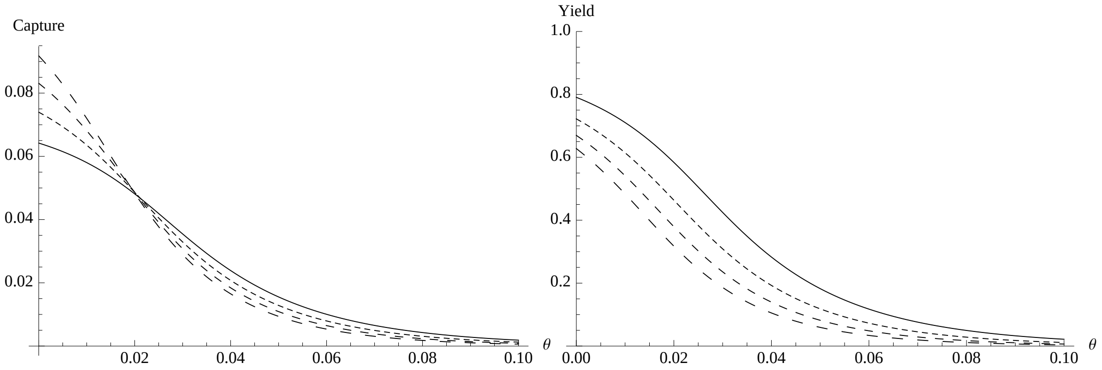


Figure 2.5: Reactionary model with increased values of desired capture rate, $\bar{c}$. The previous value of 0.08 is given by the solid line, and each subsequent dashed line represents an increase of 25%

2.7 ALTERNATIVE FUNCTIONS FOR MODELLING PARASITE-INDUCED REDUCTIONS IN CAPTURE

Throughout this paper, an exponential function has been used to model the parasite-induced reduction in capture. This function was useful as it was relatively simple, for some of the models, to determine equilibrium values and stability. In choosing the exponential function, however, some assumptions were made about the nature of the relationship between the mean parasite burden and the capture rate. Most crucially, the shape of the exponential function implies that most of the reduction in the capture occurs with the first few parasites, with high parasite burdens having a less marked effect. In reality, it is more likely that any impact on rod capture would be negligible until tens of parasites were present per fish.

The two most novel findings which resulted from the exponential decrease in capture were that 1) the host population size, for the coexistence equilibrium, was higher when compared with a model without a capture reduction, and 2) that the system exhibits hysteresis, which can allow the parasite to survive at lower host densities than would otherwise be possible (depending on the initial conditions). In this section we investigate whether other functions give the same results, or whether these results rely on the choice of the exponential function.

The constant stocking model is now rewritten as:

$$dH/dt = s - cHf(P/H) - \alpha P \tag{2.40}$$

$$dP/dt = \beta HW - P(\mu + \alpha) - cPf(P/H) - \alpha k \frac{P^2}{H} \tag{2.41}$$

$$dW/dt = \lambda P - dW - \beta HW, \tag{2.42}$$

with the function $f(P/H)$ defined as a monotonically decreasing function on the interval $P/H \in [0, \infty)$, with $f(0) = 1$ and $f(P/H) \to 0^+$ as $H \to \infty$. By setting the first two equations equal to 0 and solving each for $f(P/H)$, it is possible to obtain a general expression for the mean parasite burden $\frac{P^*}{H^*}$ in terms of H^*

$$\frac{P^*}{H^*} = \frac{1}{\alpha(k-1)} \left[\frac{\beta H^* \lambda}{\beta H^* + d} - \mu - \alpha - s/H^* \right]. \tag{2.43}$$

This can be substituted back into the first equation:

$$H^* = \frac{s - \alpha P^*}{cf(P/H)}. \tag{2.44}$$

Which gives

$$H^* = \frac{1}{2} \left[\frac{d\gamma_g + s\beta k}{\beta(\lambda - \gamma_g)} + \sqrt{\left(\frac{d\gamma_g + s\beta k}{\beta(\lambda - \gamma_g)} \right)^2 + \frac{4dsk}{\beta(\lambda - \gamma_g)}} \right], \tag{2.45}$$

where $\gamma_g = \mu + \alpha - c(k-1)f(P/H)$. This can now be compared with the host population density for the model without a capture rate reduction:

$$H^* = \frac{1}{2}\left[\frac{d\gamma + s\beta k}{\beta(\lambda-\gamma)} + \sqrt{\left(\frac{d\gamma + s\beta k}{\beta(\lambda-\gamma)}\right)^2 + \frac{4dsk}{\beta(\lambda-\gamma)}}\right], \tag{2.46}$$

where $\gamma = \mu + \alpha - c(k-1)$.

Although the value of P/H is unknown, from the definition of the function f, $0 < f(P/H) \leq 1$. Since $P/H > 0$ is a necessary condition for existence of a coexistence equilibrium, it follows that $f(P/H) < 1$. Thus the host equilibrium density is higher with a capture rate reduction than without it, for any function $f(P/H)$, and so 1) holds for a general function, f.

To show 2) recall that, in the original, constant capture model, (and others throughout this paper), the coexistence equilibrium was stable for positive equilibrium values. In particular, the condition that the expression for P^* give a positive solution was key in determining whether the parasite would be able to survive.

From $P^* = \frac{s - cHf(P/H)}{\alpha}$ it is evident that one condition for a positive parasite equilibrium is $s > cHf(P/H)$, and substituting this into equation 2.45 and solving for s, it can be deduced that the minimum value of s for which P^* is positive is:

$$\frac{cdf(P/H)(\mu + \alpha + cf(P/H))}{\beta(\lambda - \mu - \alpha - cf(P/H))} \tag{2.47}$$

This is evidently smaller than the minimum stocking level for the original model

$$\frac{cd(\mu + \alpha + c)}{\beta(\lambda - \mu - \alpha - c)}, \tag{2.48}$$

and thus the parasite population is positive for lower values of s when there is a reduction in capture rate. Since linear stability analysis shows that the host-only equilibrium is stable whenever the original condition $s < \frac{cd(\mu+\alpha+c)}{\lambda-\mu-\alpha-c}$ is met, hysteresis may occur for any monotonically decreasing function, $f(P/H)$, when

$$\frac{cdf(x)(\mu + \alpha + cf(x))}{\beta(\mu + \alpha + cf(x))} < s < \frac{cd(\mu + \alpha + c)}{\beta(\mu + \alpha + c)}. \tag{2.49}$$

The extent of the bistability will depend on the function chosen, but the result that bistability occurs as a result of capture rate reduction is consistent with the exponential reduction results.

Although it is useful to know that the threshold may be reduced, and that hysteresis may occur, it would be more useful from a practical point of view to determine a threshold beyond which the parasite could not survive.

At the start of this section it was stated that the mean parasite burden in terms of H^* was given by:

$$\frac{P^*}{H^*} = \frac{1}{\alpha(k-1)}\left[\frac{\beta H^* \lambda}{\beta H^* + d} - \mu - \alpha - s/H^*\right]. \tag{2.50}$$

This saturates as $H^* \to \infty$ at

$$P_{max} = \frac{1}{\alpha(k-1)}(\lambda - \mu - \alpha). \tag{2.51}$$

This means that any decreasing function f has a minimum of $f(P_{max})$ - thus the effect on the capture rate is limited because the mean parasite burden is bounded above.

This in turn means that bistability is limited to the region

$$\frac{cdf(P_{max})(\mu + \alpha + cf(P_{max}))}{\beta(\mu + \alpha + cf(P_{max}))} < s < \frac{cd(\mu + \alpha + c)}{\beta(\mu + \alpha + c)}, \tag{2.52}$$

although the actual lower bound may be higher than this. This is an important result since, for any function, f, a threshold value of s can be found. If the stocking level is dropped below this threshold, then the parasite will be unable to survive as the parasite burden cannot possibly become high enough to reduce the capture rate sufficiently for it to survive.

For example - with the exponentially reduced model dropping s below

$$\frac{ce^{-\theta P_{max}} d(\mu + \alpha + ce^{-\theta P_{max}})}{\beta(\lambda - \mu - \alpha - ce^{-\theta P_{max}})}, \tag{2.53}$$

would result in the extinction of the parasite.

2.7.1 *Reactionary Model*

By similar logic the threshold host density required for the parasite survival in the reactionary model is given by

$$H_{crit} = \frac{d(\mu + \alpha + cf)}{\beta(\lambda - \mu - \alpha - cf)}, \tag{2.54}$$

which is again lower than the constant capture model. The mean parasite burden relative to the host population, now given by $\frac{H}{\alpha k}\left[\frac{\beta H^{*}\lambda}{\beta H^{*}+d}-\mu-\alpha-cf\right]$, is also higher, while the condition for stability of the host-only equilibrium remains the same.

2.7.2 *Replacement and Compensatory Models*

In the replacement model, the results that the parasite persists longer and therefore induces more host mortalities when any function f is used (compared with a model without a capture reduction) hold. This is a fairly trivial result which can be seen by noting that 1) the host population is in decline whenever $P > 0$, and 2) the parasite population declines at a slower rate.

The compensatory model (with $q = 1$) always maintains the host population at its initial density. For any f, it can be noted that the minimum host density required to sustain the parasite is $H_{crit} = \frac{d(\mu+\alpha+cf)}{\beta(\lambda-\mu-\alpha-cf)}$, and so the parasite can survive under circumstances where it previously could not. The mean parasite burden is also higher for any f, and therefore the capture rate is impacted even though the host population density is unaffected.

2.8 DISCUSSION

The models in this paper were constructed with the primary aim of determining the impact of different stocking methods on a parasitic infection such as *Argulus* spp., in order to make recommendations of management strategies which will reduce the parasite burden.

In the baseline model, which assumed that fish reproduced naturally rather than being artificially stocked, the parasite-induced reduction in capture rate lowered the parasite exclusion threshold, under some circumstances allowing both fish and parasite to survive even when the birth rate, a, was lower than the capture rate, c. Biologically, there are two ways in which coexistence could arise with $a < c$ in this model. If an infection was already established, with $a > c$, and the host then suffered a reduction in fecundity due to the infection, then the parasite could continue to exist so long as c did not become substantially higher. Similarly if c was increased only slightly above a in reaction to an infection, then the parasite may continue to persist at a similar level unless the condition $a > \frac{\alpha}{\theta}(1 + \ln \frac{c\theta}{\alpha})$ is violated - in other words, unless the capture rate is further increased.

The replacement stocking method was shown to result in a low enough density of fish to make long term parasite survival impossible. Adopting the replacement method of stocking, at least temporarily, in the event of an outbreak, appears to be a sensible course of action. Once the capture rate stabilises it would be advisable to wait at least the duration of one parasite life cycle before restocking to a higher level, as hatching parasite eggs could potentially re-infect the fish. Since the growth rate of the parasite is linked to temperature, and factoring in their over-wintering capabilities, this period could extend beyond one calendar year. The effect of the parasite-induced reduction in capture was less pronounced in the replacement model than the others - while the duration of infection, and number of mortalities were impacted, the outcome (extinction of the parasite) was identical. It should be noted that as *Argulus* spp. is a generalist parasite, wild fish populations may provide a reservoir for the infection even if this method is used - in the absence of such populations, however, the replacement model looks like a simple, cost-effective, if slightly time-inefficient, method of eliminating *Argulus* spp..

The constant stocking method was shown to be beneficial to the parasite when the catch rate, c, was low, and the stocking rate, s, was high. The fact that the parasite birth rate must exceed its combined loss rates - including the capture rate - in order for the coexistence equilibrium to be stable shows that *Argulus* spp. can be eradicated by ensuring that the fish are caught quickly, even when very high numbers of fish are stocked. This is consistent with the findings of Taylor et al. [50] and Taylor et al. [51], which concluded that slow stock turnover was an important *Argulus* spp. risk factor. The reactionary model showed that the practice of increasing stocking in reaction to an infection may have the desired effect of increasing the number of fish caught, but could increase the parasite burden. This is logical as increasing stocking will increase the host density and consequently create more favourable conditions for the parasite.

The constant and reactionary stocking models were similar in that they allowed the parasite to survive if the host density exceeded some threshold H_{crit}. The reduction in capture rate reduced the stocking threshold beyond which the parasite was able to survive in both these models, but this was dependent on the initial conditions. This would suggest that while the number of fish added to the water must be high for an *Argulus* spp. to successfully invade a fishery, the stocking level may have to be reduced well below this threshold in order to exclude it. In other words, because the capture rate has been lowered by the parasite, the stocking rate must be further lowered in order to eradicate it.

The compensatory model, whereby fishery managers attempt to estimate the number of parasite-induced mortalities and replace them by increasing the stocking level accordingly, was constructed to show what would happen if the fish population was successfully maintained at its original value. This method was shown to allow the parasite population to survive if and only if the starting fish density exceeded the quantity H_{crit}. Under this stocking regime, it is extremely important to ensure that any compensation for parasite induced mortalities, in the form of additional stocking, is undertaken with great care - if there are more than H_{crit} fish per m^3 in the water, and mortalities are over-estimated by even a small percentage, then a small influx of parasites could result in a long term infection. Underestimating the number of mortalities may negatively impact the number of fish caught, but will eventually result in the parasite dying out - albeit more slowly than simply replacing the caught fish. The idea that simply replacing dead fish could be sufficient to maintain an infection may seem somewhat counterintuitive, but should serve as a warning to fishery managers that what may seem like a common sense approach to stocking could do more harm than good.

The effect of the parasite-induced reduction in capture on the compensatory model was straightforward - the critical host density required for parasite survival dropped, allowing the parasite to survive with fewer fish present. This result is fairly intuitive since parasites are being removed at a slower rate. This model suffered in terms of yield, parasite burden and capture rate, but to a lesser extent than the constant and reactionary models.

Overall, the reduction in capture rate is a useful mechanism for *Argulus* spp., as well as a phenomenon which can be detrimental to the economics of fisheries. Stocking methods which rise and fall along with the capture rate (for example the replacement and compensatory methods) result in less severe consequences for yield and capture relative to any parasite-induced reductions in capture, as illustrated in figure 2.4.

For the constant, compensatory or reactionary models, a host density of less than $H_{crit} = \frac{d(\mu+\alpha+c(H,P))}{\beta(\lambda-\mu-\alpha-c(H,P))}$ will not sustain an infection when there is no capture rate reduction. If using compensatory stocking then it would be wise to avoid stocking more than the sum of the losses due to mortalities and capture. For the constant and reactionary models this threshold can be exceeded, but only if the turnover of fish happens very quickly, i.e. $c(H,P) > \lambda - \mu - \alpha$.

While estimation of the function $c(H,P)$ in the field is non-trivial, if an infection is established then it may be relatively simple to see how much lower the capture rates are relative to their infection-free values. Thus, if the capture is known to have halved then the minimum stocking density would be given by $\frac{d(\mu+\alpha+0.5c)}{\beta(\lambda-\mu-\alpha-0.5c)}$, which translates to a minimum stocking level of $\frac{0.5cd(\mu+\alpha+0.5c)}{\beta(\lambda-\mu-\alpha-0.5c)}$ for the constant model.

More work is needed to improve the realism of these *Argulus* spp. models; for instance the ability of the parasite to attach to another host following mortality of its original host should be added, and seasonality in the parasite's life cycle is expected to show that the timing of stocking events could impact the parasite's ability to persist. Simulations were run in order to see whether stocking at regular intervals (rather than in a continuous manner) had a significant effect on the results presented here - the results were consistent with those presented here, showing uniform cycles around the population densities.

Low stock turnover has been linked to *Argulus* spp. infections in the UK (e.g.Taylor et al. [50]), and the models presented in this paper appear to confirm this - in all cases the rates at which fish were added to and removed from the system were key in determining the abundance of the parasite, as well as the threshold at which it could survive. This is an intuitive result which can be understood by noting that increasing the capture rate (and therefore the rate of stock turnover) also increases the rate at which parasites are removed from the water.

Far from showing that fishery managers “must" stock according to a particular method, the models in this paper have demonstrated that almost any method is permissible so long as certain, fairly straightforward, guidelines are followed. This means that any recommendations resulting from this research will be simple to implement for fisheries managed in many different ways.

While methods such as replacement and reactionary may be used in fisheries, the extent to which fishery managers are able to maintain a consistent host density (required for the compensatory model) and the desired capture rate required for the reactionary model are likely to be unpredictable and variable between sites. The replacement method may be beneficial but would consistently result in parasite extinction, confounding results and precluding any equilibrium analysis. Therefore in following chapters the constant stocking model is used as a baseline due to its simple parameterisation and comprehensibility, with s being simply the number of fish stocked per cubic metre per day. In the next chapter the constant stocking model is used as a baseline, and a number of features are added to improve its biological realism.

3

FURTHER MODEL ALTERATIONS

In this chapter a number of alterations are made to the baseline model presented in chapter two, in order to improve its biological realism, and tailor it further to fit the *Argulus foliaceus* system. These changes include: allowing a proportion of argulids to survive in the environment when the host dies due to infection; adding a separate compartment to represent parasite eggs being laid off the host; adding a host mortality rate; and modifying the shape of the parasite-induced capture reduction function.

These features were implemented separately prior to combining, in order to determine the impact of each new feature. At the end of this chapter these changes are brought together to form a more detailed baseline model, which will be used throughout subsequent chapters.

The constant stocking model described in chapter two is used throughout due to its simplicity, and in order to facilitate comparisons between the models.

3.1 PARASITE REATTACHMENT

In chapter two it was assumed that when an infected host dies, its parasites died with it, however Bower-Shore reported both survival of the parasite after host mortality and reattachment within half an hour when exposed to a new host [7]. This life cycle trait of *A. foliaceus* is in contrast to a similar parasite *Ergasilus sieboldi* which also affects trout but will die if its host dies. Accordingly, a new term was added to the model in order to allow parasites to attach to another host when their original host died. A fixed proportion, δ, of attached parasites survive the death of their host and move back into the free-living compartment. These parasites are then able to attach to a new host at rate β.

The model is now:

$$\frac{dH}{dt} = s - cH - \alpha P \tag{3.1}$$

$$\frac{dP}{dt} = \beta HW - P(\mu + \alpha + c) - \alpha k \frac{P^2}{H} \tag{3.2}$$

$$\frac{dW}{dt} = \lambda P - dW - \beta HW + \delta\alpha \left[P + k\frac{P^2}{H} \right]. \tag{3.3}$$

Setting these equations equal to zero and rearranging demonstrates that two equilibria are present: a host-only equilibrium $(\frac{s}{c}, 0, 0)$, where the host density is dependent only on the number of fish stocked and caught, identical to that from previous models, and a coexistence equilibrium given by:

$$H^* = \frac{1}{2}\left[\frac{d\gamma_1 - k\beta\delta s + s\beta k - cdk}{\beta(\lambda - \gamma_1 + \gamma_k)} + \sqrt{\left[\frac{d\gamma_1 - k\beta\delta s + s\beta k - cdk}{\beta(\lambda - \gamma_1 + \gamma_k)} \right]^2 - \frac{dsk}{\beta(\lambda - \gamma_1 + \gamma_k)}} \right] \tag{3.4}$$

$$\frac{P^*}{H^*} = \frac{\beta H^*(\lambda + \delta\alpha - \gamma_1) - d\gamma_1}{\alpha k(\beta H^*(1 - \delta) + d\alpha k)} \tag{3.5}$$

$$W^* = P^* \frac{\lambda + \delta\alpha(1 + \frac{P^*}{H^*})}{\beta H^* + d} \tag{3.6}$$

where $\gamma_1 = \mu + \alpha + c$ and $\gamma_k = \delta\alpha - c\delta k + ck$. This is similar to the constant stocking model from chapter two, but the inclusion of δ (> 0) causes a decline in the host equilibrium density, and an increase in the attached parasite density.

The host-only equilibrium, $(\frac{s}{c}, 0, 0)$, is stable if

$$s < \frac{cd\gamma_1}{\beta(\lambda + \delta\alpha - \gamma_1)}, \tag{3.7}$$

which again is reminiscent of previous models where keeping the stocking level low provides insufficient numbers of hosts to sustain the parasite. Equation 3.5 can be rearranged to show that for P^* to be positive, the condition

$$H^* > H_{crit} = \frac{d\gamma_1}{\beta(\lambda + \delta\alpha - \gamma_1)}. \tag{3.8}$$

must be met. This minimum value of H^* is lower than in the model without reattachment (where $H_{crit} = \frac{d\gamma_1}{\lambda - \gamma_1}$), as is the minimum stocking value required to sustain the parasite given in equation 3.7. This implies that the possibility of reattachment allows the parasite to survive when fewer fish are being stocked, and the host density is lower than if all parasites died along with the host to which they are attached.

3.1.1 *Conclusions*

As noted above, allowing parasites to reattach when their original host dies reduces the threshold density of hosts, H_{crit}, above which the parasite can survive. As is intuitively obvious, this additional mechanism for parasite survival makes it easier for the parasite to persist.

3.2 PARASITE-INDUCED CAPTURE REDUCTION

Although it has already been shown in chapter two that any monotonic decreasing function for reduction in capture due to parasite burden will: 1) increase the host density at the coexistence equilibrium and, 2) cause the model to exhibit hysteresis (see section 2.7), it is necessary to choose a suitable function in order to perform simulations in later chapters. Although little data is available to parameterise this function, anecdotal evidence suggests that a small number of parasites have little or no impact on the behaviour of the fish, while heavier burdens can cause significant reductions in capture [52]. The exponential function, while more suitable for analytical comparisons between stocking methods in chapter two, is not representative of the relationship between parasite burden and capture as it results in a significant reduction in capture for the first few parasites.

3.2.1 *Hill function reduction in capture*

Here, a downward hill function is introduced, which takes the following form:

$$c(H,P) = c\frac{\rho^n}{\rho^n + (P/H)^n}. \tag{3.9}$$

For positive values of ρ, the mean parasite burden required to half the capture rate by 50%, and n, the shape parameter, this function decreases monotonically from 1 to 0 as the parasite burden, P/H increases. This function not only produces a more realistic relationship between parasite burden and capture than the exponential function (see figure 3.1), but also benefits from being easier to interpret biologically, as ρ is the mean parasite burden required to halve the capture rate. The shape parameter, n, is not easily derived from data, but increasing it makes the sigmoid shape more pronounced, as seen in figure 3.1.

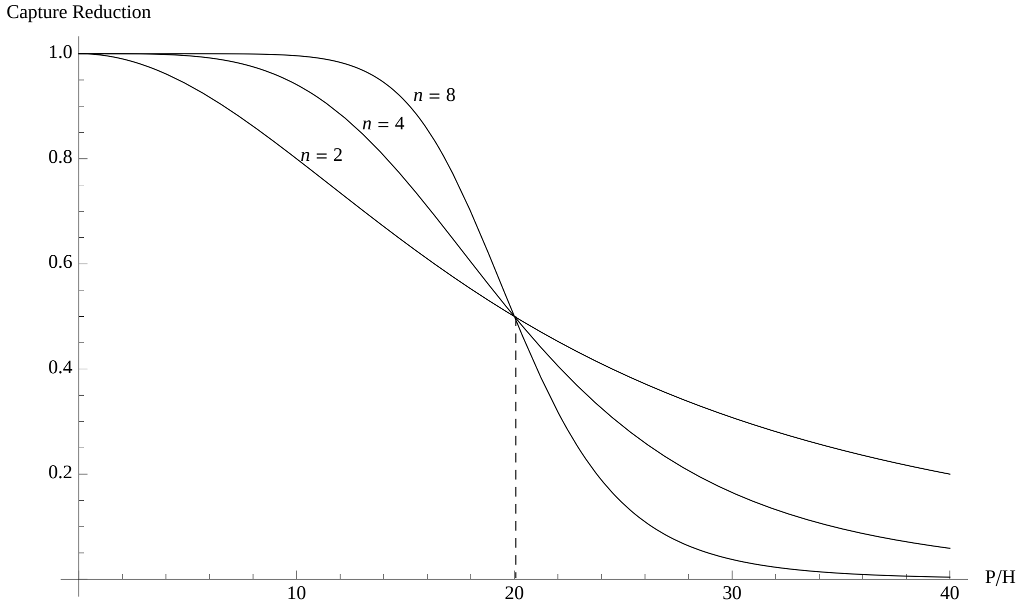


Figure 3.1: Relationship between the reduction in fish capture as the number of parasites per host increases, given by a downward hill function with $\rho = 20$: a mean parasite burden of 20 halves the capture rate, while increasing n makes the sigmoid shape more pronounced.

Including this function within the chapter two baseline model gives:

$$dH/dt = s - cH\frac{\rho^n}{\rho^n + (\frac{P}{H})^n} - \alpha P \tag{3.10}$$

$$dP/dt = \beta HW - P(\mu + \alpha) - cP\frac{\rho^n}{\rho^n + (\frac{P}{H})^n} - \alpha k\frac{P^2}{H} \tag{3.11}$$

$$dW/dt = \lambda P - dW - \beta HW \tag{3.12}$$

The host only equilibrium is again identical to the baseline model and is given by $(s/c, 0, 0)$. The characteristic equation for this equilibrium is:

$$(\Lambda + c)(\Lambda^2 + \Lambda(\gamma + d + \beta s/c) + \gamma(d + \beta s/c) - \lambda\beta s/c) = 0 \tag{3.13}$$

The first eigenvalue is $\Lambda_1 = -c$, and the remaining eigenvalues are negative when $\gamma(d + \beta s/c) - \lambda\beta s/c) > 0$, ie. $s < \frac{cd\gamma}{\beta(\lambda-\gamma)}$. The stability of the host-only equilibrium is thus independent of both ρ and n.

3.2.2 *Coexistence equlibrium*

By letting $x = \frac{\rho^n}{\rho^n + (\frac{P}{H})^n}$ and solving the first two equations set equal to 0 for x, the following expressions can be obtained:

$$x = \frac{s - \alpha P^*}{cH^*} \tag{3.14}$$

$$x = \frac{1}{c}\left[\frac{\beta H^* \lambda}{\beta H^* + d} - \mu - \alpha - \alpha k \frac{P^*}{H^*}\right] \tag{3.15}$$

Setting these two equations equal to each other gives P^* in terms of H^*:

$$P^* = \frac{H^*}{\alpha(k-1)}\left[\frac{\beta H^* \lambda}{\beta H + d} - \mu - \alpha - s/H^*\right]. \tag{3.16}$$

From this it can be deduced that, for P to be positive, the following condition must be met:

$$\beta H^*(\lambda - \mu - \alpha) - \beta s > d(\mu + \alpha) + ds/H^* > 0 \tag{3.17}$$

This gives the following conditions for positivity of the attached parasite equilibrium density:

$$\lambda > \mu + \alpha \tag{3.18}$$

$$H^* > \frac{s}{\lambda - \mu - \alpha} \tag{3.19}$$

and finally:

$$H^{*2} - H\frac{\beta s + d(\mu + \alpha)}{\beta(\lambda - \mu - \alpha)} - \frac{ds}{\beta(\lambda - \mu - \alpha)} > 0. \tag{3.20}$$

This is identical to the condition for positivity of the exponentially reduced model evaluated in chapter two.

$$H^* > \frac{1}{2}\left[\frac{\beta s + d(\mu + \alpha)}{\beta(\lambda - \mu - \alpha)} + \sqrt{\left[\frac{\beta s + d(\mu + \alpha)}{\beta(\lambda - \mu - \alpha)}\right]^2 + \frac{4ds}{\beta(\lambda - \mu - \alpha)}}\right]. \tag{3.21}$$

Determining the stability of this equilibrium directly is non-trivial, as even for $n = 1$, the value of H^* is the solution of a fourth-order polynomial. However, in earlier models it was shown that the stability of coexistence equilibria is dependent on the existence of equilibrium values. Numerical simulations run for a variety of parameter estimates are consistent with this result, and show that where the host-only equilibrium is stable and the expression for the parasite burden is positive, the outcome of an infection is dependent on the initial number of parasites present at the start of the simulation.

3.2.3 *Simulations for the model with a hill function*

In order to compare the behaviour of the model with the hill function with that of the exponentially-reduced model, simulations were run. Figure 3.2 shows the approach to equilibrium of the three models: constant capture, exponentially-reduced capture, and downward hill reduced capture. All three models exhibit the same qualitative behaviour, albeit with different equilibrium values. This is because the value of the reduction function at the equilibrium points are different. Depending on the parameters used, either the hill or the exponential model could result in higher parasite burden or high capture rate. Even when the functions are parametrised equivalently (see below) the functions will intersect at one or more points, and if other parameters within the model are changed then the functions will cease to be equivalent. When the models are parametrised equivalently, e.g. for $\rho = 2$ and $n = 2$:

$$\frac{\rho^n}{\rho^n + (P/H)^n} = e^{-\theta P/H} \tag{3.22}$$

$$\frac{2^2}{2^2 + (2.5)^2} = e^{-2.5\theta} \tag{3.23}$$

$$ln(4/10.5)/2.5 = \theta \approx 0.386 \tag{3.24}$$

the equilibrium and the temporal behaviour are almost identical for both models, as seen in figure 3.3. Figure 3.4 shows that the reduction in capture could be slightly more severe depending on the parasite burden, which in turn is dependent on the other parameters in the model.

The hysteresis result from chapter two, whereby the initial conditions dictate which of the two stable equilibria the model ultimately arrives at holds true for this model, this is shown in figure 3.5, which is a parametric plot of the host (horizontal axis) and attached parasite (vertical axis) population densities, and shows a clear divide between starting points resulting in coexistence (on the upper right of the plot - i.e. where initial values of H and P are relatively high) and those resulting in the extinction of the parasite.

The hill function is used throughout the remainder of this thesis in the belief that it more accurately represents the relationship between capture rates and parasite burden observed in

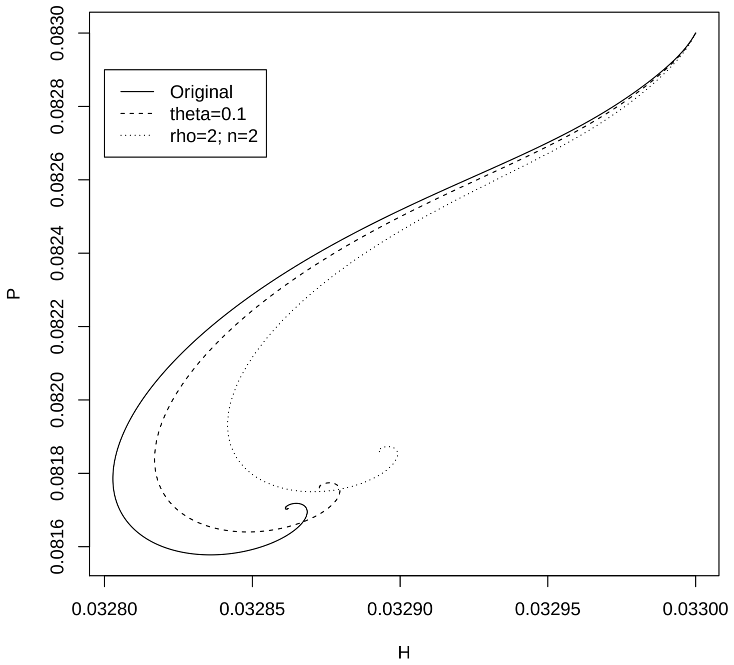


Figure 3.2: Approach to equilibrium for the constant (black), exponentially reduced (grey), and downward hill reduced (dashed) capture models with arbitrarily chosen capture-reduction parameters ρ, n, and θ.

the field. Attempts are made in chapter four to find appropriate values of the parameters ρ and n.

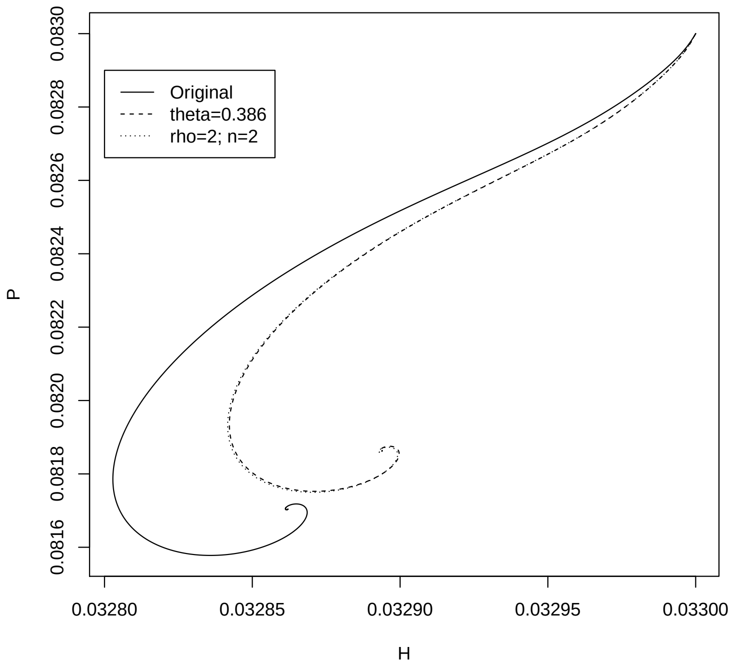


Figure 3.3: Approach to equilibrium for the constant (black), exponentially reduced (grey), and downward hill reduced (dashed) capture models with the reduced models parameterised equivalently

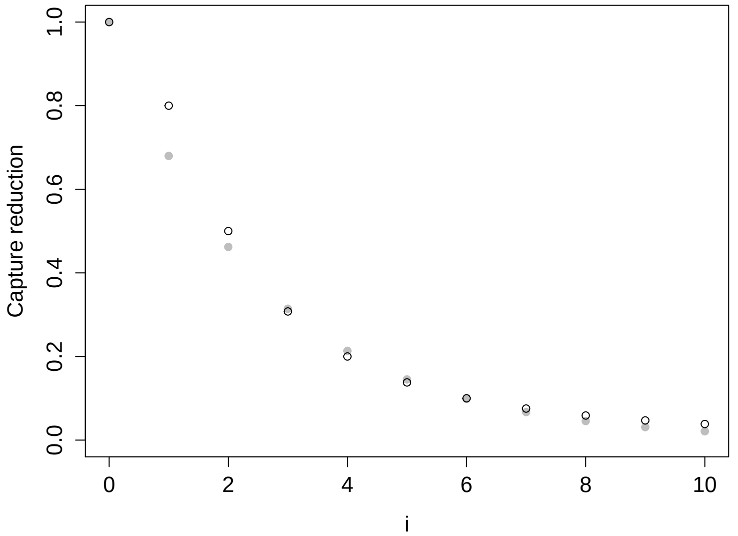


Figure 3.4: Capture reduction function - hill function in black and exponential function in solid grey. The functions are similar but depending on the parasite burden either model can produce a slightly stronger reduction in capture.

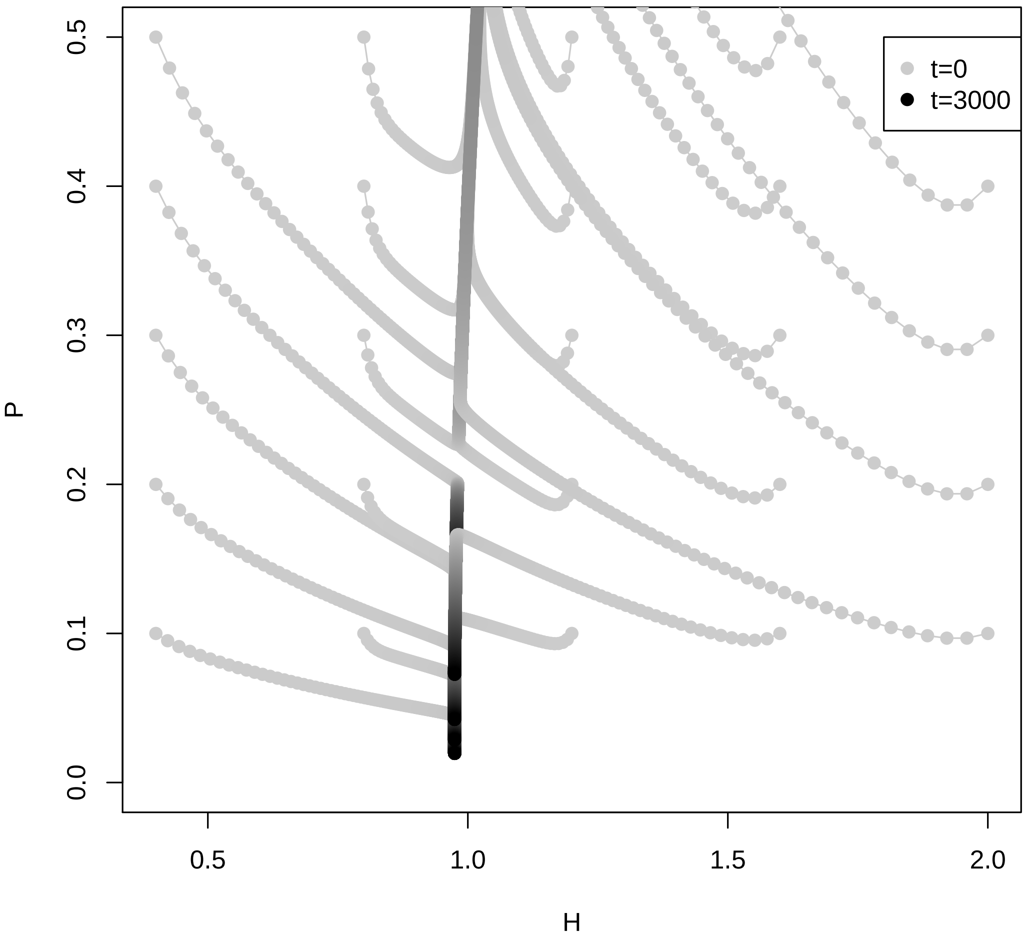


Figure 3.5: Parametric plot of the hill-reduced model with different initial conditions. The palest grey points represent $t = 0$ and the progression of time is shown by the gradual change in shade to black. When $P(0)$ and $H(0)$ are small the parasite fails to survive, shown by the dark points at the bottom of the plot, but otherwise the parasite manages to invade and establish itself long term, shown by the darker points toward the top of the plot (actual equilibrium point outside the plot area).

3.2.4 *Per-fish reductions in stocking*

In the models with the exponential and hill function reductions in capture, results showed that once an infection was established, the parasite could provide a refuge from capture for infected fish. Furthermore, in all of the models we found that once established, the reduction in host capture caused by the parasite could make it harder to eradicate the parasite. To determine that this was not a consequence of the manner in which the model was written, the model was expanded to capture the fact that the reduction in capture rate is not evenly spread across the fish population, but most likely has a more marked effect on heavily-parasitised fish. To do this a number of simulations were run in which the reduction in capture was applied proportionally so that fish with a heavier parasite burden were harder to capture. The probability density function for the negative binomial distribution, with $P(i)$ giving the proportion of fish harbouring i parasites, is given by

$$P(i) = \binom{k' + i - 1}{k' - 1} (1-p)^i p^{k'}$$

where $p = k'/((P/H) + k')$, and so as $n \to \infty$, $\sum_{i=1}^{n} \left[\binom{k'+i-1}{k'-1} (1-p)^i p^{k'} \right] \to 1$. Therefore as $n \to 1$ the following model produced the same results as the model with no reduction in capture (shown in figure 3.6):

$$\begin{aligned}
\frac{dH}{dt} &= s - cH \sum_{i=1}^{n} \left[\binom{k' + i - 1}{k' - 1} (1-p)^i p^{k'} \right] - \alpha P \\
\frac{dP}{dt} &= \beta HW - P(\mu + \alpha) - cP \sum_{i=1}^{n} \left[\binom{k' + i - 1}{k' - 1} (1-p)^i p^{k'} \right] - \alpha k \frac{P^2}{H} \\
\frac{dW}{dt} &= \lambda P - dW - \beta HW.
\end{aligned} \tag{3.25}$$

Next the exponential reduction in capture was added as an example, so the model took the form:

$$\begin{aligned}
\frac{dH}{dt} &= s - cH \sum_{i=1}^{n} \left[e^{-i} \binom{k' + i - 1}{k' - 1} (1-p)^i p^{k'} \right] - \alpha P \\
\frac{dP}{dt} &= \beta HW - P(\mu + \alpha) - cP \sum_{i=1}^{n} \left[e^{-i} \binom{k' + i - 1}{k' - 1} (1-p)^i p^{k'} \right] - \alpha k \frac{P^2}{H} \\
\frac{dW}{dt} &= \lambda P - dW - \beta HW.
\end{aligned} \tag{3.26}$$

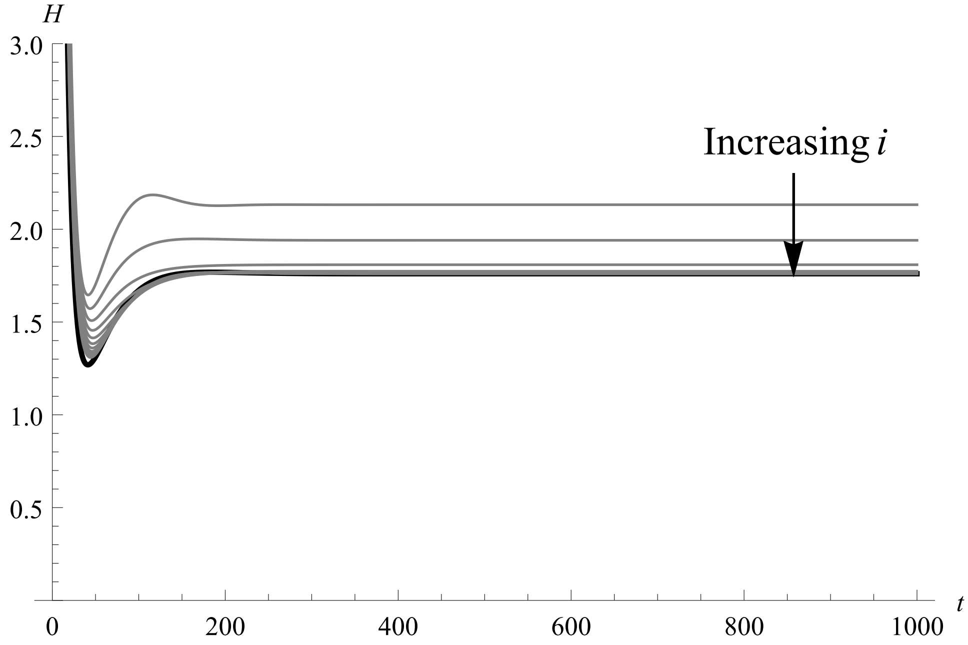


Figure 3.6: Simulation results for the full capture, constant stocking model, as i, the maximum number of parasites per host, is increased. As i increases (grey lines, from top to bottom), the model moves towards its original form (with no capture reduction), shown as a thick black line.

In this way, the difference in capture rates between heavily parasitised fish and those with few or no parasites is acknowledged in the model by weighting the terms appropriately so that fish with i parasites are caught at rate ce^{-i}.

Figure 3.7 shows that the distributive model sits somewhere between the original and exponentially-reduced models in terms of host, parasite and free-living densities.

To check that the lower threshold result, whereby the parasite can survive at a lower host density because of the reduced capture rate, holds, parameters were chosen such that the parasite population would die out with no reduction in capture, but survive for particular initial conditions in the exponentially-reduced host capture model.

As figure 3.7 shows, the parasite population also survives in the new model, albeit at a slightly lower density than previously observed. The reduced threshold result is still therefore valid when the parasite distribution is taken into account within the capture rates.

On closer inspection after completing this work it became clear that the model described in this section was not fit for purpose, as effectively the distribution of parasites would be likely to change over time, and the sole effect of this addition to the model is a rescaling of

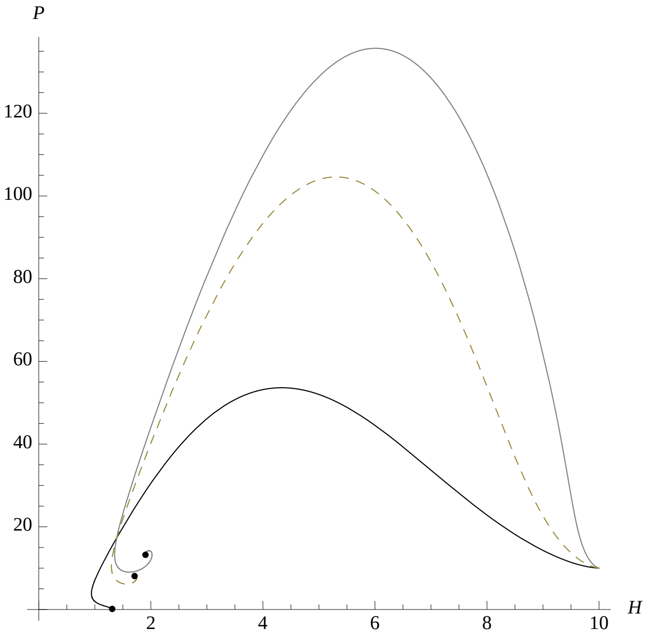


Figure 3.7: Parametric plot of the three models. The solid black line is the constant capture model, the grey solid line is the exponentially reduced, and the dashed is the new, distribution sensitive model.

the parameters in the original exponential model. In order to verify the model in the manner intended, an individual-based model would be required, through which the distribution of parasites could be tracked. While the following chapters mainly make use of simulations, this would add a level of complexity to the model which would make any analytical results more difficult to achieve, and simulations more computationally intense.

Moving forward, the decision was taken to retain the downward hill reduction in capture. As previously stated, the exponential function was useful for finding analytical results, but the shape seems less likely to be representative of the relationship between parasitism and capture than this function, as it implies that the drop off in capture is quite sharp for few parasites. The parameters in the downward hill function also have the benefit of being more readily understood and interpreted, since ρ can be comprehensively defined as the number of parasites per host for which the capture rate is halved.

3.3 EGG EQUATION

To this point the models have assumed the parasite emerges from adult stages ready to attach to a host; however *Argulus* spp. lay eggs off the host which is likely to delay reproduction timing and make parasite recruitment less dependent on host survival. To account for this a fourth compartment representing parasite eggs is now added in order to improve the realism of the model, and to allow the parasites to over-winter as eggs in the seasonal models, which will be studied in chapter four. While female *A. foliaceus* leave the host to lay eggs, this is already accounted for in the attached mortality rate μ_P, as *A. foliaceus* mortality is high after egg-laying, so adding these parasites back into the free-living compartment would produce misleading results. In this section the new model and parameters are introduced and the model analysed. A comparison of the model with the baseline model follows.

Several new parameters are introduced here, and these are: egg-laying and hatching; h is defined as the hatching rate per day (1/incubation period), and ε is the rate at which eggs are laid (eggs per day per attached parasite). The model with constant capture rate assumed is now:

$$dH/dt = s - cH - \alpha P \tag{3.27}$$

$$dP/dt = \beta HW - P(\mu_p + \alpha + c) - \alpha k \frac{P^2}{H} \tag{3.28}$$

$$dW/dt = hE - \mu_w W - \beta HW \tag{3.29}$$

$$dE/dt = \varepsilon P - hE - \mu_e E \tag{3.30}$$

The host-only equilibrium is given by $(s/c, 0, 0, 0)$, which is again identical to the host-only equilibrium in the baseline model, and in the equilibrium analysis has the characteristic equation:

$$(\Lambda + c)[\Lambda^3 + \tag{3.31}$$

$$\Lambda^2(\mu_p + \alpha + c + h + \mu_e + \beta s/c + \mu_w) + \tag{3.32}$$

$$\Lambda[(\mu_p + \alpha + c)(h + \mu_e + \beta s/c + \mu_w) + (\beta s/c + \mu_w)(h + \mu_e)] + \tag{3.33}$$

$$(\mu_p + \alpha + c)(\beta s/c + \mu_w)(h + \delta) - \beta s/ch\varepsilon] \tag{3.34}$$

From which it is evident that the first eigenvalue is given by

$$\Lambda_1 = -c, \tag{3.35}$$

and is therefore always negative.

The conditions under which the remaining eigenvalues are negative were found by using the Routh-Hurwitz conditions for a third order polynomial, since one of the eigenvalues is already known; these conditions are 1) $a_1 > 0$; 2) $a_3 > 0$; and 3) $a_1 a_2 < a_3$.

The first of these is always met for positive parameters, and the second is true with the condition that:

$$\varepsilon < \frac{c}{\beta s h}(\mu_p + \alpha + c)(\beta s/c + \mu_w)(h + \mu_e) \tag{3.36}$$

For positive parameters, condition 3) is always true. Thus, the host-only equilibrium is stable when condition 3.36 is met - in other words, when the parasite egg-laying rate is too low to maintain the parasite population relative to the loss rates of the parasite in the egg, attached and free-living stages.

For the coexistence equilibrium:

$$H^* = \frac{\beta ks + \mu_w \gamma_k}{\beta(\frac{h\varepsilon}{h+\mu_e} - \gamma_k)} \tag{3.37}$$

$$\pm \sqrt{\left[\frac{\beta ks + \mu_w \gamma_k}{\beta(\frac{h\varepsilon}{h+\mu_e} - \gamma_k)}\right]^2 + \frac{4\mu_w ks}{\beta(\frac{h\varepsilon}{h+\mu_e} - \gamma_k)}} \tag{3.38}$$

$$P^* = \frac{H^*}{\alpha k}\left[\frac{\beta H^* h\varepsilon}{(\beta H^* + \mu_w)(h * \mu_e)} - \mu_p - \alpha - c\right] \tag{3.39}$$

$$E^* = \frac{\varepsilon P^*}{h + \mu_e} \tag{3.40}$$

$$W^* = \frac{hE^*}{\beta H^* + \mu_w} \tag{3.41}$$

where $\gamma_k = \mu_p + \alpha + c - ck$. For H^* to be a unique positive equilibrium, the egg-laying rate must be sufficiently high:

$$\varepsilon > \frac{h+\delta}{h}(\mu_p + \alpha + c - ck), \tag{3.42}$$

and in order for the parasite equilibrium density to be positive, the condition $\varepsilon > \mu_p + \alpha + c$ must be met, and a minimum H^* is required:

$$H^* > \frac{d(\mu_p + \alpha + c)}{\beta(\frac{h\varepsilon}{h+\mu_e} - \mu_p - \alpha - c)}. \tag{3.43}$$

When the expression for H^* is substituted in to this, it becomes the opposite of the condition for stability of the host-only equilibrium. As in previous models, positivity of the parasite equilibrium density is a sufficient condition for the stability of the coexistence equilibrium, and parasite survival is dependent on the attachment and reproductive rates exceeding losses due to capture and mortalities.

3.3.1 *Comparison with the model without egg-laying*

Table 3.1 provides a comparison of the model without egg-laying with the new model, which includes a compartment for the egg population. The two models are equivalent in equilibrium density and stability when $\frac{h\varepsilon}{h+\mu_E} = \lambda$, and both are capable of producing the same qualitative results. The addition of this equation in isolation makes little difference to the model, but is necessary for work in later chapters.

Table 3.1: Equilibrium densities and stocking threshold for parasite survival for the two models

	Without egg-laying	With egg-laying
Host density (infected)	$\frac{\beta ks-d\gamma}{\beta(\lambda-\gamma)}+\sqrt{(\frac{\beta ks-d\gamma}{\beta(\lambda-\gamma)})^2+\frac{4dks}{\beta(\lambda-\gamma)}}$	$\frac{\beta ks-d\gamma}{\beta(\frac{\varepsilon h}{h+\mu_E}-\gamma)}+\sqrt{(\frac{\beta ks-d\gamma}{\beta(\frac{\varepsilon h}{h+\mu_E}-\gamma)})^2+\frac{4dks}{\beta(\frac{\varepsilon h}{h+\mu_E}a-\gamma)}}$
Parasite density	$\frac{H^*}{\alpha k}\left[\frac{\beta H^*\lambda}{\beta H^*+d}-\mu-\alpha-c\right]$	$\frac{H^*}{\alpha k}\left[\frac{\beta H^*h\varepsilon}{(\beta H^*+d)(h+\mu_E)}-\mu-\alpha-c\right]$
Threshold stocking level	$\frac{cd(\mu+\alpha+c)}{\beta(\varepsilon-\mu-\alpha-c)}$	$\frac{cd(\mu+\alpha+c)}{\beta(\frac{\varepsilon h}{h+\mu_E}-(\mu+\alpha+c))}$

3.4 NATURAL HOST MORTALITIES

At this stage, for completeness, host mortalities at a rate of $\mu_H = 1/(\mathrm{L}-\mathrm{A})$ day^{-1} were added to the model, where L gives the lifespan of the fish, and A the age at which fish are typically stocked into the fishery. This varies according to the age of fish stocked into the fishery and environmental factors affecting their survival, its inclusion in the model is necessary for biological realism - failure to include this would mean that without capture and parasite-induced mortalities, the host population could survive indefinitely even if no fish were being stocked.

3.5 MOVING FORWARD: THE FULL MODEL

The model including the alterations made throughout this chapter, which is used in subsequent chapters, is now given by:

$$dH/dt = s - \mu_H H - cfH - \alpha P \tag{3.44}$$

$$dP/dt = \beta HW - P(\mu_P + cf + \alpha) - \alpha k\frac{P^2}{H} \tag{3.45}$$

$$dW/dt = hE - \mu_W W - \beta HW + \delta\alpha P(1 + k\frac{P}{H}) + \delta\mu_H P \tag{3.46}$$

$$dE/dt = \varepsilon P - hE - \mu_E E \tag{3.47}$$

The shorthand f denotes the downward hill function for reduction in capture.

The host-only equilibrium is given by $H^* = \frac{s}{\mu_H + cf}$. For this equilibrium the characteristic equation is given by:

$$(\Lambda + \mu_H + c)[\Lambda^3 \tag{3.48}$$

$$+\Lambda^2[\mu_p + \alpha + c + \mu_W + \frac{\beta s}{\mu_H + c} + h + \mu_E] \tag{3.49}$$

$$+\Lambda[(\mu_P + \alpha + c)(\mu_W + \frac{\beta s}{\mu_H + c} + h + \mu_E) + (h + \mu_E)(\mu_W + \frac{\beta s}{\mu_H + c}) - \frac{\delta \alpha \beta s}{\mu_H + c}] \tag{3.50}$$

$$+(\mu_p + \alpha + c)(h + \mu_E)(\mu_W + \frac{\beta s}{\mu_H + c}) - \frac{\beta s}{\mu_H + c}(\delta \alpha (h + \mu_E) + h\epsilon)] \tag{3.51}$$

The first eigenvalue is $\Lambda_1 = -\mu_H - c$, and the remaining three eigenvalues are negative when $a_3 > 0$, i.e. when $\frac{h\epsilon}{h+\mu_E} < \left[(\mu_P + \alpha + c)(\frac{\mu_W(\mu_H+c)}{\beta s} + 1) - \delta\alpha\right]$. The other Routh Hurwitz conditions for stability are always met. Inclusion of host mortalities reduce the equilibrium host density and consequently the parasite's ability to survive, but the qualitative results are unchanged.

3.6 CONCLUSIONS

The alterations made in this chapter make no difference to the range of qualitative results produced by the model, but naturally have an impact on its quantitative results. By altering the shape of the parasite-induced capture reduction function, the model now more realistically reflects the relationship between parasite burden and fish capture. The addition of the egg compartment to the model will facilitate the inclusion of seasonality in chapter four, and it is important to include natural host mortalities in order to accurately model the fish population.

4

SEASONALITY, SITE DATA, AND MODEL FITTING

In this chapter the aim is to capture the seasonal life cycle of *Argulus foliaceus* throughout the course of the year. *A. foliaceus* numbers are highly variable across the seasons as the parasite exhibits temperature-dependent growth, hatching and death rates [7]. It is necessary to include these dynamics in the model as these fluctuations in numbers may mean that anti-parasite interventions, to be investigated in chapter six, are more likely to be effective at certain times of the year; similarly there may exist times during the year during which stocking batches of fish may carry a higher risk of exacerbating an *Argulus* spp. infection.

In this chapter an overview of the parasite burden data presented by Taylor et al. [52] is provided, as well as stocking data for one of these sites. These stocking figures are then incorporated into the model, so that the predicted parasite burden values can be compared to the data.

Seasonality has been added to the model in two stages: in section 4.2.1 the egg-laying parameter, ε, is replaced with a function which varies according to the temperature, given by a sinusoidal function of time, and in section 4.2.2 a discrete cut-off temperature beyond which the parasite is unable to hatch, lay eggs or attach to a host is introduced, to represent *A. foliaceus*'s overwintering behaviour.

Finally, the model is fitted to the available data, by optimising a series of the parameters for which values were not available in the literature.

4.1 FISHERY SITE DATA

In this section parasite burden data collected from five sites, and studied in [52] are presented, as well as stocking and capture data from site three in the same study. While the sample sizes are fairly small (a maximum of 30 fish were sampled during each sampling event), the aim is to show that the model represents the parasite dynamics across the year, and to find reasonable values of the attachment rate β, parasite-induced host mortality rate α, parasite burden required to halve the capture rate ρ and the shape parameter for the hill function, n, for use in simulations in subsequent chapters.

4.1.1 *Parasite burden data*

Parasite burden data collected between May 2002 and May 2003 are presented in figure 4.1 (joined to show January to December). In all cases parasite numbers are stable and relatively low from December until April. In sites 1-3 parasite numbers were low in May 2002, and higher in May 2003.

In 2002 the parasite burden increased in all sites from May onwards. While sites 1, 4 and 5 reached their peak in September or October, there is a sharp dip in abundance between the August and September sampling events in sites 2 and 3. A similar drop is also seen in July at site 4.

Looking specifically at site three, data from which will be used to parameterise the model, the sharp dip between August and September is unique to this and site two, which is under the same management as this site, and at which an intervention is believed to have taken place between the August and September sampling visits. Sites one, four and five had their peak parasite burden in September or October, but both sites two and three have a drop between August and September, with the populations experiencing secondary peaks in October and November respectively.

4.1.2 *Stocking data*

The stocking and capture data is given in table 4.1. Stocking data were available for both sites two and three from the study; however, data from site two was not used in parametrising

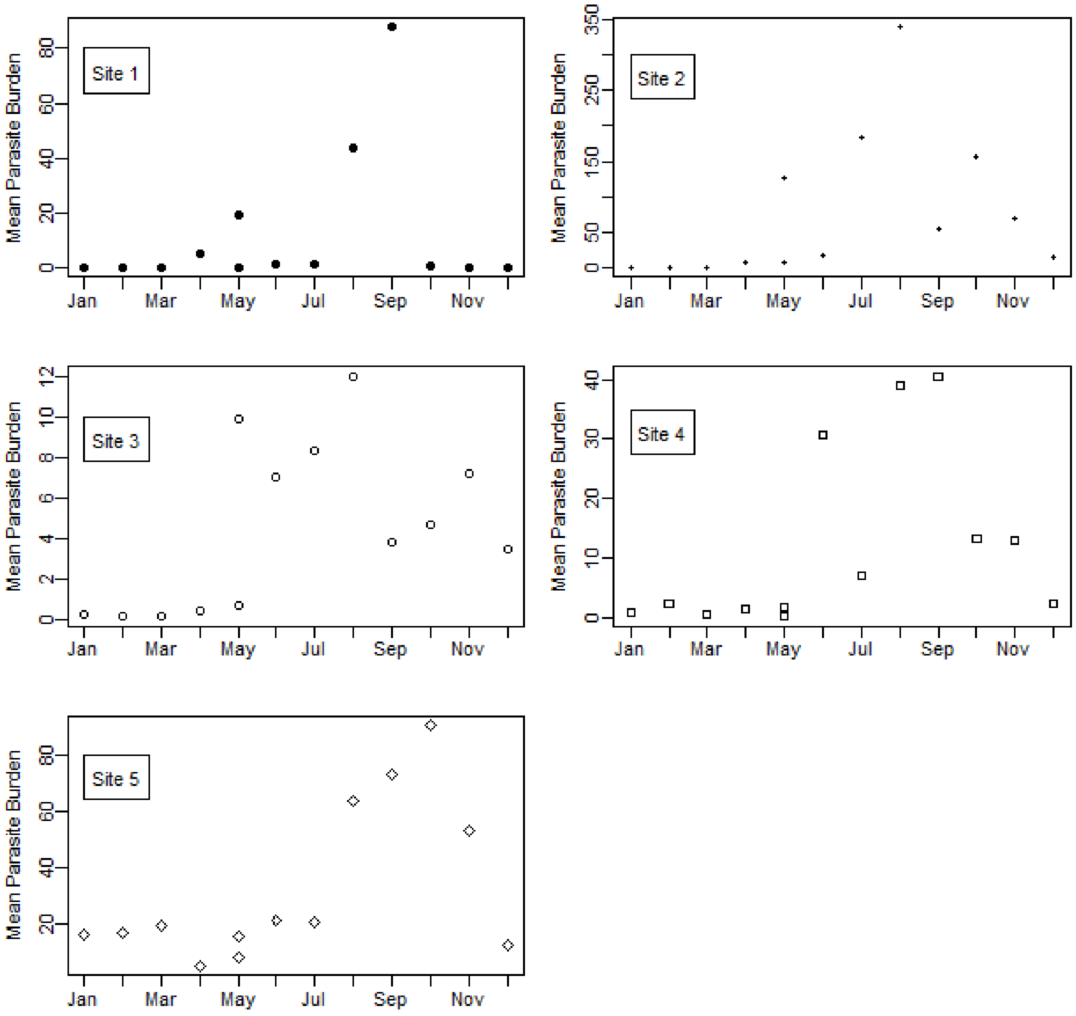


Figure 4.1: Plot of parasite burden for each of the five sites

the model, as an undisclosed intervention against *Argulus foliaceus* is believed to have been used during the study period [52]. The stocking data was added to the model by dividing the numbers of fish stocked by 365/12 (as stocking figures were given for each month) and the volume of water at each site to give daily stocking rates per unit volume. Data for both May 2002 and May 2003 were available, and so the mean of these two values was used. In the following sections where seasonality is added to the model, the mean of the stocking rates was used. The actual figures are then incorporated into the model at the end of the chapter in order to compare the actual parasite burden figures to the model predictions.

Table 4.1: Adjusted stocking, capture and parasite burden data used in fitting the model: the mean of the May values were used for all three measures.

Site 3	Stocked	Caught	Parasite Burden
May	1461	1318	5.26
Jun	840	656	7.00
Jul	710	497	8.30
Aug	121	258	12.00
Sep	350	275	3.75
Oct	452	367	4.67
Nov	690	417	7.20
Dec	1115	975	3.40
Jan	1100	787	0.22
Feb	600	588	0.10
Mar	1324	1211	0.13
Apr	1308	911	0.36

4.2 ADDING SEASONALITY TO THE MODEL

In chapter three, model features including an egg compartment and natural host mortalities were included to improve its realism; this chapter therefore begins with a model of the following form:

$$dH/dt = s - \mu_H H - cfH - \alpha P \tag{4.1}$$

$$dP/dt = \beta HW - P(\mu_P + cf + \alpha) - \alpha k \frac{P^2}{H} \tag{4.2}$$

$$dW/dt = hE - \mu_W W - \beta HW + \delta\alpha P(1 + k\frac{P}{H}) + \delta\mu_H P \tag{4.3}$$

$$dE/dt = \varepsilon P - hE - \mu_E E \tag{4.4}$$

Descriptions of the parameters have been provided in previous chapters, but for reference these are summarised in table 4.2. The equilibrium values in this model, with the parameters used throughout, are approximately $H^* = 0.00389$, $P^* = 0.0145$, $W^* = 0.0260$ and $E^* = 0.451$ per cubic metre. At the fishery level for site three, this translates to around 845 fish being present in the fishery, which compares favourably with the fishery's reported standing stock level of 900 fish, and a mean of 3.73 attached parasites per host which is within the range seen throughout the year on site (between around zero and 12 parasites per host). There are around 80% more free-living than attached parasites - this population being fed partly by the detachment of parasites from dying hosts (at a rate of around 0.00023 day^{-1}), but mainly through hatching from the egg population, which occurs around 50 times faster (roughly 0.012 $\text{day}^{-}1$). Eggs are more prevalent still, with around 116 times more eggs than hosts at any given time owing to the large number of eggs laid per parasite.

Table 4.2: Descriptions of model parameters

Parameter	Description
s	Stocking rate
c	Capture rate
α	Increased host mortality due to infection
μ_i	Natural mortality rate of population i
β	Rate of attachment
h	Hatching rate
ε	Egg-laying rate
δ	Proportion of parasites surviving host death

4.2.1 *Temperature-dependent egg-laying*

As described in chapter one, the life-cycle of *Argulus* spp. in the UK is seasonal; eggs overwinter and lie dormant without developing while the water temperature is below $8-10°\text{C}$, and the parasite matures faster at higher temperatures. In this section, seasonality is added by modelling water temperature as a function of time, based on data collected from fisheries in 2002-2003 Taylor et al. [52]: this data is presented in figure 4.2. The least squares regression curve found from this data is given by $\text{Temp}(°\text{C}) = 11.98 + 7.99\sin\left[\frac{2\pi(\text{d.o.y.}-127.98)}{365}\right]$, where $d.o.y.$ is the day of the year (e.g. 1 denotes the first of January). This is then incorporated into the egg-laying rate using the following formula, which gives the time taken for an argulid to reach adulthood (and begin laying eggs), as estimated by Taylor et al. [51].

$$D = \frac{3900}{(0.434T + 0.361)^2} days \quad \forall T \geq 0. \tag{4.5}$$

The sex ratio is assumed to be 1:1; while some studies have indicated a male bias, this is generally attributed to females leaving the host to lay eggs near the end of the parasite life cycle. An average of 228 eggs laid per female [37] is used, so that the egg-laying rate at a given timepoint is given by $228 * 0.5/D$ per attached parasite per day. While much research has been focused on determining the off-host survival of *Argulus* spp., little data is available on the lifespan or mortality rates of attached parasites, however mortality after egg-laying is high [7] [24]. For this reason $1/D$, with D given by the equation above, is used for the mortality rate. While some females may lay their eggs over several events, the number of events has been shown to have no significant effect on the total number of eggs laid [17].

Figure 4.3 shows time series plots of the four populations before and after the addition of sinusoidal egg-laying. As would be expected, all four populations are more variable, and the population densities now fluctuate around the original, static equilibrium values of the previous model. Within around five years, the model reaches a cyclic equilibrium, with each population moving through the same pattern of growth and decline each year.

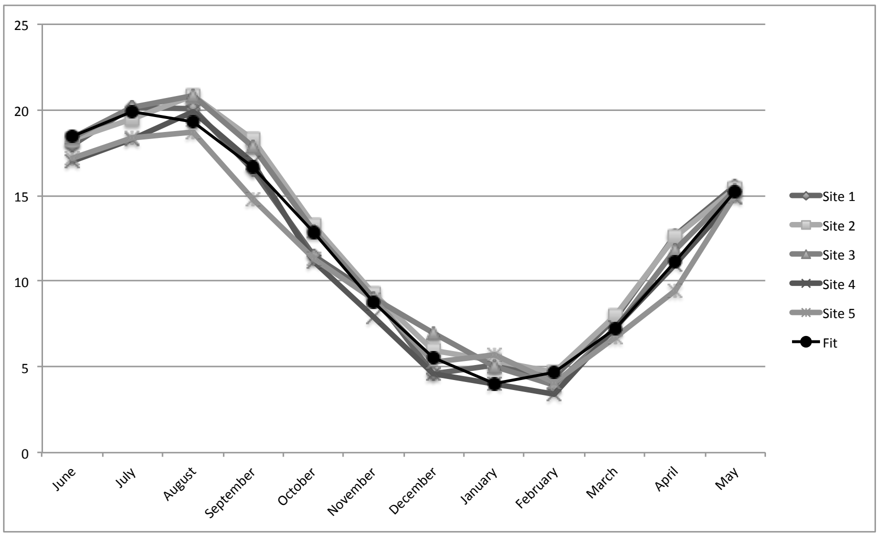


Figure 4.2: Water temperature (°C) from five fisheries across England - 2002/03 - recreated from [52].

In subsequent sections it is often difficult to directly compare time series plots of the seasonal models, and in these cases parametric plots are useful for highlighting the differences. Figure 4.4 shows parametric plots of the same two models, with and without sinusoidal egg-laying, but while the parasite density is still given on the vertical axis, now the host population is on the horizontal axis. The plot shows a simulation period of ten years; the first four years are clearly defined, but about halfway through the simulation each year becomes indistinguishable from the next.

The main consequence of including seasonality in the model is that the parasite is more prevalent at certain times of the year than others; this is consistent with observations in fisheries, where *Argulus* spp. typically causes more problems in summer rather than winter. Whereas the non-seasonal model provides a static parasite burden of 3.72, the seasonal model predicts annual fluctuations between 1.2 and 8.6 attached parasites per host in the winter and summer respectively, which is similar to the data for site three (figure 4.1), which predicts a mean parasite burden of upto 12 parasites per host in the summer.

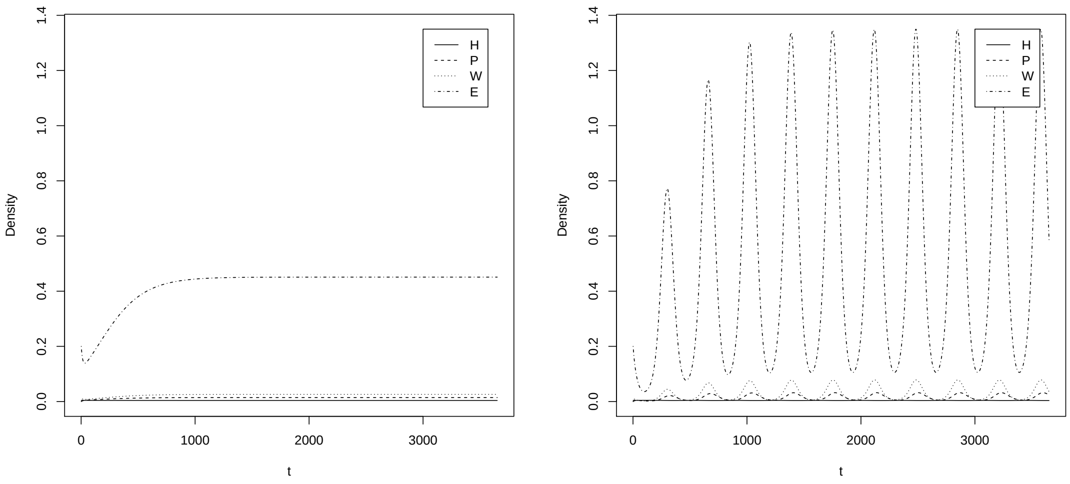


Figure 4.3: Time series plots of host (H), attached parasite (P), free-living parasite (W) and parasite egg stages (E) before (left) and after (right) sinusoidal egg-laying was added to the model. The parameters in the non-seasonal model are as in the seasonal model, but with the temperature set to its annual mean of 12°C.

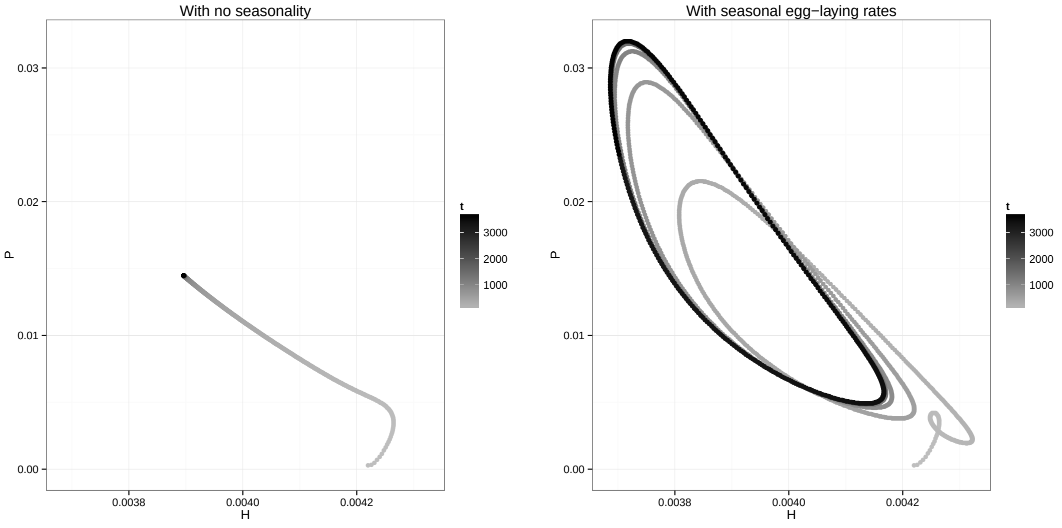


Figure 4.4: Parametric plots the host-parasite dynamics before (left) and after (right) sinusoidal egg-laying was added to the model. The host population is on the horizontal axis, and the attached parasite population is on the vertical axis. The colour of the plot points is a function of time, starting at $t = 0$ (lightest grey) and finishing after ten years, at t=3650 (black).

4.2.2 *Parasite over-wintering*

With temperature-dependent egg-laying in place, the next step is to incorporate over-wintering into the model, so that egg-laying does not occur when the temperature is lower than 8°C. Although the scientific literature is no more specific that 8-10°C, here the lower value of 8°C is used, to be representative of the worst-case scenario. In addition to egg-laying, parasite attachment and hatching also cease in the winter months, while eggs benefit from reduced mortality rates [37] (see Appendix A). Figures 4.5 and 4.6 show time series plots of the model with over-wintering compared to the model without (the left hand plots are identical to those from the previous section, but the scales have been adjusted for comparison). Over-wintering increases the variability of both the host and parasite populations, and increases the maximum mean parasite burden (attached parasite density divided by host density) to 15 - though it also drops as low as 0.095 when the egg-laying rate is low.

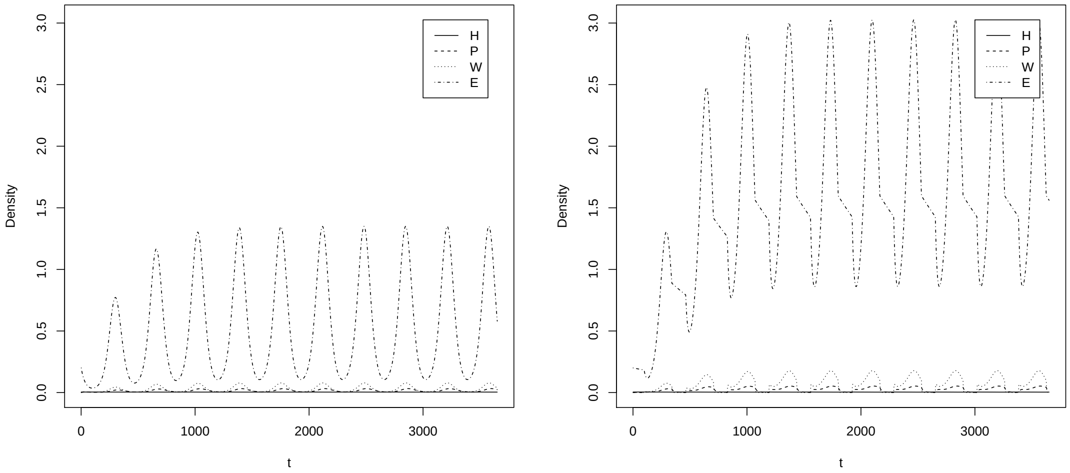


Figure 4.5: Time series plots of host (H), attached parasite (P), free-living parasite (W) and parasite egg stages (E) before (left) and after (right) overwintering was added to the model.

Figure 4.7 shows the final year of the ten-year run. The host population, bearing in mind that the stocking rate is constant throughout the year, here, varies between 0.0034 and 0.0043 fish per cubic metre - this scales up to $746 - 939$ at the fishery level, which still compares well with the reported standing stock level for site three. The egg population declines slowly when

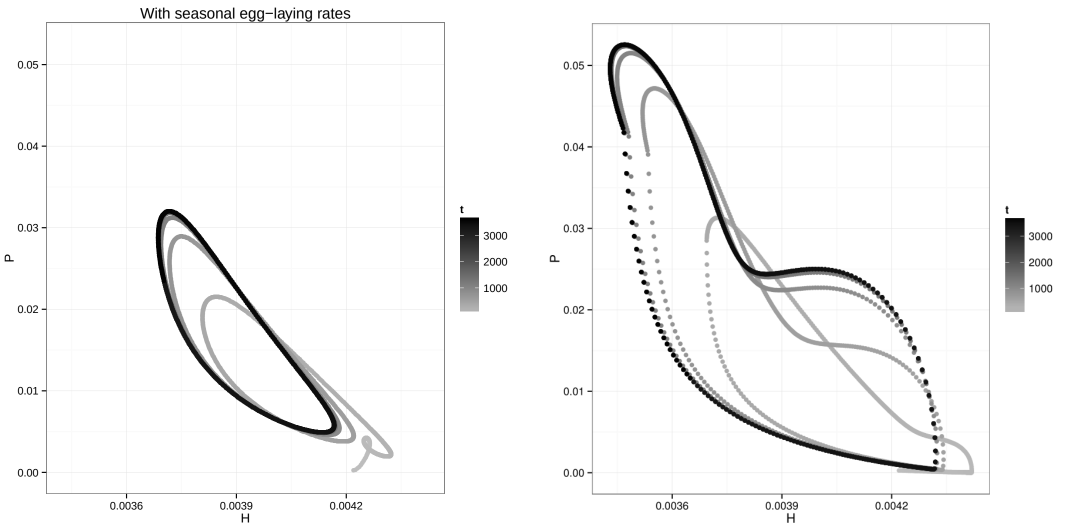


Figure 4.6: Parametric plots the host-parasite dynamics before (left) and after (right) an over-wintering period was added to the model. The host population is on the horizontal axis, and the attached parasite population is on the vertical axis. The colour of the plot points is a function of time, starting at t=0 (lightest grey) and finishing after ten years, at t=3650 (black).

the temperature is low throughout winter, as no eggs are being laid and the eggs are subjected to a (albeit low) mortality rate. The density of eggs drops as hatching begins in April, before rising steadily from May until October as the egg-laying rate increases due to both the higher temperature and the higher density of egg-laying individuals. While hatching continues throughout October and November, the egg-laying rate declines causing the population to drop to roughly the same level as January. The over-wintering period then begins, slowing the egg mortality rate. The free-living parasite population is low throughout winter and increases sharply in April when the eggs begin to hatch. As these parasites attach to hosts there is a drop in the free-living parasite population between April and May before growing again due to the higher levels of egg-laying. The decrease in temperature also affects the free-living population, though this effect is seen slightly later than in the egg population - as temperature only affects the free-living population indirectly through the egg population. The attached population follows a similar pattern, though again the peak in density is seen later than in the egg and free-living populations which feed it. Moving on to the right hand plot of figure 4.7, roughly the same pattern can be observed in the parasite burden (attached parasite density divided by the host density). The mean parasite burden drops below one parasite per 10 fish by the end of winter, and rises above a mean of 15 parasites per host in October.

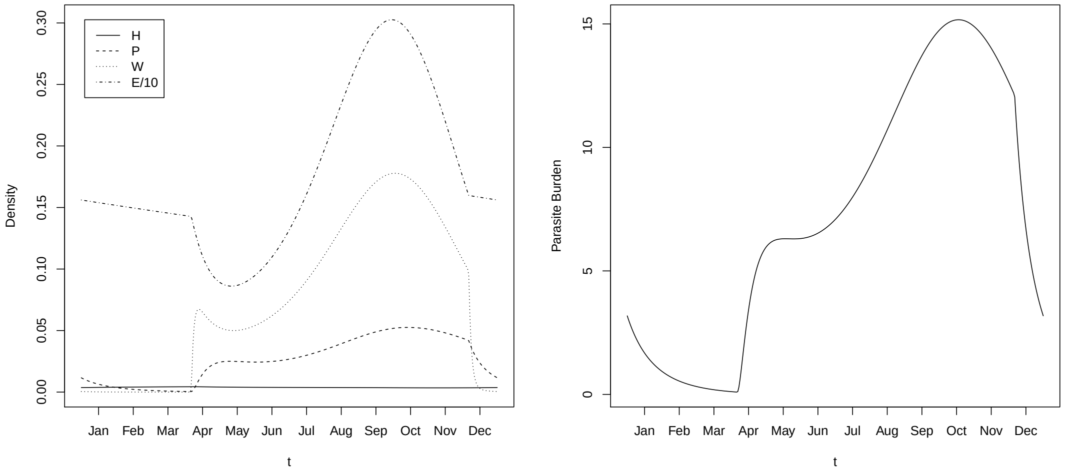


Figure 4.7: One year (last of a ten year simulation) time series plot of host (H), attached parasite (P), free-living parasite (W) and parasite egg stages (E) in the overwintering model (left). The egg population density has been divided by 10 in order to show all the populations together. The right hand plot shows the mean parasite burden throughout the year - this is found simply by dividing the attached parasite population density (P) by the host population density (H).

The next section briefly describes how the model parameters were fit to the available fishery data, before the model with and without seasonality is compared to the data to show how the alterations made here affect the ability of the model to predict seasonal variations in parasite abundance, and the impact on capture rates.

4.3 PARAMETER FITTING AND SENSITIVITY ANALYSIS

The parameters α (parasite-induced host mortality rate) and β (parasite attachment rate) were fit to the data using the box-constrained limited-memory Broyden-Fletcher-Goldfarb-Shanno (L-BFGS-B) method within the optim function in R. This method was chosen as upper and lower bounds on the parameters can be specified (so that all parameters are greater than zero, for example). In order to achieve this the current set of parameters are compared to the constraints at each step, and then only the "free" parameters are optimised using the L-BFGS method, which is an optimisation algorithm generally used for estimating large numbers of parameters.

The metrics used to assess the fit were the capture rates and parasite abundance. The observed values were as presented in table 4.1, with the capture rate divided by the volume of water. As the data were collected from the sites over a period of two weeks each month, it was decided that the best way to compare the data to the parasite burden predicted by the model was to use the predicted value halfway through each month. In order to calculate the expected values from the model, the last year of a ten-year simulation was used, and an additional compartment added to the model, in order to keep track of the total number of fish caught. From this, the number of caught fish at the beginning of each month was subtracted from the number of caught fish at the end of the month, and these were compared to the scaled values provided by the fishery owner.

The optim function was set up to minimise the square of the differences in the capture and parasite burden values. A Chi-squared approximation was used where the value to minimise was initially given by:

$$\sum_i \frac{(O-E)^2}{E} \tag{4.6}$$

However, as the capture values were high relative to the parasite burden values, the latter fit very poorly to the available data (not shown). The values were therefore scaled so that the sum of scores for the parasite burden and the sum of scores for the capture rate each had a theoretical maximum of 1. Since each $\frac{(O-E)^2}{E}$ has a maximum of E as $E \to \infty$, each capture score was divided by the sum of capture scores, and each parasite score was divided by the sum of parasite scores, so that the function being minimised became:

$$\sum_{i=1}^{12} \frac{(O_{ci}-E_{ci})^2}{E_{ci}\sum E_{ci}} + \frac{(O_{pi}-E_{pi})^2}{E_{pi}\sum E_{pi}} \tag{4.7}$$

This places equal importance on the parasite burden and capture data, and returned parameter estimates of $\alpha = 0.0015$ and $\beta = 7.12$ and a score of 0.312. While more sophisticated methods may be available to fit parameters to the model, suitable data was only available for one site, and limited data were available to verify it. Optim provided a quick and significant improvement in the model; where the previous set of parameters, $\alpha = 0.001$ (as in chapter two) and $\beta = 0.0384$ (see Appendix A), resulted in parasite extinction with the site three stocking data, the values found by optim compare well with the observed data (as seen in the next section).

While the new β value of 7.12 is much higher than the previous estimate of 0.0384, the latter value was calculated from a study that was not specifically designed to estimate the rate of parasite attachment. Anecdotal evidence also suggests that attachment experiments with the parasite can be difficult in the laboratory due to a high level of predation by the fish upon the parasite. This may explain why the value is higher when fitted to data from the wild.

As well as α and β, it was also necessary to find reasonable parameters to use for the capture reduction parameters ρ, the mean parasite burden required to halve the capture rate, and n, the shape parameter for the capture reduction function, as required for the hill function described in chapter three. Initial attempts to estimate these using optim were confounded by the relationship between the two parameters, and were ultimately unsuccessful - even with extreme initial guesses, the optimised parameters changed very little. Eventually fitting of these parameters was done somewhat crudely by eye - this involved plotting the score (using the function for minimisation given above) against a wide range of values of ρ and n. Typically within each n-space there was an optimum value of ρ, where higher values of n required lower values of ρ. The best set of parameters found were $\rho = 15$ and $n = 2$ - indicating that the capture rate would be halved for a mean parasite burden of 15 per fish, with the sigmoidality of the function determined by n, resulting in the shape shown in figure 4.8.

With these values, optim was then run again to see if the optimal values of α and β were different, but these remained the same. The four optimised parameters are shown in table 4.3, and these are used throughout this and subsequent chapters.

Tornadograms provide graphical representations of model sensitivity to a range of parameters; each parameter is increased and decreased by a fixed percentage, and the resultant

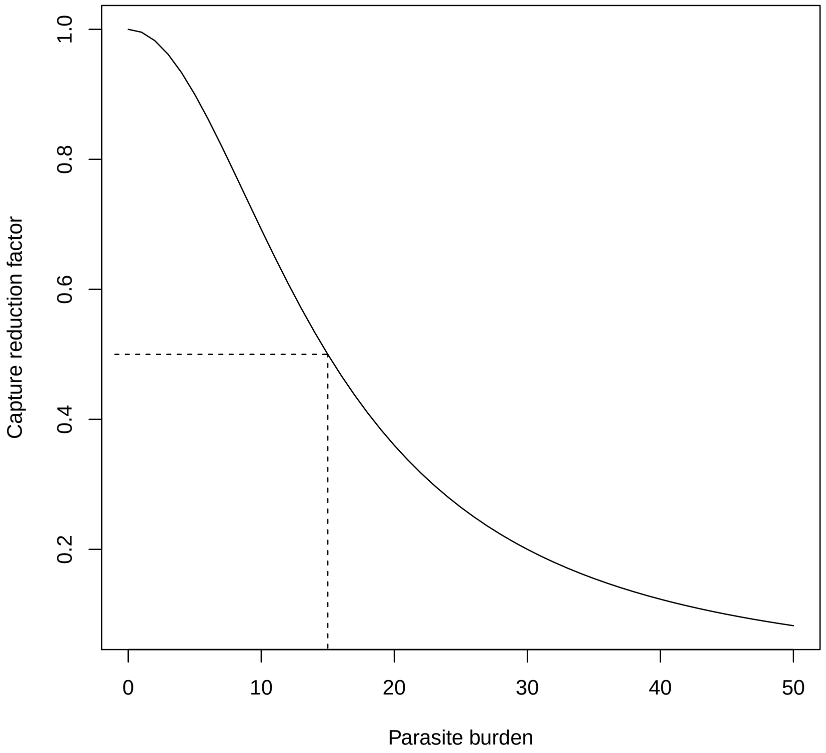


Figure 4.8: The downward hill function for capture reduction, where the reduction in capture for a parasite burden of P/H is given by $\frac{\rho^n}{\rho^n+(P/H)^n}$, with $\rho = 15$ and $n = 2$.

effect on the model is depicted on a bar chart showing the impact of these changes on a particular output. Such figures, showing the sensitivity of the seasonal model to parameters in terms of deviation from the fitted values are shown in figure 4.9; for example a 1% increase in the attachment rate, β results in roughly a 0.6% reduction in capture, and an increase of around 2.5% in parasite abundance. The model is most sensitive to β in terms of both parasite abundance and capture. The next most sensitive parameter is α, the rate at which the parasite induced mortality in the host, followed by the capture reduction parameters ρ and n. This suggests that β would be a useful parameter to estimate in future experiments, though as stated previously this is difficult to achieve under laboratory conditions, and is likely to vary with different environmental conditions [52].

Table 4.3: Model parameters fitted using optim.

Parameter	Fitted Value
α	0.0015
β	7.12
ρ	15
n	2

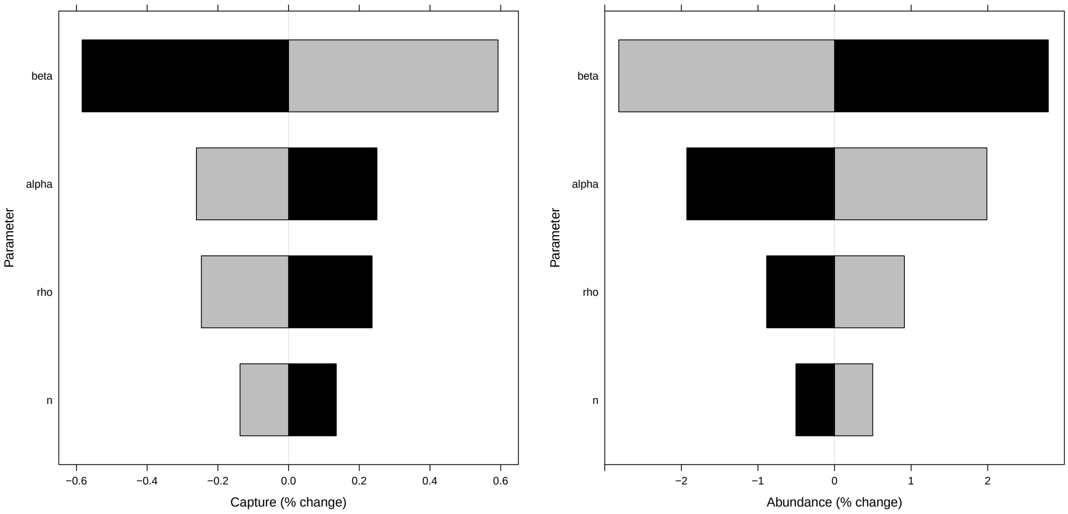


Figure 4.9: Tornadograms showing how changes in parameters affect the number of fish caught (top) and parasite abundance (bottom). The black bars represent an increase of 1% to the parameter, while the grey bars represent a decrease of 1%.

4.4 INCLUSION OF STOCKING DATA IN THE MODEL

In order to compare the model to the data, the temporal stocking data presented earlier in this chapter was first incorporated into the model, and the recorded parasite burden and capture data compared to the predicted values from 1) the non-seasonal model from the beginning of this chapter, 2) the intermediate seasonal model with seasonal egg-laying, and 3) the final model including overwintering described above, to see how the inclusion of these different aspects of seasonality affected the fit.

A linear interpolation of the stocking values, corrected for time (divided by 365/12) and volume (217366m^3) is shown in figure 4.10. This gives $s(t)$, which is the number of fish stocked per cubic metre on a particular day.

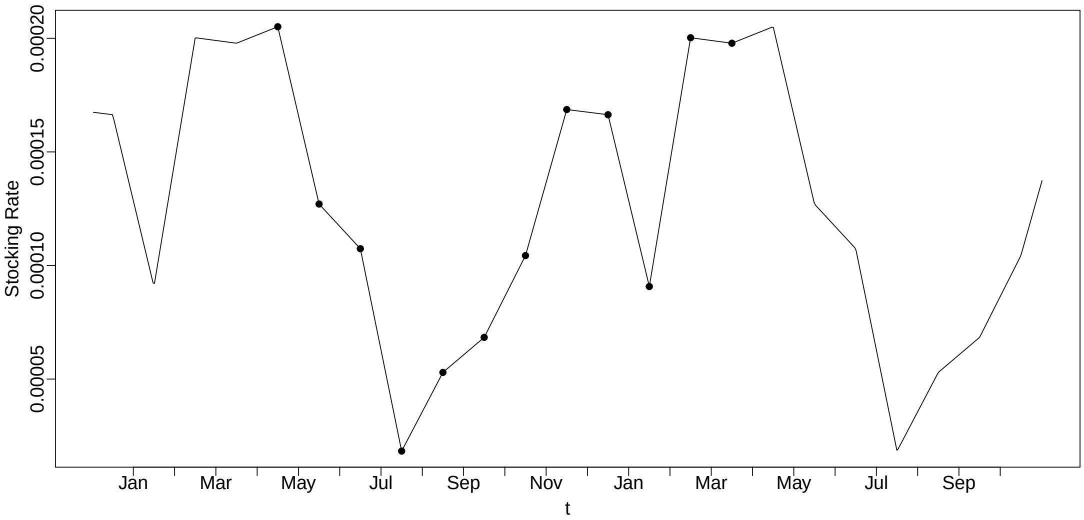
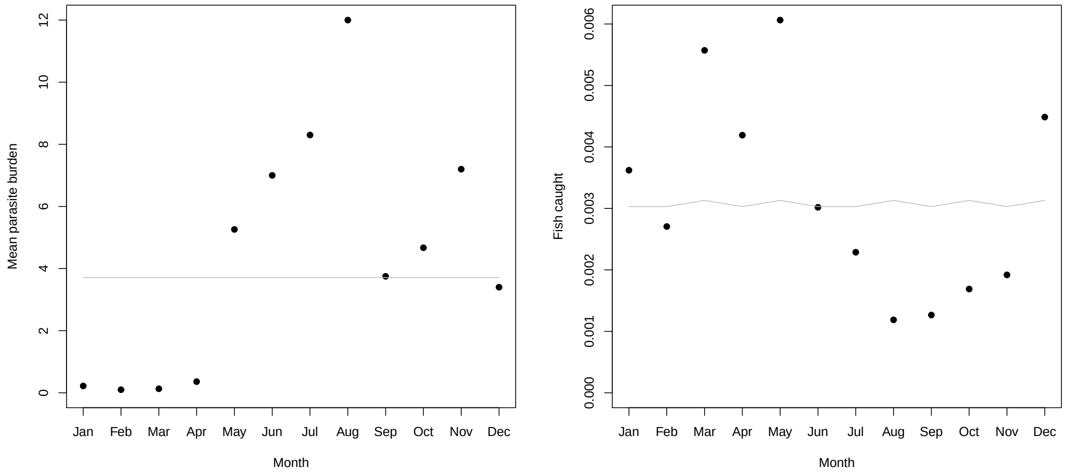


Figure 4.10: Line showing linear interpolation of stocking rates from site three. The actual data (divided by 365/12 for inclusion on the plot) is given by the black points. The figures on the vertical axis represent the number of fish stocked per cubic metre per day. The figures are extrapolated to cover the length of the simulation period, in the absence of longer term data.]

Figure 4.11 shows actual parasite burden (4.11a) and the capture (4.11b) data from site three plotted along with the predicted values, for the non-seasonal model used at the beginning of this chapter - with the actual stocking values. While the model approximates the mean parasite burden and capture rates across the year reasonably well, unsurprisingly, this model is not capable of representing the changes in parasite abundance throughout the year. The variation in stocking throughout the year causes slight fluctuations in the capture rate, but not enough to cause any noticeable variation in the parasite burden.

When temperature dependent egg-laying is included - as illustrated in figure 4.12 - the fit is improved, with a noticeable peak in parasite burden (4.12a) occurring in August, and lower numbers throughout the winter months. There is still room for improvement as, relative to the data, the parasite burden is over-estimated in winter, and under-estimated in summer -

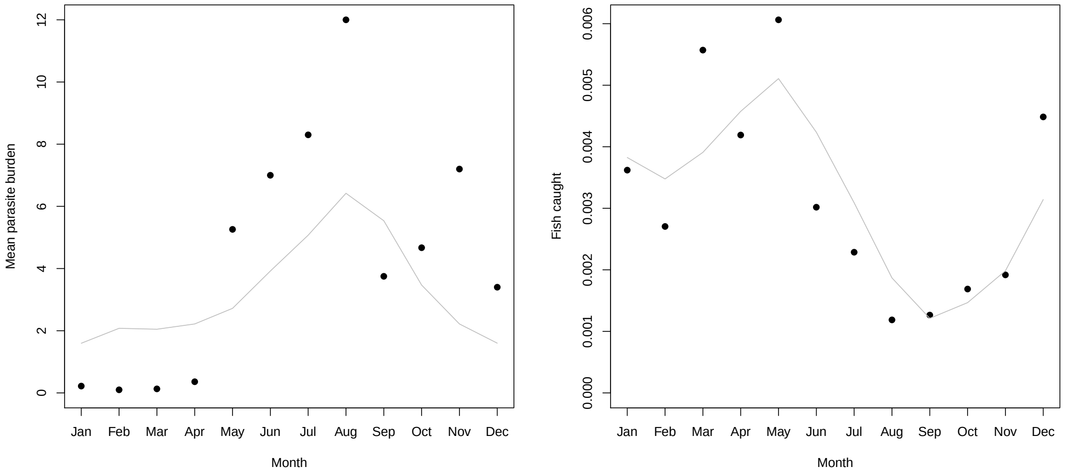


(a) (b)

Figure 4.11: Parasite burden and capture rate comparisons of the model (with no seasonality) against the data from site 3.

suggesting that further development of the model is needed to capture the extent of the effect of temperature on the host-parasite dynamics.

Finally, in figure 4.13, the over-wintering dynamics are included in the model. This model better represents the low numbers of parasites seen over the winter months when attachment, hatching and egg-laying are unable to occur due to low temperatures. Even with fitted parameters, however, the model does not predict the fall in parasite burden seen between August and September. As suggested earlier in this chapter, this could potentially be a consequence of an undisclosed intervention against the parasite, but could also be attributed to low sample sizes - for example only three fish were sampled in August. Another possibility is that due to the instantaneous occurrence of the various parasite dynamics (egg-laying, hatching, attachment), it is not able to capture the emergence of distinct cohorts throughout the year. In future models the inclusion of delays in the hatching and egg-laying rates may counter this problem. Including such dynamics in the model in this thesis, however, would seem ill-advised given the lack of this drop in the other sites presented at the start of this chapter, and would risk over-fitting the model to the site in question.



(a) (b)

Figure 4.12: Parasite burden and capture rate comparisons of the model (with sinusoidal egg-laying but no overwintering) against the data from site 3.

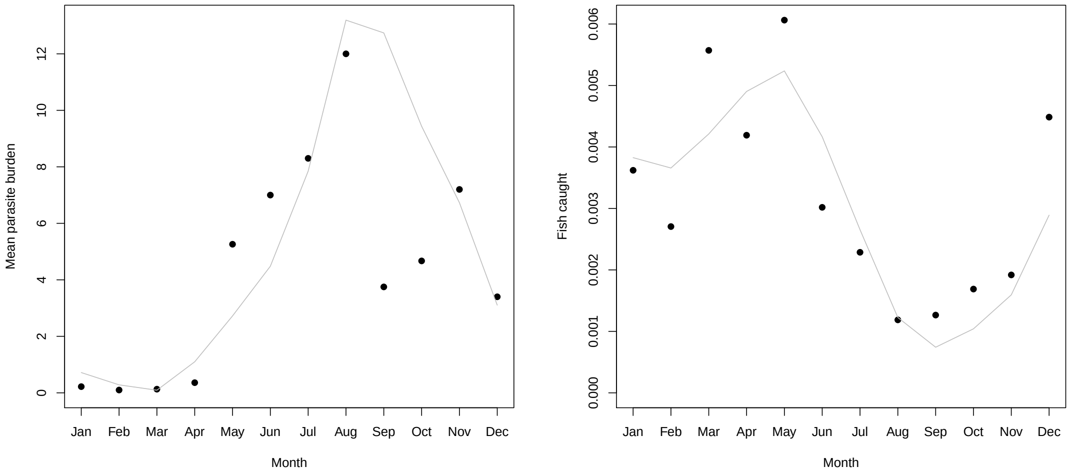


Figure 4.13: Parasite burden and capture rate comparisons of the model (with sinusoidal egg-laying and overwintering) against the data from site 3.

4.5 CONCLUSIONS

In this chapter seasonality has been added to the model in two stages. Firstly the fact that *A. foliaceus* lays eggs faster in warm temperatures, and more slowly at low temperatures was taken into account by modelling temperature as a sinusoidal function of time and using a temperature-dependent function estimated by Taylor et al. ([52]) for the rate of parasite maturation to determine the rate at which eggs were laid. The model was then further developed so that below a temperature of 8°C, the parasite eggs over-wintered and hatched stages stopped laying eggs, and these changes were shown to improve the fit of the model to both fish capture and parasite abundance data from site three.

Furthermore estimates of the parameters α and β, which have not yet been directly estimated experimentally, were found, as well as estimates of ρ and n which determine the strength and shape of the relationship between parasite burden and fish capture rates. The fact that the optimal value of the parameter ρ was as small as 15 - and therefore has a noticeable impact on fish capture for parasite numbers within the range of those seen in the field - indicates that the inclusion of the function improves the fit of the model, and justifies its inclusion in the model in this and subsequent chapters.

While the alterations improve the fit of the model, they also increase its complexity and resonance may occur if initial population densities are not chosen carefully. Simulations are therefore run for a minimum of ten years in later chapters to counter this effect when looking at the long-term effects of *Argulus* spp. and interventions against it.

Figure 4.14 shows the full model with and without the variable stocking data, and demonstrates that even when the total number of fish stocked within a year is the same, the timing of stocking events, even when approximated by a continuous function in such a manner that stocking never actually stops, has a noticeable impact on the parasite population. The model with variable stocking rates predicts lower densities of all three parasite compartments. Figure 4.15 shows the extent of the impact of variable stocking on the host population. By stocking in a manner which lowered host numbers in the latter half of the year when the highest number of parasites was present, it appears that the site may have benefited from higher rates of fish capture - with the model estimating 7857 fish caught (compared with 8260 actual captures) with the variable stocking rate, and 6601 without. The mean parasite burden per caught fish is also lower than would be expected with consistent stocking, dropping from 5.85 to 3.25 per fish. This highlights the importance of understanding the influence of stocking timing on the host-parasite dynamics, and the following chapter therefore focuses on stocking frequency, with an aim to predicting the optimal time to stock (or not stock) fish in order to minimise the impact of *A. foliaceus*.

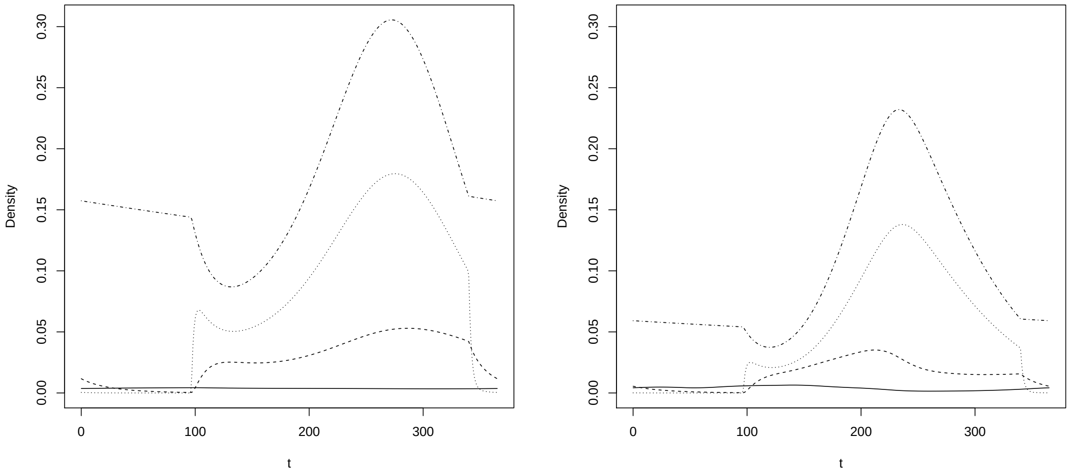


Figure 4.14: Time series plots of the model with constant (left) and variable (right) stocking data. The egg population densities have been divided by 10 for comparison.

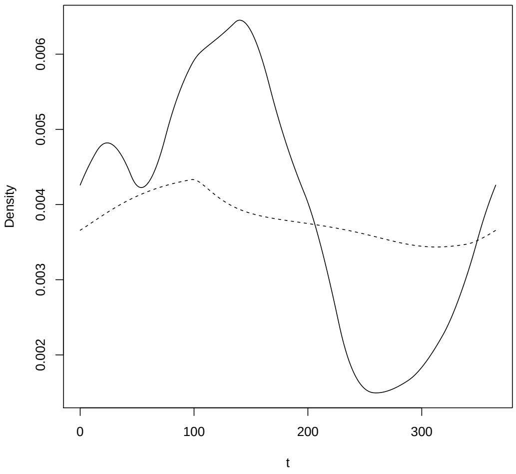


Figure 4.15: Time series plots of the host density as predicted by the model with constant (dashed) and observed variable (solid) stocking data.

5

STOCKING FREQUENCY

In chapter four, seasonality was added to the model in order to capture the temperature-dependent life history traits of *Argulus foliaceus*. There is now scope to examine the impact that altering the times of year and frequency at which fish are stocked into a fishery may have on the dynamics of *A. foliaceus*.

Current Environment Agency guidelines [2] advise that the stocking of large batches of fish on an infrequent basis is likely to exacerbate *Argulus* spp. infections. By modifying the model used in chapter four, we sought to determine whether this was the case, and hypothesised that stocking in this manner may reduce abundance throughout the year, depending on the timing of the stocking events; for example, stocking after the majority of parasite eggs have hatched in spring and the emerging free-living parasites have died due to a dearth of potential hosts. Regardless of whether stocking little and often, or “trickle" stocking, does turn out to be the ideal, as is currently accepted, financial and logistic constraints will make this impractical in many fisheries, such as smaller sites and those which are based a considerable distance from their supplier. For such fisheries it may therefore be useful to determine the best and worst times of year at which to stock fish with respect to *A. foliaceus* infections.

After examining a range of stocking frequencies the capture rate, which already included the parasite-induced rate reduction as parameterised in chapter four, was further constrained by imposing a theoretical restriction on the number of fish caught by each angler, to determine what, if any, impact this has on the effect of stocking at different times.

In this chapter the aim is to compare the impact the parasite has under different stocking regimes, with focus on the frequency and timing of stocking events. For simplicity this study was based on the constant stocking framework described in chapter two, whereby the level of stocking is consistent regardless of capture rates or mortalities. The number of fish stocked in a given year was assumed to be consistent throughout this chapter, but they were stocked in increasingly large batches and at increasingly long intervals - ranging from the baseline of continuous/daily stocking which has been assumed in earlier chapters, to a minimum stocking frequency of once per year.

In previous chapters the constant stocking method represented a case where the same number of fish, s, were stocked every day. In reality few fisheries have the ability to source fish at this frequency for this to be either practical or viable. To investigate the effect of different stocking frequencies on *A. foliaceus* infections, a new stocking function was formulated so that stocking occurred over 24 hours, on the first day of a ψ-day long period. The function $s[t]$, given in equation 5.1, defines the stocking rate at a given time point.

$$s(t) = \begin{cases} \psi s, & 0 \leq tMod\psi < 1 \\ \\ 0, & 1 \leq tMod\psi < \psi \end{cases} \tag{5.1}$$

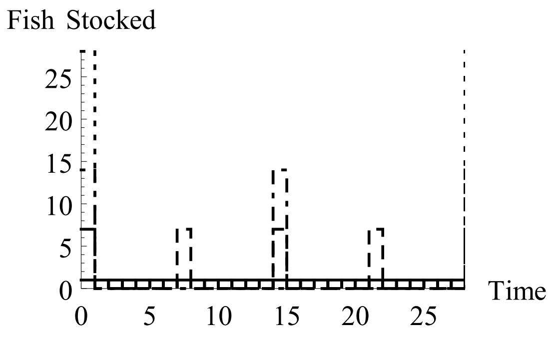


Figure 5.1: Illustration of different stocking frequencies, (ψ), when an average of one fish is stocked per day over a 28-day period (e.g. $s = 1$). Daily ($\psi = 1$, solid), weekly ($\psi = 7$, dashed), fortnightly ($\psi = 14$, dot-dashed) and monthly ($\psi = 28$, dotted) are shown.

Therefore $s[t] = s\psi$ on the day stocking occurs, and $s[t] = 0$ for the remainder of the stocking cycle; thus, the total number of fish added to the water throughout a given period should be the same regardless of ψ. Figure 5.1 provides a graphical representation of the stocking patterns for some different values of ψ - each of these values is a factor of 28, and so the total number of fish stocked over the 28 days is the same regardless of ψ. Throughout this chapter, increases in ψ will result in an increase in the length of time between stocking events, and also in the number of fish stocked on each occasion.

Initially a range of simulations were run using $\psi = 1$ through to $\psi = 365$ for one year to see if there was any obvious relationship between this parameter and the number of fish caught. Figure 5.2 shows the total number of fish stocked over one year per cubic metre, along with the total number of fish caught, and illustrates how the stocking frequency can change the number of fish caught over a five-year period.

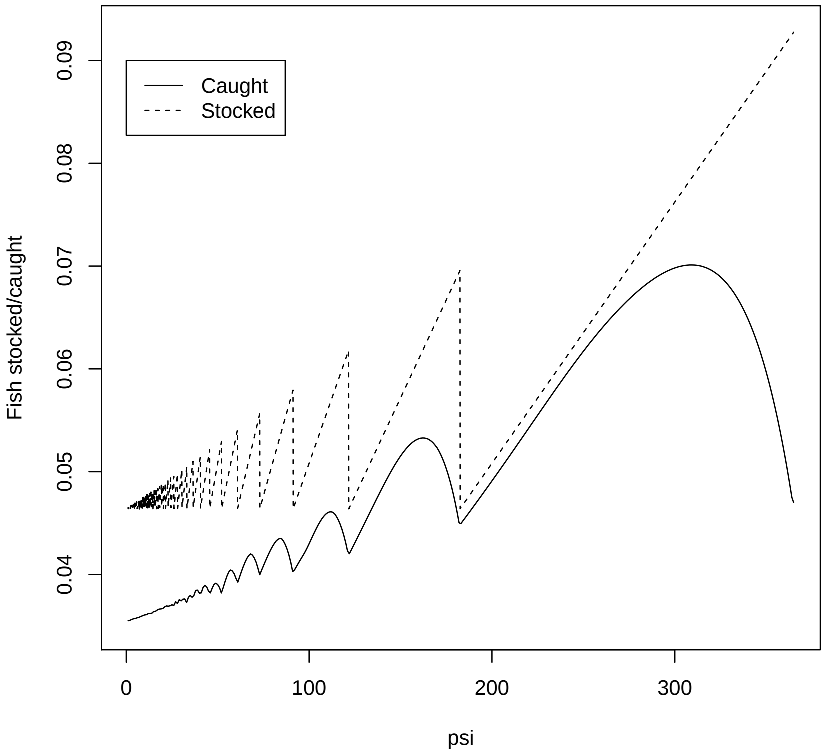


Figure 5.2: Number of fish stocked (dashed) and caught (solid) per cubic metre over one year, using the seasonal model from the end of chapter four, plotted against different stocking periods, ψ.

The oscillations, increasing in amplitude along with ψ, are symptomatic of the fact that values of ψ which do not evenly divide the simulation period have been included. If fish are stocked during the first day of a ψ-day-long cycle, and the simulation period in days, $tmax$, is not a multiple of ψ, then, as illustrated above, the results of the simulations will vary not only because of the variation in stocking frequency, but because the number of fish stocked is not fixed. For example, if simulations were run for 8 days, and stocking occurred every 7 days, then $7s$ fish would be stocked on the first day, and another $7s$ fish would be stocked on the last day, so $14s$ fish would be stocked altogether. Meanwhile if stocking occurred every 1, 2, 4, or 8 days then $8s$ fish would be stocked. If $tmax$ is not a multiple of ψ then $\psi s(tmaxDiv\psi + 1)$ fish will be stocked rather than the $s * tmax$ that would be stocked otherwise.

It is clear from this that the number of extra fish stocked has a strong impact on the rate of capture; however, towards the peaks of each of the cycles in the number of fish stocked, the capture rate begins to decline. This is because, as the period between stocking approaches a factor of 365 from below, the final stocking event happens too close to the end of the simulation for many of the extra fish to be caught.

The points at the troughs of these oscillations, at which points the number of fish stocked is equal, appear to show an underlying general trend for an increase in captures as the period between stocking events increases. This suggests that the parasite may struggle to survive when fish are stocked as infrequently as this, but could also be caused by the fact that these fish are stocked earlier and have more time to be caught, as in this example stocking events occur on the first day of the stocking period. The irregular shape of the oscillations in the capture rate in figure 5.2 are perhaps an early indication of interactions between the impact of the parasite and the timing of stocking events relative to seasonal aspects of the parasite life cycle.

It was decided that stocking periods which divide 365 would be used in order to avoid oscillations which could prove a confounding factor in the results. This is not unrealistic as in the field stocking is unlikely to occur exactly (for example) every 120 days, and is more likely to occur on the first Monday of every quarter. In order to represent the range of stocking periods employed by fisheries across the UK, values of ψ between 1 and 365 were chosen, to

Table 5.1: Stocking frequencies and corresponding values of ψ.

Stocking frequency	ψ
Continuous/Daily	1
Weekly	365/52
Fortnightly	365/26
Monthly	365/12
Quarterly	365/4
Biannually	365/2
Annually	365

represent stocking procedures ranging from daily to annual; these values are given in table 5.1.

As mentioned at the start of this chapter, the timing of stocking events may prove important in influencing the population dynamics of *A. foliaceus*. When fish are stocked weekly, doing so on a Thursday instead of a Monday is unlikely to make much difference; however, when fish are stocked as infrequently as once or twice per year, doing so while the parasite lies dormant in January may be more beneficial to the fishery than, for example, stocking immediately before the over-wintered parasites begin to hatch. Consequently, the impact of timing was also examined by incorporating an offset into the model (see equation 5.2) that determines the day within the stocking period on which fish are stocked. If the offset is zero and the stocking period is 365 then fish are stocked when $0 \leq t < 1$. If the offset is 12 then stocking occurs when $12 \leq t < 13$, and so on. The offset can therefore be assigned any value such that $\texttt{Offset} < \psi - 1$.

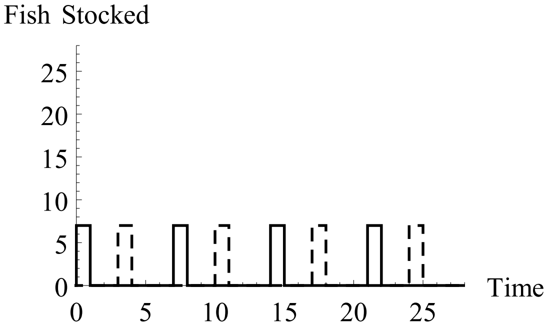


Figure 5.3: Comparison of two weekly stocking procedures, with different stocking offsets. An offset of 0, where fish are stocked on the first day of the cycle, from $t = 0$ to $t = 1$, is given by the black line, while the dashed line represents an offset of 3, meaning stocking occurs between $t = 3$ and $t = 4$.

$$s(t) = \begin{cases} \psi s, & \texttt{Offset} \leq tMod\psi < \texttt{Offset} + 1 \\ 0, & \texttt{Offset} + 1 \leq tMod\psi \\ 0, & tMod\psi < \texttt{Offset} \end{cases} . \tag{5.2}$$

Figure 5.3 illustrates weekly stocking procedures with different offsets - the number of fish stocked throughout the period is identical, but the stocking events take place at different times.

In order to counter the effects of resonance and to allow comparison of the long term effects of each stocking frequency, for each value of ψ the total number of fish caught, mean parasite burden per caught fish, and fish lost due to parasite-induced mortalities within the final year of a ten year simulation period were recorded by creating extra compartments in the model.

5.2 RESULTS

5.2.1 *Continuous/daily stocking*

The first model represents daily, or continuous stocking, and has already been seen in previous chapters. This is repeated here in order to provide a baseline to which the following stocking procedures can be compared.

Table 5.2 shows, as a percentage of the total number of fish stocked, the fish caught and lost as a result of parasite-induced mortalities when an *A. foliaceus* infection is present under this stocking regime. The mean parasite burden per caught fish is also provided in the table, and a time series plot of the final year of the simulation period is given in figure 5.4 - this is identical to the model with non-variable stocking that was presented at the end of chapter four, and shows the host-parasite dynamics that result from a consistent influx of fish.

Table 5.2: Percentage mortalities and capture of the total number of fish stocked, and mean parasite burden per caught fish over five years, with continuous stocking

Offset	Mortalities	Captures	Parasite Burden
N/A	31	65	5.73

5.2.2 *Weekly Stocking*

Next, the model was run with fish stocked on a weekly basis which, as per table 5.1, corresponds to a value of $\psi = 365/52$ in the model. In table 5.3, which summarises the best and worst stocking offsets with respect to the impact of *A. foliaceus* infection, a small decline in the mean parasite burden is apparent when the offset is 1 rather than 5, but the difference caused by stocking on a different day of the week is marginal.

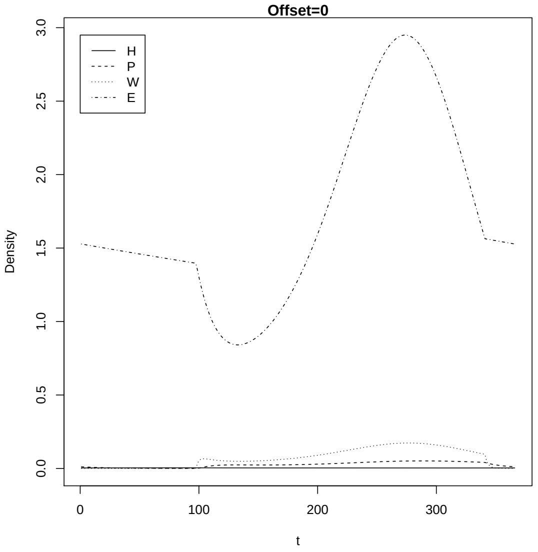


Figure 5.4: Time series plot for the final year of a ten year simulation, for the continuous stocking model. Hosts (solid), attached parasites (dotted), free-living parasites (dot-dashed) and egg (dashed) population densities are plotted against time on the horizontal axis.

Table 5.3: Percentage mortalities and capture of the total number of fish stocked, and mean parasite burden per caught fish over five years, for different offset values, with weekly stocking ($\psi = 365/52$).

Offset	Mortalities	Captures	Parasite Burden
1	30.3	65.6	5.70
5	30.4	65.6	5.71

Compared with the baseline model above, the capture rate increased by 0.6%, and parasite-induced mortalities dropped by 0.5-0.6% depending on the offset, while the mean parasite burden has dropped by 0.02-0.03 parasites per host (a change of less than 1%).

The results of the weekly stocking model are plotted in figure 5.5, which shows the proportion of fish caught, and lost to parasite-induced mortalities - natural mortalities also account for around 4% - for the full range of offset values. On this scale there is no visible difference between the day of the week on which fish were stocked, and indeed it is highly unlikely that this would cause any substantial difference in real life. Time series plots, not shown here, are almost indistinguishable from the continuously stocked model except on a very large scale where the stocking events themselves are visible. When compared with daily stocking, weekly stocking appears to be beneficial to the fishery and detrimental to the parasite in terms of all the measures used. The differences are slight, but this suggests that there is little or no benefit to be gained by stocking fish any more frequently than once per week when dealing with *A. foliaceus*.

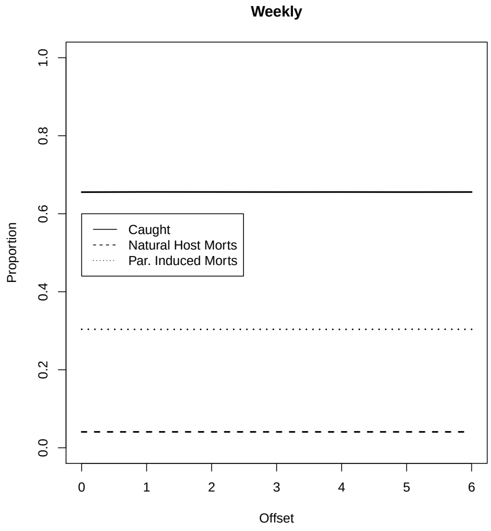


Figure 5.5: Proportion of stocked fish caught, lost to parasite-induced mortalities, and lost through natural mortalities for the full range of offset values under weekly stocking.

5.2.3 *Fortnightly stocking*

With fortnightly stocking little difference was observed by stocking on a different day within the two week period, as illustrated by figure 5.6. Table 5.4 shows a 0.2% increase in mortalities and a 0.2% decrease in fish capture when fish are stocked on day 12 rather than day 4, as well as a small rise in the mean parasite burden. Notably the effect of the parasite on all three metrics has decreased relative to weekly stocking, for all of the offset values. The differences from the baseline of up to 1% in the capture rate, 1% in the mortality rate and 0.14 in the mean parasite burden (2.4%) are, as with weekly stocking, marginal, and this again suggests that there is little to be gained by stocking fish more frequently than once per fortnight.

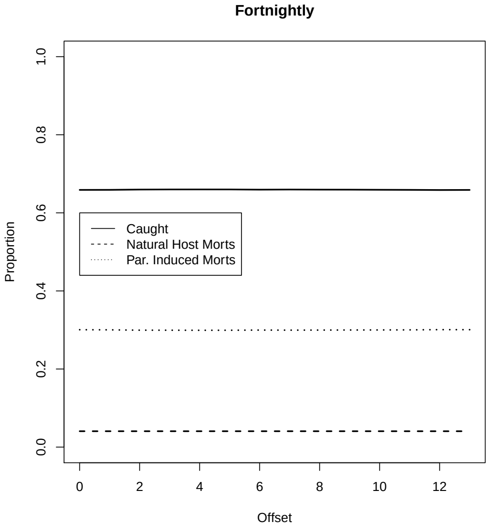


Figure 5.6: Proportion of stocked fish caught, lost to parasite-induced mortalities, and lost through natural mortalities for the full range of offset values under fortnightly stocking.

Table 5.4: Percentage mortalities and capture of the total number of fish stocked, and mean parasite burden per caught fish over five years, for different offset values, with fortnightly stocking ($\psi = 365/26$).

Offset	Mortalities	Captures	Parasite Burden
4	29.9	66.0	5.59
12	30.1	65.8	5.64

5.2.4 *Monthly stocking*

A further increase in ψ to 365/12, representing monthly stocking, now means that around thirty times more fish are being stocked on each occasion, relative to the baseline model with daily stocking. A very small increase can be seen in the capture rate towards the right hand side of figure 5.7, which coincides with a small dip in parasite-induced mortalities. Again the overall mortality rate is lower, and the capture rate higher, than for the more frequent stocking regimes described previously, but the differences are still marginal with only a 2-3% increase in fish capture, and a corresponding drop in parasite-induced mortalities compared with the baseline model. Time series plots (figure 5.8) now show visible, though slight, increases in the host population during the stocking period, after which the free-living parasite population declines slightly due to increased rates of attachment, causing the attached parasite population to grow. The egg population begins to grow at a rate which slows prior to the next stocking event, as host numbers drop between stocking events. Notably the worst stocking offset is 8, which means fish are being stocked at $t = 99.25$ (9th of April), while the parasite begins hatching at $t = 98$ (8th of April) when the temperature reaches 8°C. This is a fairly intuitive result, as stocking at this time provides freshly-hatched parasites with hosts to which they can attach.

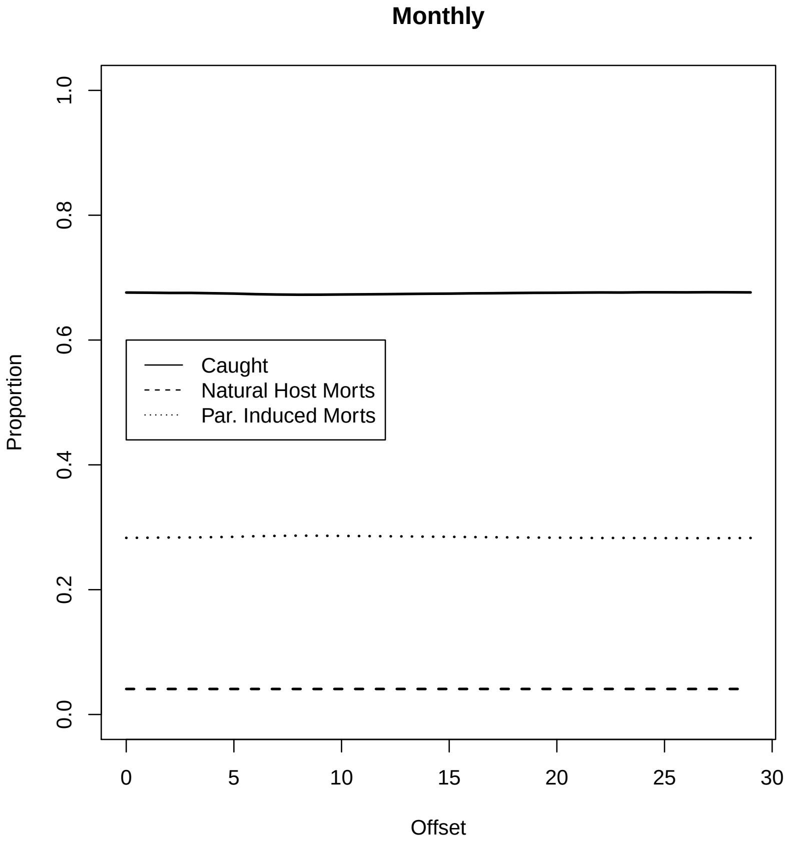


Figure 5.7: Proportion of stocked fish caught, lost to parasite-induced mortalities, and lost through natural mortalities for the full range of offset values under monthly stocking.

Table 5.5: Percentage mortalities and capture of the total number of fish stocked, and mean parasite burden per caught fish over five years, for different offset values, with monthly stocking ($\psi = 365/12$).

Offset	Mortalities	Captures	Parasite Burden
8	28.7	67.3	5.25
27	28.2	67.7	5.23

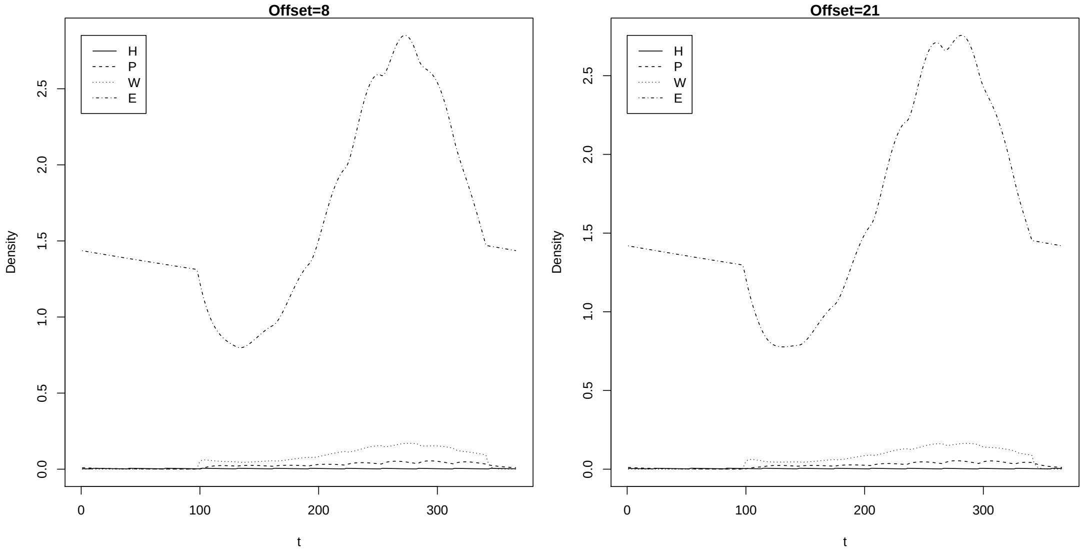


Figure 5.8: Time series of the monthly stocking model. Hosts (solid), attached parasites (dotted), free-living parasites (dot-dashed) and egg (dashed) population densities are shown.

5.2.5 *Quarterly stocking*

The pattern of reduced parasite numbers continues as ψ increases and fish are stocked only four times per year. The worst offset is now 8, which corresponds to fish being stocked on the ninth day of each quarter; however this still leads to better capture rates and lower parasite burdens than the more frequent stocking patterns. The optimal offset is when fish are stocked on the 67th day of each quarter, and examination of time series plots in figure 5.10 shows that this is the case as parasites are hatching at roughly $t = 98$ (8th of April), which means that the fish density is fairly low when free-living parasites begin to emerge in need of a host, and many parasites have died due to low attachment rates by the time the next stocking event occurs. Figure 5.9 and table 5.6 show that parasite-induced mortalites have dropped from 30% in the baseline model to between 23.5 and 14.6% depending on the timing of these less-frequent stocking events.

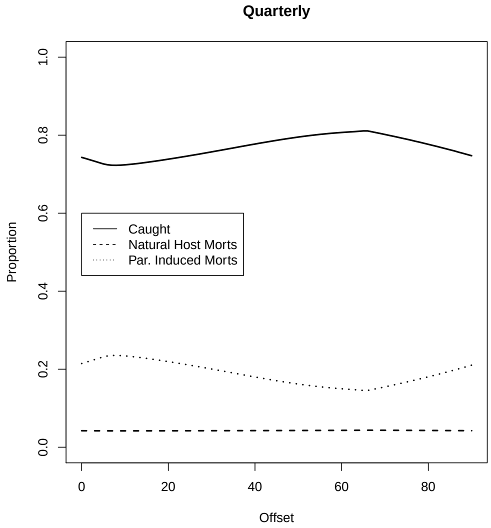


Figure 5.9: Proportion of stocked fish caught, lost to parasite-induced mortalities, and lost through natural mortalities for the full range of offset values under quarterly stocking

Table 5.6: Percentage mortalities and capture of the total number of fish stocked, and mean parasite burden per caught fish over five years, for different offset values, with quarterly stocking ($\psi = 365/4$).

Offset	Mortalities	Captures	Parasite Burden
8	23.5	72.3	4.18
66	14.6	81.1	2.49

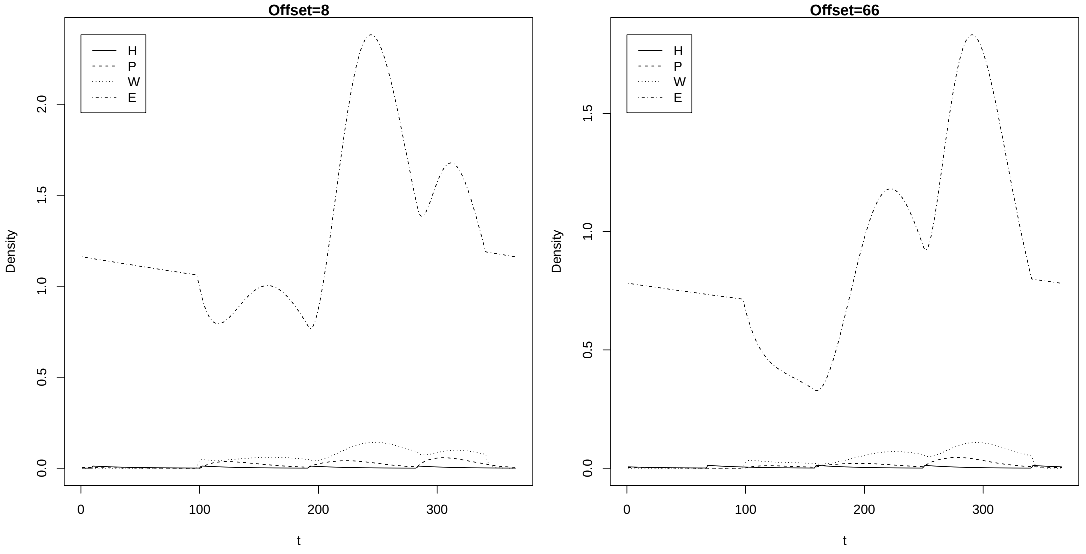


Figure 5.10: Time series of the quarterly stocking model. Hosts (solid), attached parasites (dotted), free-living parasites (dot-dashed) and egg (dashed) population densities are shown.

5.2.6 *Biannual stocking*

With biannual stocking ($\psi = 365/2$) parasite-induced mortalities range from between 0.8 and 12%, both of which are again lower than all previous values seen for lower stocking frequencies. Figure 5.11 and table 5.7 show that the optimal stocking time for the fishery is on the 157th day of each six-month period (i.e. the 5th of June and 5th of November). This corresponds to the latter stocking event occurring at the beginning of the parasite's overwintering period, meaning half of the annual supply of fish will mostly have been caught by the time the parasite begins to hatch and look for a host the following year. Similarly to the monthly and quarterly models, the time series plots in 5.12 show that stocking as the parasite eggs begin to hatch (shown by the dip in the egg population density) is beneficial to the parasite. This also means that the second stocking event occurs in October while the temperature is still high enough for the parasite to be able to reproduce.

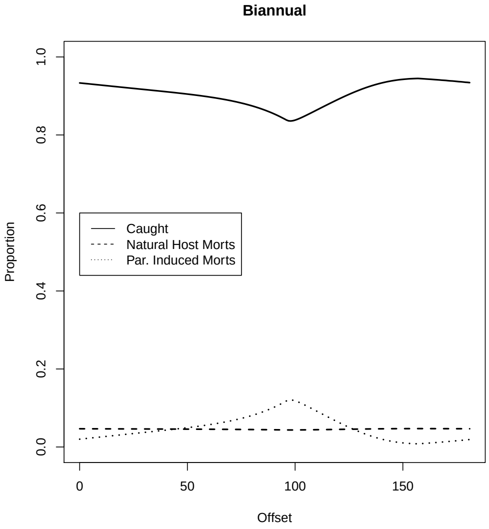


Figure 5.11: Proportion of stocked fish caught, lost to parasite-induced mortalities, and lost through natural mortalities for the full range of offset values under biannual stocking.

Table 5.7: Percentage mortalities and capture of the total number of fish stocked, and mean parasite burden per caught fish over five years, for different offset values, with biannual stocking ($\psi = 365/2$).

Offset	Mortalities	Captures	Parasite Burden
98	12.1	83.6	2.36
157	0.8	94.5	0.16

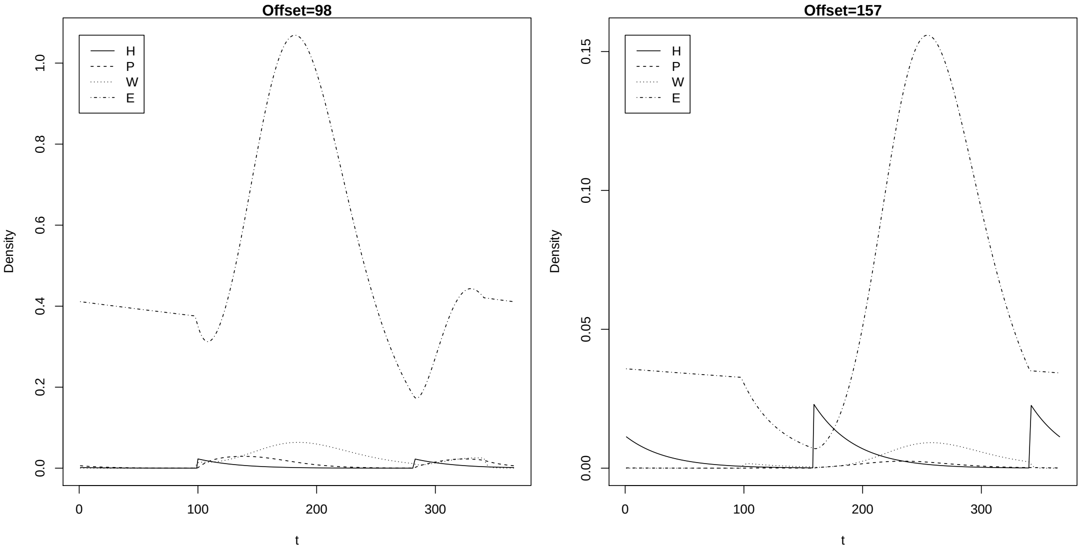


Figure 5.12: Time series of the biannual stocking model. Hosts (solid), attached parasites (dotted), free-living parasites (dot-dashed) and egg (dashed) population densities are shown.

5.2.7 *Annual stocking*

Finally, under annual stocking ($\psi = 365$) the parasite is completely unable to survive if fish are stocked in the first 37 days of the year ($offset \leq 36$) or after day 293 ($offset \geq 292$); i.e. between mid-October and early February. This can be seen in figure 5.13, which shows captures and natural host mortalities accounting for 100% of fish, with around 5% dying naturally, and the remaining 95% being caught. Time series of the best and worst stocking offsets under annual stocking are shown in figure 5.14. The peak in parasite numbers occurs when fish are stocked on day 173 (25th of June) - not immediately prior to eggs hatching as in the other examples, but when high numbers of susceptible fish are available at the time when the parasite is able to reproduce quickly due to high temperatures.

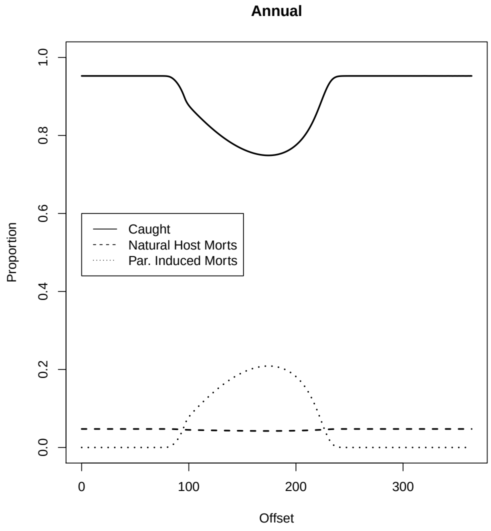


Figure 5.13: Proportion of stocked fish caught, lost to parasite-induced mortalities, and lost through natural mortalities for the full range of offset values under annual stocking.

At this stage the previous strategy of stocking after most free-living parasites have died is no longer an optimal solution for the fishery. As only one stocking event has to be scheduled, the option of stocking outside of the parasite's active period is available, whereas when there were two events, as was the case with biannual stocking, stocking at the very start of the year would also have meant stocking at the start of July when the parasite is reproducing rapidly. It is worth noting that the parasite is active between early April and mid-December (according

Table 5.8: Percentage mortalities and capture of the total number of fish stocked, and mean parasite burden per caught fish over five years, for different offset values, with annual stocking ($\psi = 365$).

Offset	Mortalities	Captures	Parasite Burden
< 37 or > 293	0	95.3	0
173	20.9	74.9	2.52

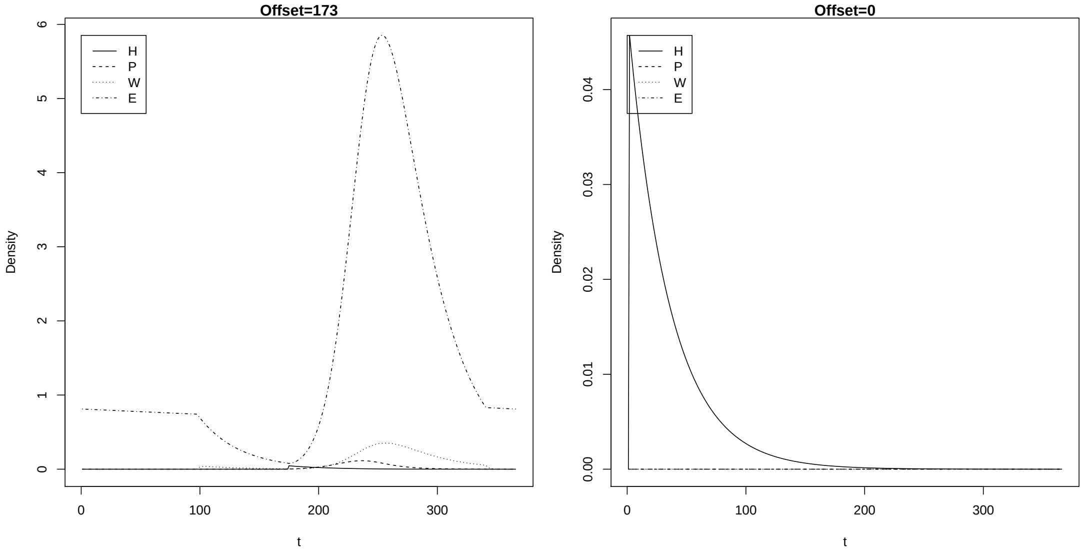


Figure 5.14: Time series of the annual stocking model. Hosts (solid), attached parasites (dotted), free-living parasites (dot-dashed) and egg (dashed) population densities are shown.

to the temperature function detailed in chapter four), and thus simply stocking outside of this period is not sufficient to eradicate the parasite, as stocking from mid-February still results in a sufficient host density later in the year to maintain the parasite population. What is also noticeable here is that unlike previous examples, the move from biannual to annual stocking does not necessarily result in a reduction in the impact of the parasite. This is because annual stocking allows for 100% of fish to be stocked at the optimal time for the parasite, while with biannual stocking adding 50% of fish at this point would mean that the other 50% would have to be stocked at the end of the season.

5.2.8 *Conclusions*

The models described in this section have confirmed that the timing of stocking events may be important in managing *A. foliaceus* infections. This is not entirely surprising as in chapter two it was demonstrated that a sufficiently high density of hosts must be present in order to sustain an infection. Therefore it is intuitively obvious that stocking in such a manner that fewer hosts are available for *A. foliaceus* attachment at the time of year when parasites are seeking hosts will inhibit its ability to survive. Table 5.9 provides a summary of the best and worst offsets for each stocking period, ψ, and demonstrates the apparent trend of fish capture rates and mortalities improving as fish are stocked less frequently. Figure 5.15 shows plots of the best and worst offsets in terms of parasite-induced mortalities, fish capture rates and parasite burden, and demonstrates that as stocking events become less frequent, their timing becomes more and more important in managing an *A. foliaceus* infection. For example there is no visible difference between the best and worst offset with weekly stocking (shown by $\psi = 365/52$ on the horizontal axes), but for quarterly stocking mortalities are reduced by around 40% when fish are stocked on the 66th day of each quarter rather than the 8th. As seen with monthly stocking an offset of 8 corresponds to early April, when parasite eggs are beginning to hatch, so it is unsurprising that stocking at this time appears to be detrimental to the fishery.

Time series plots such as figure 5.14 show that as the fish capture rate is proportional to the density of fish, the capture rate is extremely high immediately after stocking. This results in around 75% of fish being caught within around 50 days of the stocking event. While the results in this section have shown that *A. foliaceus* benefits from a consistent influx of fish - i.e. frequent stocking, this is also true of anglers, and attempts to manipulate the fish density in this manner may consequently prove detrimental to the fishery if there are few fish to be caught throughout most of the year.

Nevertheless, there do exist fisheries that stock infrequently; though such businesses are unlikely to survive if most of their fish are caught so soon after stocking with extremely low capture rates throughout the rest of the year. In the next section the capture rate is capped to see what impact batch stocking may have when the capture rate is constrained and fish remain in the water for longer periods of time before being caught. This management practice is common in the UK, where fishery owners often permit anglers to capture (up to) a fixed number of fish per visit for a certain admission fee. The reason for this is simply that the owners want to see a good return from their stock, but where this rod limit is fairly constrictive - for example if most anglers would be able to catch five fish, but are only allowed to take four, it will increase the residence time of the fish and could therefore influence *A. foliaceus* dynamics.

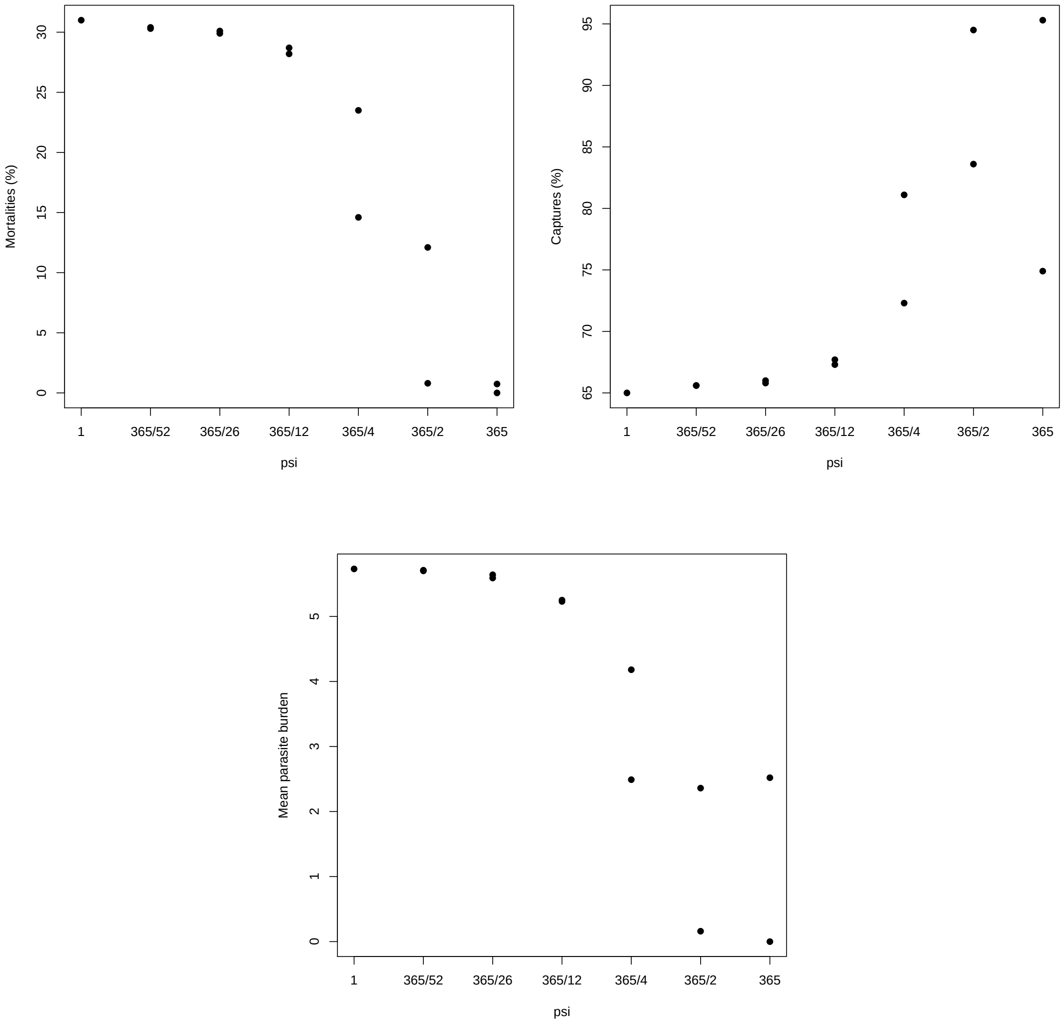


Figure 5.15: Summary of the stocking frequency results. Best and worst offsets for each value of ψ are shown - plot points are summarised in table 5.9

Table 5.9: Stocking frequency and stocking offset results with unconstrained capture (no rod limit). The best and worst offsets in terms of fish capture, mortality and parasite burden are shown for each offset.

Stocking Frequency	ψ	Offset	Mortality (%)	Capture (%)	Mean parasite burden
Continuous	1	0	31	65	5.73
Weekly	7.02	1	30.3	65.6	5.7
	7.02	5	30.4	65.6	5.71
Fortnightly	14.04	4	29.9	66	5.59
	14.04	12	30.1	65.8	5.64
Monthly	30.42	8	28.7	67.3	5.25
	30.42	27	28.2	67.7	5.23
Quarterly	91.25	8	23.5	72.3	4.18
	91.25	66	14.6	81.1	2.49
Biannually	182.50	98	12.1	83.6	2.36
	182.50	157	0.8	94.5	0.16
Annually	365	0	0	95.3	0
	365	173	20.9	74.9	2.52

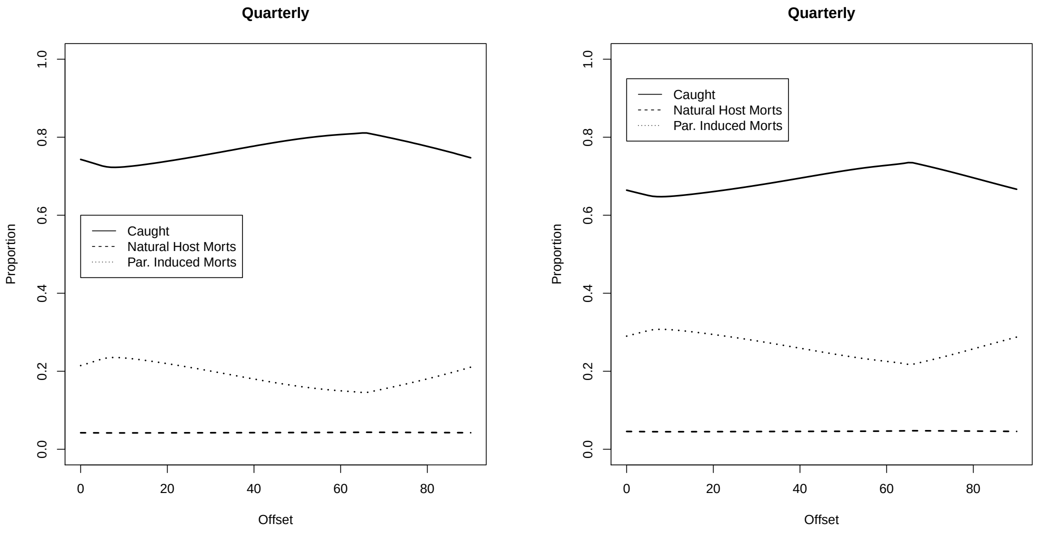
Since capture rates were high immediately after stocking, a limit on the number of fish that can be caught per day was imposed. At site three (used for parameterisation in chapter four), footfall data was obtained, and there was an average 0.00005 anglers per m^3 per day. Taking a high estimate of a bag limit of 4 fish per angler, this gives a theoretical maximum of $cH = 0.0002$ per m^3 fish caught per day. The model was adapted so that the capture rate (including the parasite-induced reduction in capture) was capped at 0.0002 fish per day per cubic metre, in order to determine the impact of this practice on the host-parasite dynamics.

Summary plots showing fish captures and mortalities versus the stocking offset for the weekly, fortnightly and monthly stocking models are very similar to those seen in the previous section with no rod limit, and so are not presented here. This is because the capture rate only becomes high enough for the rod limit to have an effect when fish are stocked four or fewer times per year, due to the high number of fish present following the stocking of a large batch of fish.

5.3.1 *Quarterly stocking*

A comparison of quarterly stocking with and without the rod limit is shown in figure 5.16. The left hand plot, figure 5.16a, is identical to the one presented in the previous section without a rod limit, but is reproduced here for comparison. While the shape of the plots are similar, and indicate that the rod limit does not affect the optimal stocking time in this case, unsurprisingly the capture rate is consistently lower with the rod limit, by around 7%. Parasite-induced mortalities are also around 7% higher, suggesting that parasites have more time to attach to hosts, and that the parasite-induced mortality rate is now higher relative to the capture rate than in the model without a rod limit.

Figure 5.17 shows comparisons of time series plots for the best and worst stocking offsets in the quarterly models with (5.19b) and without (5.19b) a rod limit. As already seen in figure

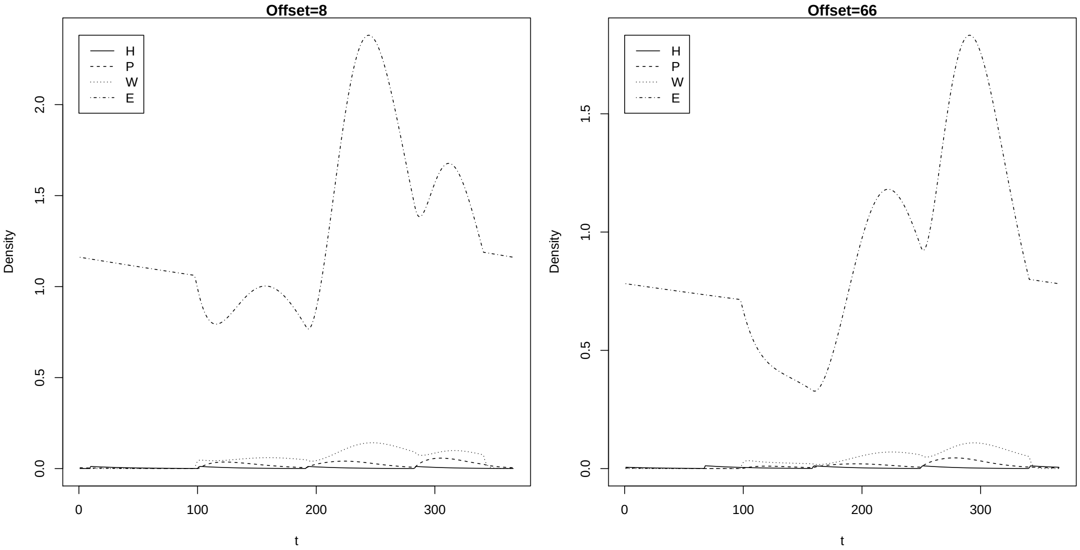


(a) Without rod limit

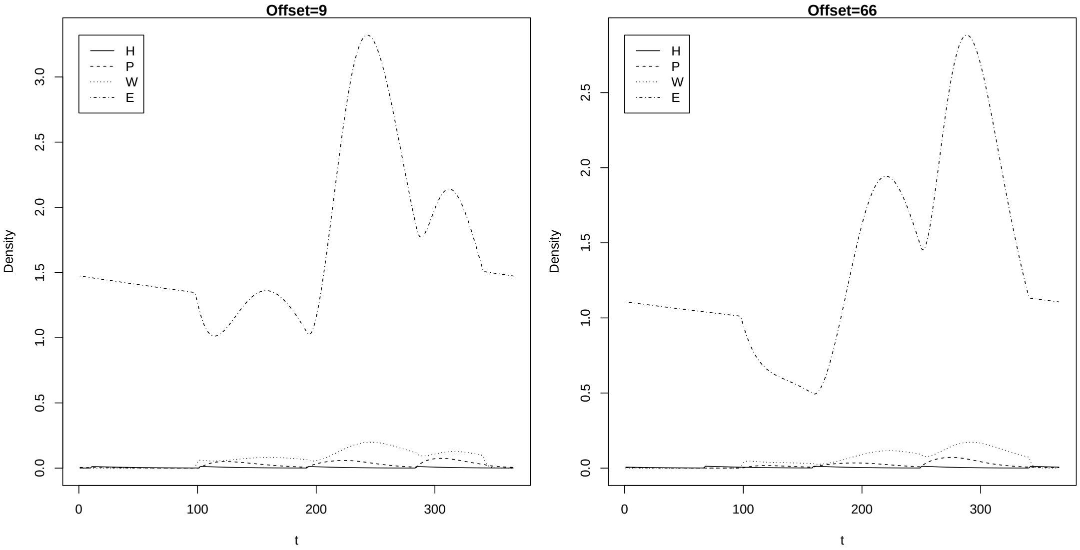
(b) With rod limit

Figure 5.16: Proportion of stocked fish caught, lost to parasite-induced mortalities, and lost through natural mortalities for the full range of offset values under quarterly stocking with and without a rod limit imposed.

5.16a, the effect of the timing of stocking events is very similar for both models, with the parasite benefiting from a stocking event in April, and two further batches being stocked before the beginning of its overwintering period. Parasite numbers are consistently higher with a rod limit due to increased host availability throughout the year.



(a) Without rod limit

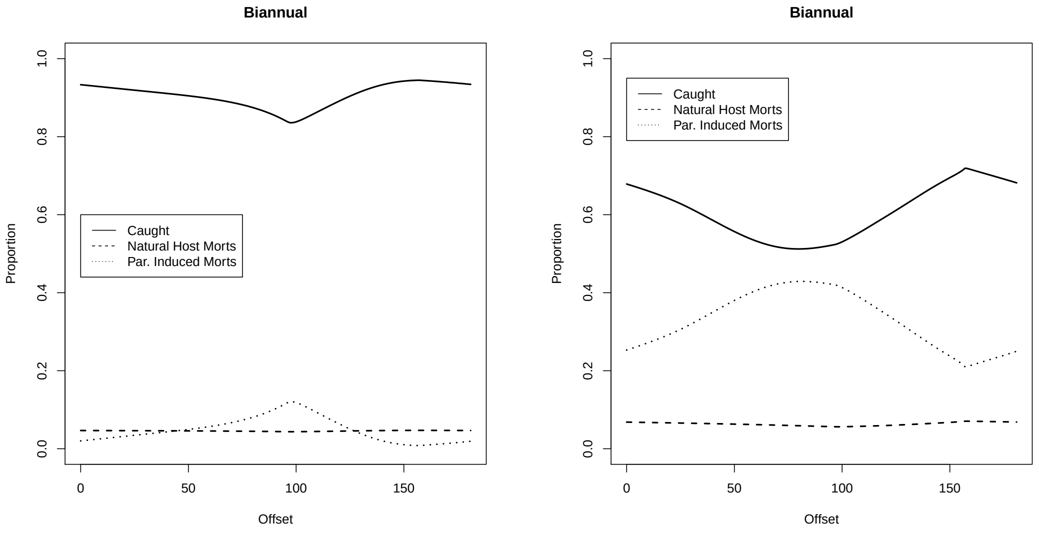


(b) With rod limit

Figure 5.17: Time series of the quarterly stocking models without (top) and with (bottom) a rod limit. Hosts (solid), attached parasites (dotted), free-living parasites (dot-dashed) and egg (dashed) population densities are shown.

5.3.2 *Biannual stocking*

Figure 5.18 shows comparisons of the biannual stocking model with a rod limit with the model without a rod limit. In a similar manner to the quarterly stocking model, imposing a rod limit has reduced the capture rate for all stocking offsets, as well as increasing the level of parasite-induced mortalities in the model. Now, however, the timing of the worst stocking time has also changed, as seen by comparing the shape of the lines in figures 5.18a and 5.18b - the worst time to stock is now day 89 rather than day 98 (late March rather than early April).

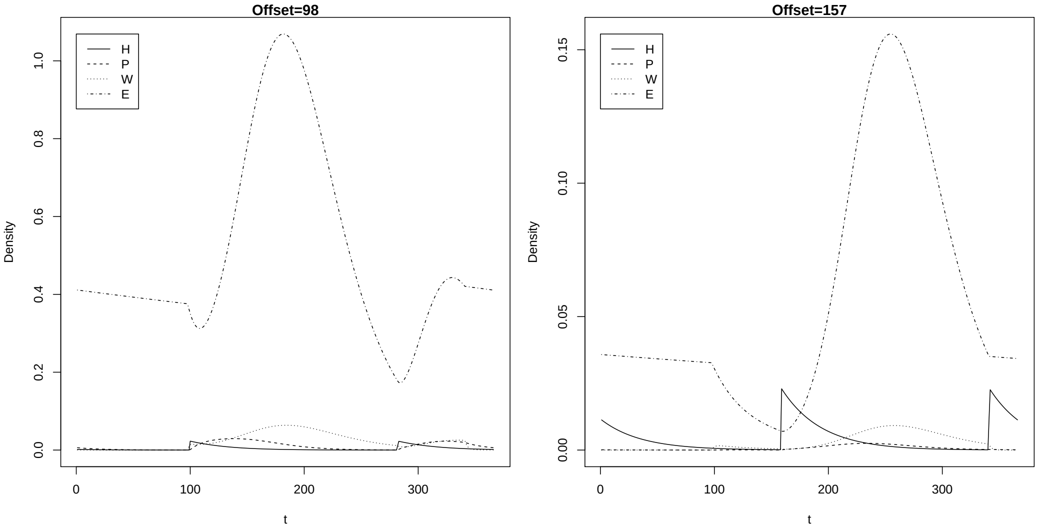


(a) Without rod limit

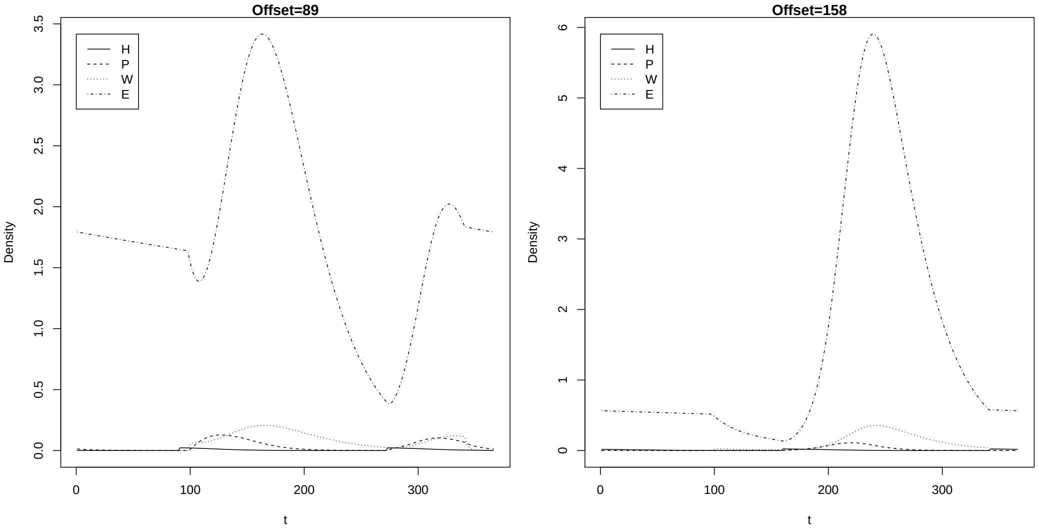
(b) With rod limit

Figure 5.18: Proportion of stocked fish caught, lost to parasite-induced mortalities, and lost through natural mortalities for the full range of offset values under biannual stocking with and without a rod limit imposed.

From the time series plots shown in figures 5.19, it is clear that this is because more of the fish stocked 9 days prior to the parasite beginning to hatch are present in the water when the rod limit is included in the model. This means the second stocking event takes place earlier in the year, at a time when the temperature is slightly higher and the parasite is able to reproduce more quickly. Notably with the rod limit the peak in parasite egg numbers is higher when the offset is 158, but this plot represents the best time to stock, as the second stocking event occurs outside the period where *A. foliaceus* is able to reproduce.



(a) Without rod limit



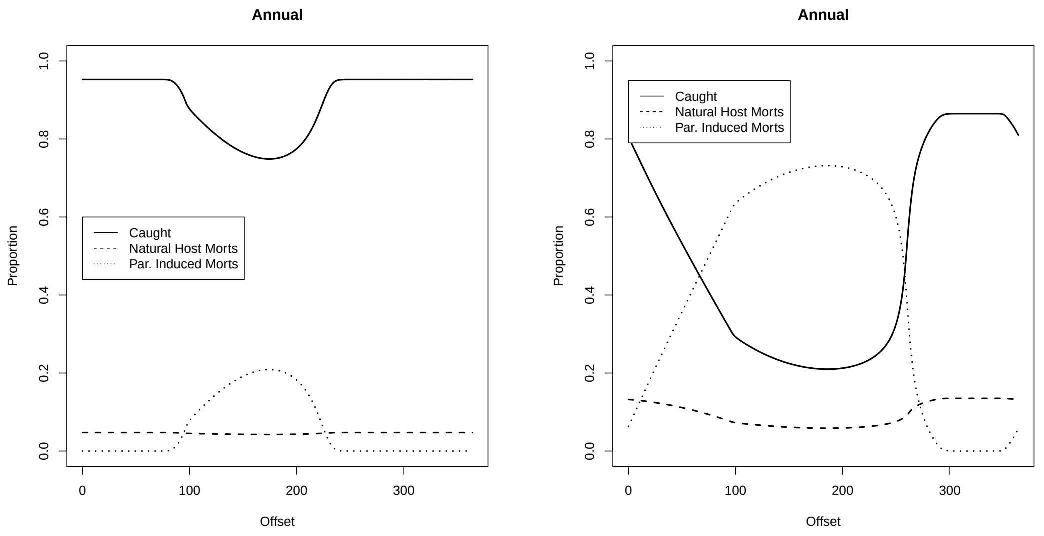
(b) With rod limit

Figure 5.19: Time series of the biannual stocking models without (top) and with (bottom) a rod limit. Hosts (solid), attached parasites (dotted), free-living parasites (dot-dashed) and egg (dashed) population densities are shown.

5.3.3 *Annual stocking*

Figure 5.20 compares the annual stocking model without a rod limit and the annual model with a rod limit. The difference between the two models is dramatic, with the "safe" winter stocking period considerably shortened when the rod limit is included in the model. While previously stocking any time between mid-October and early February resulted in the eradication of the parasite, now there is only a small window of opportunity between early November and early December during which fish can be stocked without providing a sufficient host density for the parasite the following year. As well as this change in the effect of the timing of stocking events, the model with a rod limit generally results in much worse results for the fishery; previously parasite-induced mortalities reached a maximum of 20.9% when fish were stocked at the start of June, whereas with the rod limit parasite-induced mortality wipes out 72.8% of stocked fish stocking occurs in mid-July. The mean parasite burden is also the highest of any of the models seen in this chapter, at 8.85 parasites per host. It is also evident from these plots that even when fish are stocked at such a time that the parasite cannot survive, the capture rate is lower as a result of the rod limit. This is unsurprising, as the capture rate is lower relative to natural host mortality rate, and this results in more fish dying before anglers are able, or permitted, to catch them.

Figure 5.21 shows time series of the worst and best times to stock fish without (5.21a) and with (5.21b) a rod limit. In the model with a rod limit the pattern of growth and decline over the year across the three parasite population compartments is similar, though these peak slightly later in the year when the rod limit is included due to the later timing of the stocking event. It is perhaps counter-intuitive that the parasite fares better with this later timing of stocking, as we might expect that, with fish being caught more slowly, earlier stocking would leave more fish present when the parasite the temperature is highest at the beginning of August (day 219), and it is able to lay eggs more quickly. In the model without a rod limit, however, the parasite suffers more due to a lack of hosts between stocking events, and earlier availability of hosts and a slightly higher host density through the summer months is

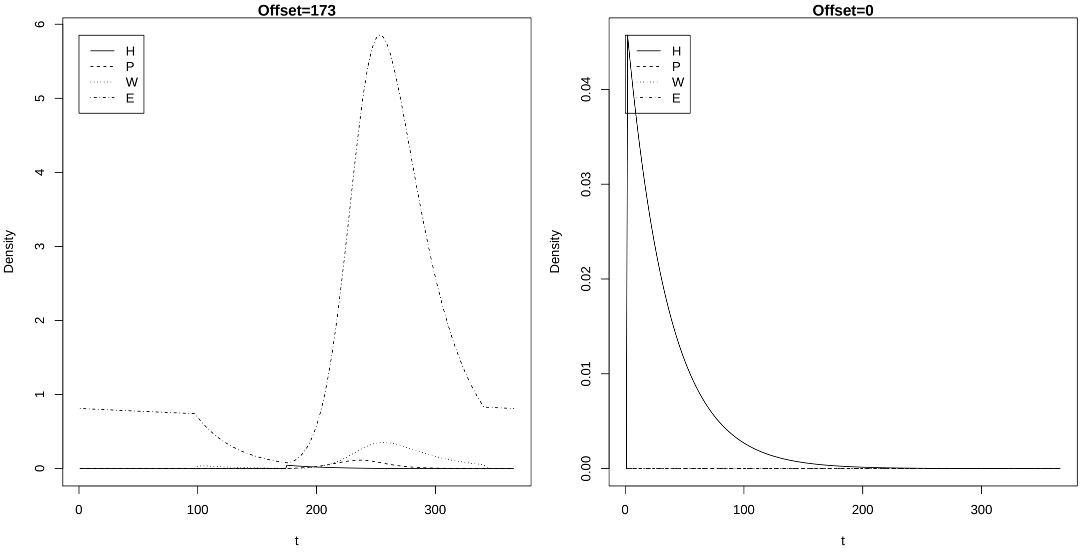


(a) Without rod limit

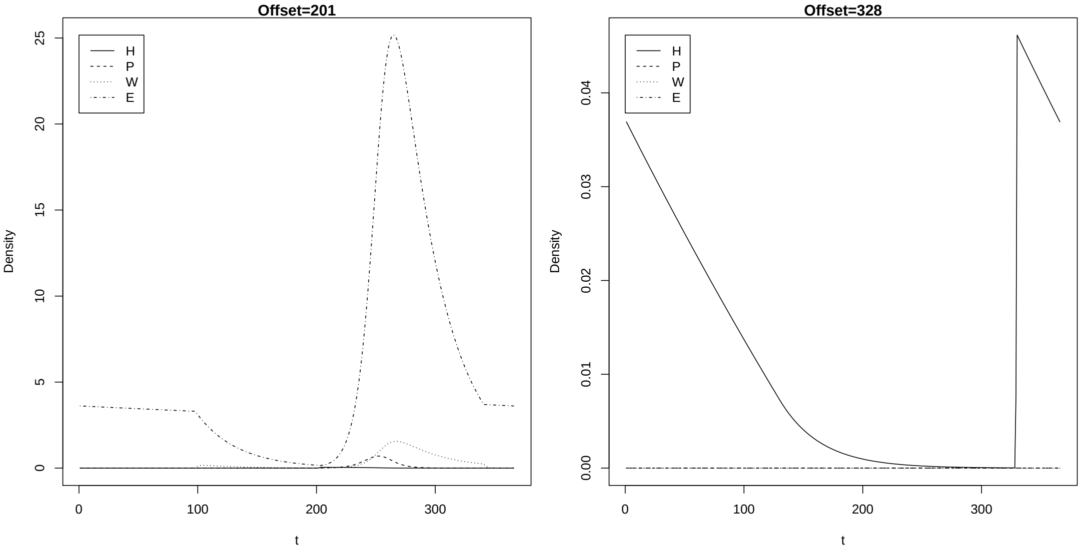
(b) With rod limit

Figure 5.20: Proportion of stocked fish caught, lost to parasite-induced mortalities, and lost through natural mortalities for the full range of offset values under annual stocking with and without a rod limit imposed.

preferable to stocking later in the year when a higher proportion of fish stocked will survive into the winter months, during which time the parasite will not be able to attach to hosts.



(a) Without rod limit



(b) With rod limit

Figure 5.21: Time series of the annual stocking models without (top) and with (bottom) a rod limit. Hosts (solid), attached parasites (dotted), free-living parasites (dot-dashed) and egg (dashed) population densities are shown.

5.3.4 *Summary - rod limit*

Table 5.10 provides a summary of all the models with a rod limit, with higher rates of mortality and lower rates of capture for all stocking less frequent than once per quarter, when compared with the model with no rod limit, as the constraints on the capture rate only take effect when fish are stocked in large batches. Figure 5.22 shows plots of the models with a rod limit against the previous models without a rod limit. Similarly, the models are indistinguishable for stocking events occurring more frequently than once per quarter, but for longer stocking intervals, and larger batches, the model becomes both more variable for different offsets, and generally the fishery fares worse under these circumstances, with a higher parasite burden, more fish mortalities and, unsurprisingly, lower rates of capture when compared with the model with no rod limit.

The comparisons of quarterly, biannual and annual stocking frequencies shown in figures 5.16, 5.18 and 5.20 have shown that as fish are stocked in larger batches, the timing of stocking events becomes increasingly important. With quarterly stocking the percentage of fish caught varies between around 65 and 74%, while with annual stocking the capture rate can drop as low as 21% when fish are stocked towards the end of July, but as high as 86.5% when fish are stocked towards the end of the year.

Stocking in the colder months can still result in the eradication of the parasite when a rod limit is in place, as the host density is still very low for most of the year, but while stocking any time between day 292 and 36 (e.g. from mid-October to early February) would have eradicated the parasite previously, with the capture rate constrained in this manner this can only be achieved by stocking during a month-long period at the start of the over-wintering period (from early November to early December), as stocking later that this would provide enough fish to sustain parasites hatching in April the following year.

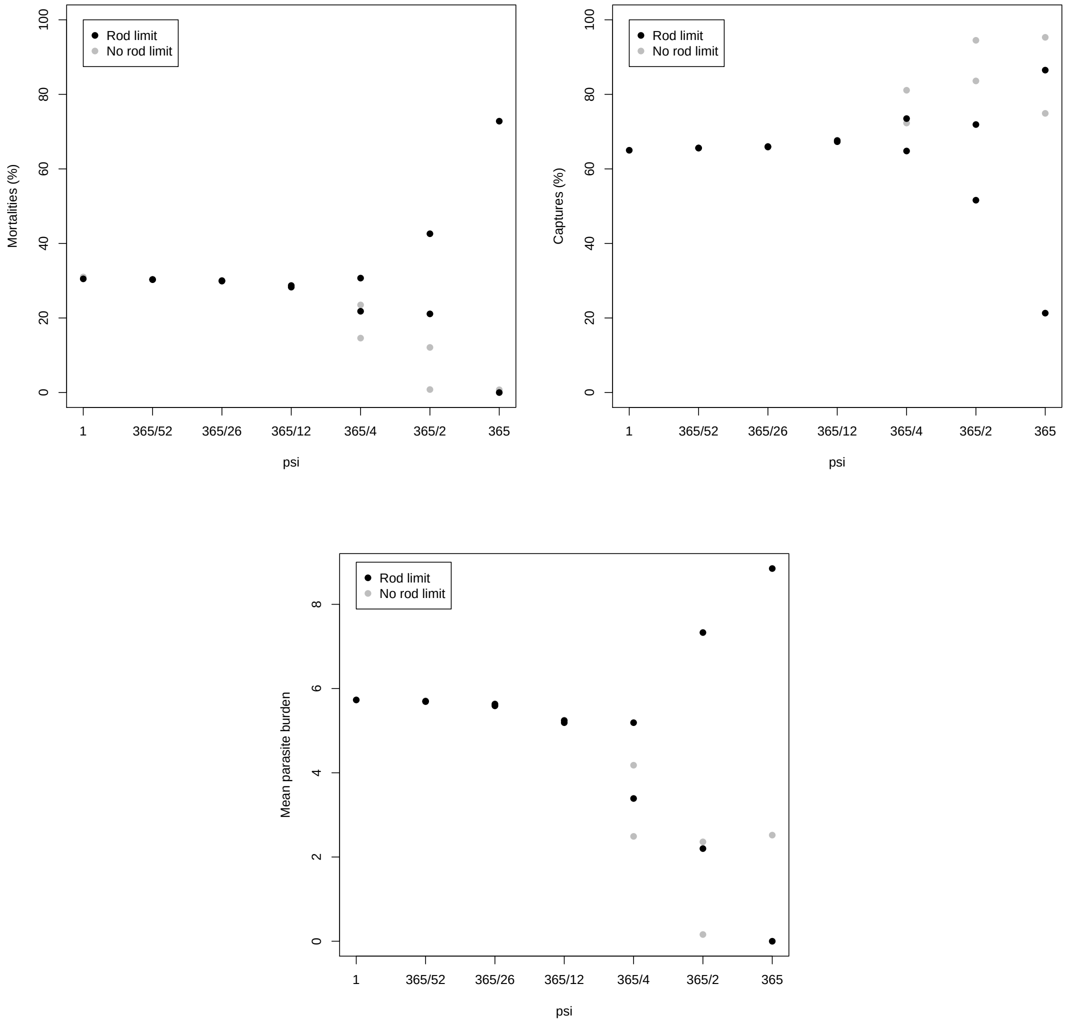


Figure 5.22: Summary of the stocking frequency results. Best and worst offsets for each value of ψ are shown - plot points are summarised in table 5.10.

Table 5.10: Stocking frequency and stocking offset results with constrained capture (a rod limit). The best and worst offsets in terms of fish capture, mortality and parasite burden are shown for each offset.

Stocking Frequency	ψ	Offset	Mortality (%)	Capture (%)	Mean parasite burden
Continuous	1	0	30.5	65	5.73
Weekly	7.02	3	30.3	65.6	5.69
	7.02	6	30.3	65.6	5.7
Fortnightly	14.04	3	29.9	66	5.59
	14.04	13	30.0	65.9	5.63
Monthly	30.42	4	28.3	67.6	5.19
	30.42	8	28.7	67.3	5.24
Quarterly	91.25	9	30.7	64.8	5.19
	91.25	66	21.8	73.5	3.39
Biannually	182.50	89	42.6	51.6	7.33
	182.50	158	21.1	71.9	2.20
Annually	365	201	72.8	21.3	8.85
	365	328	0.0	86.5	0.00

In the models presented in this chapter, capture rates are dependent on fish density, parasite burden, and of course the capture limit imposed above. Figure 5.23 shows the rates of fish capture per m^3 per day for the best stocking offsets, which take all of these factors into account. The left hand plots show the model with unconstrained capture, and the right hand plots show the equivalent models with capture limited to 0.0002 fish per m^3 per day.

Comparing the left hand plots to the right hand plots we can see that the limit is having the desired effect and no more than the fixed allowance of fish are being removed from the system when the rod limit is in place. As fish are now remaining in the water for longer post-stocking, the capture rate is less variable, and remains consistent for some time after fish have been added to the water, rather than the sharp drop seen previously.

With quarterly stocking (the top of the three plots) we can see the impact of the parasite on capture. The rod limit only takes effect when, left alone, capture would exceed the threshold. The capture rate declines after a sustained period due to declining fish numbers, but also due to the parasite-induced rate of capture. The upper plots show that capture rates fall faster after stocking in late summer when the parasite burden is at its highest. Likewise the period of high capture is shorter for the summer stocking event when compared with winter in the biannual plot shown in figure 5.23.

As the stocking frequency declines, the impact of the rod limit increases; with annual stocking the capture rate dropped below 0.0002 by day 75, but with the limit in place it remains above this level for around 5 months.

These plots illustrate the potential benefits of capture limitation for fishery managers as retaining stock for customers throughout the year is likely to be beneficial for business. As previous sections have shown, however, this strategy also benefits *Argulus* spp. and should be used with caution when the parasite is present.

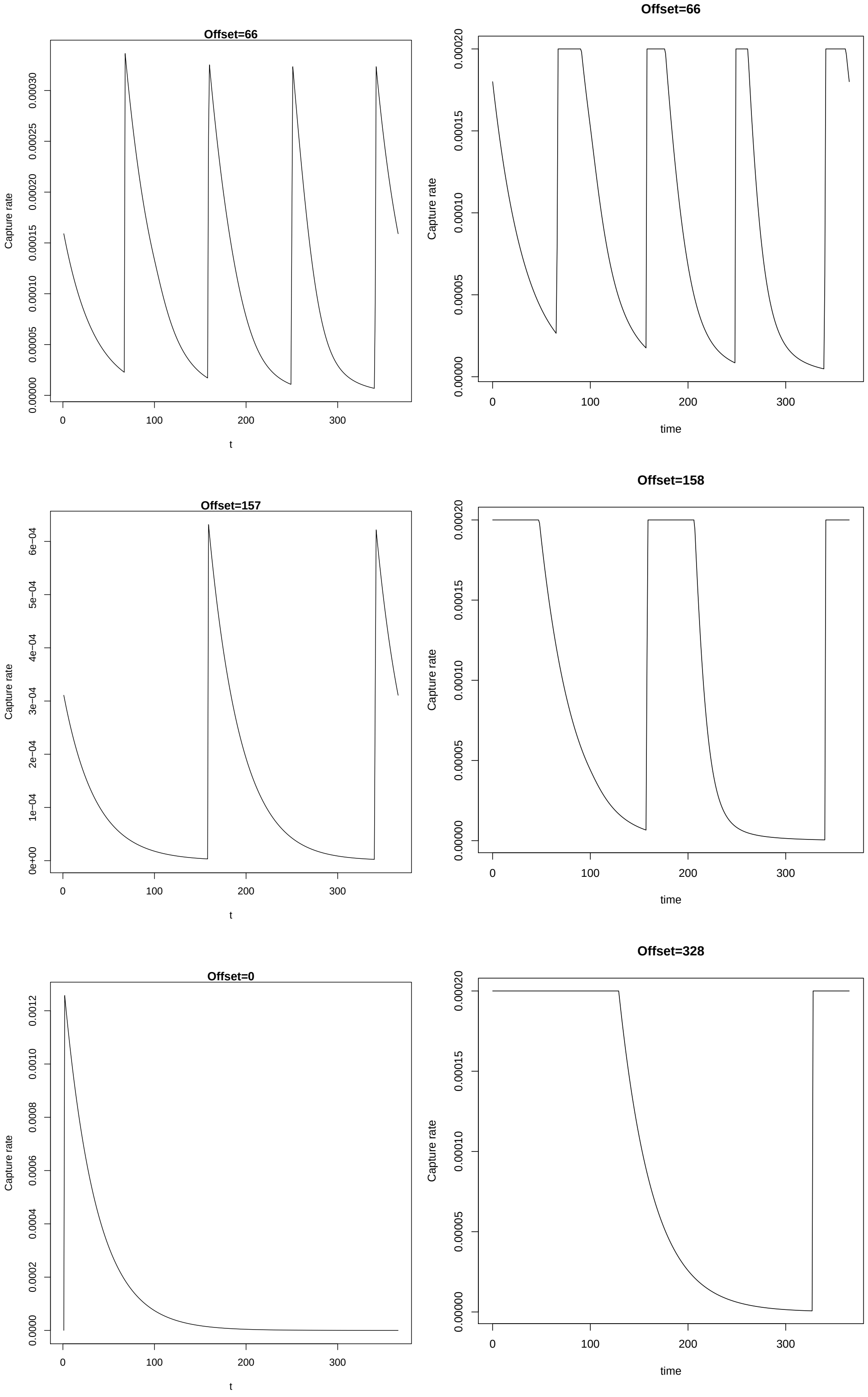


Figure 5.23: Capture rates (fish caught per m^3 per day) with unconstrained (left) and constrained (right) capture rates, with the best offsets in terms of parasite burden. Quarterly (top), Biannual (centre) and Annual (bottom) stocking frequencies are shown.

5.5 CONCLUSIONS

In this chapter the influence of the timing and frequency of fish stocking events on an *A. foliaceus* infection have been investigated. In the absence of a rod limit, as fish are stocked less frequently, and in increasingly large batches, the timing of stocking events becomes increasingly important in determining the impact of the parasite. For example the mean parasite burden, shown in the lower plot of figure 5.15, is cut by around a third when fish are stocked on the 66th day of each quarter, rather than the 8th. When stocking occurs only annually, however, the host density is below the minimum level necessary for parasite survival for such long periods that the parasite is unable to survive in the long term for certain offsets.

When the rod limit is imposed, figure 5.22 makes it clear that the rod limit makes little difference when fish are stocked frequently, as the host density is relatively consistent and remains below the level at which the limit would take effect. Similar results are seen in the respect that the importance of timing of stocking events increases as their frequency decreases. With the capture rate constrained, only stocking within a few weeks of the start of the parasite's overwintering period results in the eradication of the parasite. If the sole stocking event occurs at the peak of the parasite's egg-laying period, then more than 70% of all fish stocked may be lost due to parasite-induced mortalities, with less than 30% being caught by anglers, as during the summer months the capture rate is constrained and is outstripped the parasite-induced mortality rate. The simple interpretation of this is that fish are remaining in the water for longer, and therefore spend more time exposed to the parasite. It should be noted that while stocking occurs at evenly-spaced intervals in the models here, this need not be the case in a fishery, and therefore two stocking events over the winter period would be the equivalent of biannual stocking, and could be more viable for fisheries. Further optimisation of unevenly spaced stocking events throughout the year may be useful for individual fisheries, but is not addressed here as the benefits would be likely to change significantly depending on the times of year at which the fishery in question is busiest.

There is little difference in the peak parasite burden each year for stocking intervals of less than 56 days. Stocking regularly in small amounts is common advice for reducing *Argulus* spp. abundance in fisheries. These results show that stocking in bulk may not necessarily be detrimental if stocking is timed correctly, depending on the residence time of the fish - in other words, how long fish tend to be in the fishery before being caught.

Work in this chapter also highlights the importance of the timing of stocking events when dealing with an *A. foliaceus* infection - particularly when fish are stocked in large batches. Trickle stocking is often impractical for many fisheries due to delivery and labour costs, but is commonly seen as the ideal. While there are obvious benefits to stocking in bulk, it should be noted that the fish density is much more variable throughout the year when stocking occurs in this manner, which may cause different economic problems for the fishery.

It should be noted that these simulations provide an example of how stocking frequencies and rod limits can impact an *A. foliaceus* infection, but that stocking rates, rod limits and angler numbers will vary between sites in such a manner that it is not possible to say, in general, that annual stocking of large numbers of fish is advisable. The general findings, however, echo those from chapter two, where high host density and slow fish capture rates resulted in higher parasite densities and poor returns in terms of the number of fish caught relative to the number stocked. While the rod limit was initially included in the model as something of a sanity check to ensure that fish were not being caught unrealistically quickly, this provided further evidence that a high turnover rate of fish is highly beneficial when trying to control *A. foliaceus*.

6

CHEMICAL AND PHYSICAL INTERVENTION: SLICE AND EGG-LAYING BOARDS

In previous chapters the impact of stocking methods, procedures and timing have been examined. Where possible the fish density should be kept low in general, and particularly in the warmer months when the parasite is at its most active. In some cases, additional interventions may be desirable to further reduce parasite abundance. This may be the case where high numbers of fish are dying due to the infection, or when fishery managers are trying to keep both the quality of fish and the rate of capture high for visiting anglers.

In this chapter two methods of intervention are examined. The first of these is chemical intervention with the chemotherapeutant Emamectin benzoate (Slice), which is known to be in use at a number of sites across the UK. While not advisable, continual stocking with Slice-treated fish is known to occur in UK waters, and so the efficacy of this treatment with no restrictions, and with the current and proposed veterinary Cascade withdrawal times are of interest. With a view to promoting best practice through less frequent treatment, the optimal time to stock with Slice-treated fish is then also considered.

The second treatment is physical intervention to remove parasite eggs using egg-laying surfaces, which are periodically removed and cleaned, thus destroying the eggs. In this case the impact of the proportion of eggs laid on these surfaces as opposed to natural substrates, and the frequency of board removal, are considered.

6.1 SLICE

6.1.1 *Slice dynamics*

For treatment against sea and fish lice, Emamectin benzoate is delivered to fish in their feed prior to stocking into the fishery. In wild populations the dose delivered to fish is likely to be highly variable as other natural food sources are available, and therefore such practices should not occur. In artificially-stocked populations, however, the dose is more readily regulated as all fish can be fed a fixed amount prior to being stocked into the fishery.

Hakalahti et al. [17] demonstrated that Slice killed >80% of *Argulus coregoni* on rainbow trout in the laboratory within 3 days of a 7-day period of treatment and is therefore a potentially effective treatment. In the field (a commercial Finnish fish farm), the same authors found reductions in the mean parasite burden from 140 to 31 and 151 to 7 within 7 days of treatment in different sections of the same canal. While Slice may offer freshly-stocked fish sufficient protection to avoid infection prior to their capture, it will not affect parasites which stay attached to an untreated host which has been resident in the water for some time.

The relationship between time, temperature and slice safety and efficacy against *A. foliaceus* are, however, not well known, but Slice has been shown to be effective against *Lepeophtheirus salmonis* for a similar period of time to *A. coregoni* (ten weeks). Due to a lack of safety and efficacy data, Emamectin benzoate is currently only permitted for use against *Argulus* spp. under the veterinary Cascade system (Veterinary Medicines Directorate, Guidance on the use of the Cascade). This means that due to a lack of information on the safety and efficacy of the drug in the Argulus-Trout system, a precautionary approach is taken where the fish can only be made available for human consumption 500 degree days post completion of the treatment. In recreational fisheries "available for consumption" is synonymous with being stocked into the fishery.

As Slice is one of the only legally-available treatment options available to fisheries, it is important that it is used effectively, and imperative that it is not administered in a manner that is likely to decrease the time taken for *Argulus* spp. to develop resistance. While insufficient funds are likely to be available to produce new drugs specifically for *Argulus* spp., Slice has the potential to provide a cost-effective way to help fishery managers control *Argulus* spp. infections. A reduction in the length of the withdrawal period could slow resistance development by reducing the number of parasites which receive the small, ineffective doses of drugs that are known to drive resistance. As further information becomes available for the *Argulus* spp. system it is possible the withdrawal period could be reduced to 375 degree days. Throughout this chapter simulations are run to determine what difference stocking fish with different levels of protection might make to fisheries' capture rates, and to the parasite burden.

In this section the Slice model is formulated, and simulations are run to show the impact of treating 100% of fish with Slice prior to stocking. Next, a withdrawal period (see below) is incorporated, again with 100% treatment rate. Finally, we attempt to find the optimal time of year at which to stock with Slice-treated fish.

6.1.2 *The Model*

To allow for the addition of treated fish a compartment, H_n, was added to the model. Treated fish were stocked into this compartment, and treatment was assumed to wear off at a per capita rate m. Parasites attaching to fish in this compartment die immediately - it is assumed that the parasite is unable to cause significant harm to the host during the initial attachment. In the model parasites leave the free-living compartment at rate $\beta(H_n + H)$, but only a proportion of these, $H/(H_n + H)$, manage to successfully attach to a host, as those attaching to fish in the H_n compartment die. The other parameters in the model have been described in previous chapters, but are summarised in table 6.1.

It should be noted that the compartment H_n represents the efficacy of Slice treatment as opposed to a separate compartment of fish: as the dose of treatment delivered to each parasite

Table 6.1: Descriptions of parameters in the seasonal model

Parameter	Description
s	Stocking rate
c	Capture rate
f	Capture reduction(downward hill function)
α	Increased host mortality due to infection
μ_i	Natural mortality rate of population i
β	Rate of attachment
h	Hatching rate
ε	Egg-laying rate
δ	Proportion of parasites surviving host death

decays exponentially over time, fish stocked into this treated compartment move into the susceptible compartment.

In the absence of data specifically relating to the duration of efficacy in our species of interest, here we assume that Slice ceases to be effective, on average, 10 weeks after treatment [47]. Thus fish move from H_n to H at a rate of $m = \frac{1}{70} H_n day^{-1}$.

$$dH_n/dt = s - \mu_H H_n - cH_n - mH_n \tag{6.1}$$

$$dH/dt = mH_n - \mu_H H - cfH - \alpha P \tag{6.2}$$

$$dP/dt = \beta HW - P(\mu_P + \mu_H + cf + \alpha) - \alpha k \frac{P^2}{H} \tag{6.3}$$

$$dW/dt = hE - \mu_W W - \beta(H + H_n)W + \delta P(\alpha(1 + k\frac{P}{H}) + \mu_H) \tag{6.4}$$

$$dE/dt = \varepsilon P - hE - \mu_E E \tag{6.5}$$

The host-only equilibrium, again found by setting the model equations above equal to zero, is given by:

$$H_n^* = \frac{s}{m + \mu_H + cf} \tag{6.6}$$

$$H^* = \frac{mH_n^*}{\mu_H + cf} \tag{6.7}$$

So a higher stocking level, s, will increase the treated population and also the untreated population, due to the H_n^* term in the second equation. Conversely, higher values of the withdrawal rate, m, natural mortalities μ_H and capture (c) would result in a lower host density. The total host density is given by $H_n^* + H^* = s/(\mu_H + cf)$.

The characteristic equation used to determine the stability of this equilibrium is given by:

$$(\Lambda + \mu_H + c + m)(\Lambda + \mu_H + cf)(\Lambda^3 + a_1\Lambda^2 + a_2\Lambda + a_3) = 0 \tag{6.8}$$

Where

$$a_1 = h + \mu_E + \beta H^* + \mu_W + \gamma \tag{6.9}$$

$$a_2 = (h + \mu_E)(\gamma + \beta H^* + \mu_W) + \gamma(\beta H^* + \mu_W) - \beta H^*(\alpha + \mu_H) \tag{6.10}$$

$$a_3 = (h + \mu_E)[\gamma(\beta H^* + \mu_W) - \beta H^*(\alpha + \mu_H)] - h\varepsilon\beta H^* \tag{6.11}$$

with $\gamma = \mu_H + \mu_P + \alpha + cf$. The condition $\frac{h\varepsilon}{h+\mu_E} < \gamma(1 + \frac{\mu_W(\mu_H+cf)}{mH_N^*\beta}) - \delta(\alpha + \mu_H)$ is necessary for $a_3 > 0$, and as $a_1 > 0$ and $a_1a_2 - a_3 > 0$, provides a necessary and sufficient condition for stability of the host-only equilibrium. This essentially means that parasites must reproduce faster than they are killed, in order to survive, and the bigger H_n is, the harder this is to achieve.

The coexistence equilibrium is given by:

$$H_n^* = \frac{s}{m + cf + \mu_H} \tag{6.12}$$

$$P^* = \frac{mH_n - H(\mu_H + cf)}{\alpha} \tag{6.13}$$

$$= \frac{H^*}{\alpha k}\left[\frac{\beta H^*(h\varepsilon/(h + \mu_E) + \delta\alpha + \delta\mu_H - \gamma) - \gamma\mu_W}{\beta H^*(1 - \delta) + \mu_W}\right] \tag{6.14}$$

$$W^* = P^*\frac{\frac{h\varepsilon}{h+\mu_E} + \delta(\mu_H + \alpha + \alpha k P^*/H^*)}{\mu_W + \beta H^*} \tag{6.15}$$

$$E^* = \frac{\varepsilon P^*}{h + \mu_E} \tag{6.16}$$

with $\gamma = \mu_P + \mu_H + \alpha + cf$. The condition $\beta H^*(\frac{h\varepsilon}{h+\mu_E} + \delta\alpha + \delta\mu_H - \gamma) - \gamma\mu_W > 0$ is necessary for positive P^*: P^* is therefore positive whenever the condition for stability of the host-only equilibrium is not met.

A solution for H^* can be found by setting equal the two expressions for P^* (equations 6.13 and 6.14) and solving the quadratic:

$$H^{*2} + H^* \left[\frac{\beta k m H_n(\delta - 1) - \mu_W\gamma + \mu_W k(\mu_H + cf)}{\beta(\frac{h\varepsilon}{h+\mu_E} + \delta\alpha + \delta\mu_H - \gamma + k(1-\delta)(\mu_H + cf))} \right] \tag{6.17}$$

$$- \frac{\mu_W k m H_n^*}{\beta(\frac{h\varepsilon}{h+\mu_E} + \delta\alpha + \delta\mu_H - \gamma + k(1-\delta)(\mu_H + cf))} = 0 \tag{6.18}$$

From the condition noted above, and since $\delta < 1$, it can be concluded that the denominators are all positive. There is therefore a unique positive solution for H^*.

As seen in previous models, when $f = 1$ (in other words, when there is no parasite-induced reduction in capture) the coexistence equilibrium exists, and is stable wherever the host-only equilibrium is not.

When f is defined as a function which decreases with parasite burden, as seen in previous chapters, hysteresis is observed for a range of values where $\gamma(1 + \frac{\mu_W(\mu_H + c)}{m H_n^* \beta}) - \delta(\alpha + \mu_H) < \frac{h\varepsilon}{h+\mu_E} < \gamma(1 + \frac{\mu_W(\mu_H + cf(P_{max}))}{m H_n^* \beta}) - \delta(\alpha + \mu_H)$. Where this is the case, the parasite may either persist or die out, depending on the initial conditions; specifically, the initial parasite burden must be high in order to reduce the capture rate sufficiently for parasite establishment. As found in previous models (see chapter two), this means that the parasite may be harder to eradicate due to the parasite-induced reduction in capture rate.

6.1.3 *Slice withdrawal period*

In order to highlight the impact of the withdrawal period on the efficacy of Slice treatment, a withdrawal period was included in the model. As described before, Slice efficacy is given by the proportion of fish in the H_n compartment of the model. Rather than all fish being stocked into the H_n compartment, a proportion, $se^{-m\tau}$, are now stocked into this compartment, and the remainder, $s(1 - e^{-m\tau})$ into the H compartment, with τ being the withdrawal period. In the absence of capture and mortalities, the expression e^{-mt} gives the density of fish that would be present in the H_n compartment after a given time. The expression $e^{-m\tau}$ is therefore used to represent a withdrawal period of τ days. Formulating the model in this way means that the treatment will have worn off at exactly the same rate as it would have in the fishery. The left hand plot of figure 6.1 shows the efficacy level over time post-treatment, with exponential decay when there is no withdrawal (e.g. $\tau = 0$). With $\tau = 20$ the drug is ineffective for 20 days (as fish have not yet been stocked). When fish are then stocked on day 20, the drug is as effective as it would have been, had they been stocked immediately following treatment. The right hand plot conveys the same information, but compares fish stocked at $t = 0$, some of which have already had 20 days withdrawal.

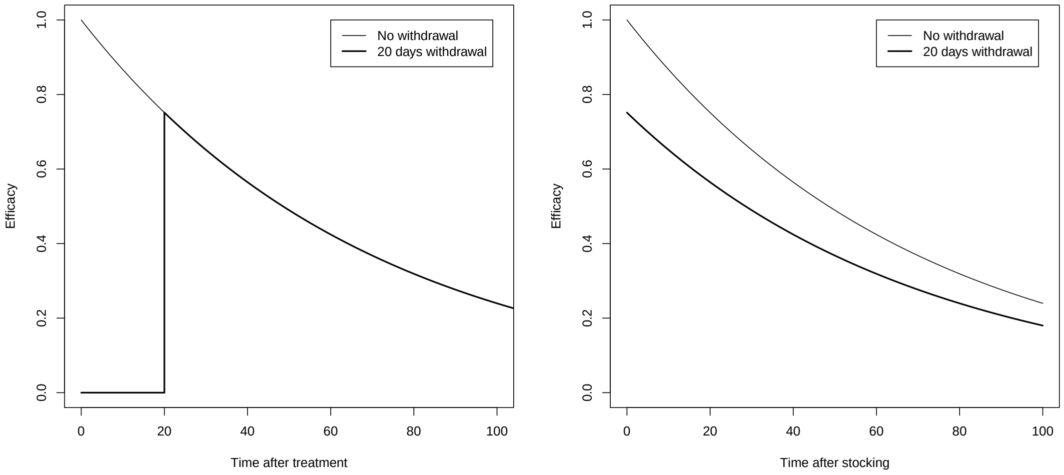


Figure 6.1: Efficacy (out of a maximum of 1) of Slice against *Argulus* after treatment (left). Efficacy post-stocking (right).

The model is now given by

$$dH_n/dt = se^{-m\tau} - \mu_H H_n - cH_n - mH_n \tag{6.19}$$

$$dH/dt = s(1 - e^{-m\tau}) + mH_n - \mu_H H - cfH - \alpha P \tag{6.20}$$

$$dP/dt = \beta HW - P(\mu_P + \mu_H + cf + \alpha) - \alpha k \frac{P^2}{H} \tag{6.21}$$

$$dW/dt = hE - \mu_W W - \beta(H + H_n)W + \delta P(\alpha(1 + k\frac{P}{H}) + \mu_H) \tag{6.22}$$

$$dE/dt = \varepsilon P - hE - \mu_E E \tag{6.23}$$

and the host-only equilibrium is given by:

$$H_n^* = \frac{sx}{m + \mu_H + c} \tag{6.24}$$

$$H^* = \frac{mH_n^* + s(1-x)}{\mu_H + c}, \tag{6.25}$$

where $x = e^{-m\tau}$.

with the combined host density equal to $\frac{s}{c+\mu_H}$. The Jacobian is:

$$\begin{vmatrix} \Lambda + \mu_H + c + m & 0 & 0 & 0 & 0 \\ \mu_H - m & \Lambda + \mu_H + c & \alpha & 0 & 0 \\ 0 & 0 & \Lambda + \mu_P + \mu_H + c + \alpha & -\beta H^* & 0 \\ 0 & 0 & -\delta(\alpha + \mu_H) & \Lambda + \mu_W + \beta(H^* + H_n^*) & -h \\ 0 & 0 & -\varepsilon & 0 & \Lambda + h + \mu_E \end{vmatrix}$$

and the characteristic equation for this equilibrium is given by:

$$(\Lambda + \mu_H + c + m)(\Lambda + \mu_H + c)(\Lambda^3 + a_1\Lambda^2 + a_2\Lambda + a_3) = 0 \tag{6.26}$$

Where

$$a_1 = h + \mu_E + \beta(H^* + H_n^*) + \mu_W + \gamma \tag{6.27}$$

$$a_2 = \gamma(\mu_w + \beta(H^* + H_n^*) + h + \mu_E) + (\mu_W + \beta(H^* + H_n^*))(h + \mu_E) - \beta H^* \delta(\alpha + \mu_H) \tag{6.28}$$

$$a_3 = (h + \mu_E)[\gamma(\beta(H^* + H_n^*) + \mu_W) - \beta(H^* + H_n^*)(\alpha + \mu_H)] - h\epsilon\beta H^* \tag{6.29}$$

and $\gamma = \mu_P + \mu_H + c + \alpha$ and $\gamma_f = \mu_P + \mu_H + cf + \alpha$. By inspection, the first two eigenvalues are negative.

The condition $\frac{h\varepsilon}{h+\mu_E} < \gamma \left(\frac{\mu_W(\mu_H+c)+\beta s}{\beta s\left(1-\frac{x(c+\mu_H)}{\mu_H+c+m}\right)} \right) - \delta(\alpha + \mu_H)$ is necessary for $a_3 > 0$, and as $a_1 > 0$ and $a_1 a_2 - a_3 > 0$, this provides a necessary and sufficient condition for stability of the host-only equilibrium.

The coexistence equilibrium is given by:

$$H_n^* = \frac{se^{-m\tau}}{m+c+\mu_H} \tag{6.30}$$

$$P^* = \frac{s(1-e^{-m\tau})+mH_n-H(\mu_H+cf)}{\alpha} \tag{6.31}$$

$$P^* = \frac{\beta H^{*2}\left[\frac{h\varepsilon}{h+\mu_E}+\delta(\alpha+\mu_H)\right]-\gamma_f H(\mu_W+\beta(H+H_n))}{\alpha k[\mu_W+\beta(H^*+H_n^*)-\delta\beta H^*]} \tag{6.32}$$

$$W^* = P^*\frac{\frac{h\varepsilon}{h+\mu_E}+\delta(\mu_H+\alpha+\alpha kP^*/H^*)}{\mu_W+\beta H^*} \tag{6.33}$$

$$E^* = \frac{\varepsilon P^*}{h+\mu_E} \tag{6.34}$$

By equating the two expressions for P^*, we find that H^* is given by the positive solution of:

$$\begin{aligned} \beta H^{*2}\left[\frac{h\varepsilon}{h+\mu_E}+\delta(\alpha+\mu_H)\right]-\gamma_f+k(1-\delta)(cf+\mu_H) \\ +H^*\left[k(\mu_W+\beta H_n)(cf+\mu_H)-\gamma_f(\mu_W+\beta H_n)-k\beta(1-\delta)(s(1-e^{-m\tau})+mH_n^*)\right] \\ -k(mu_W+\beta H_n)(s(1-e^{-m\tau})+mH_n^*)=0 \end{aligned}$$

Note that the model is equivalent to the model with no withdrwal period when $\tau = 0$. By inspection, the equilibrium parasite density increases as with withdrawal period τ increases, while the equilibrium value of the treated compartment H_n decreases. As in previous models, the fact that the H^0 coefficient is negative indicates that there is always one positive, and one negative solution. The minimum host density required to sustain the infection is now:

$$H_{crit} = \frac{\gamma_f(\mu_w+\beta H_n^*)}{\beta\left[\frac{h\varepsilon}{h+\mu_E}+\delta(\alpha+\mu_H)-\gamma_f\right]}, \tag{6.35}$$

where $H_n^* = \frac{se^{-m\tau}}{m+c+\mu_H}$.

6.2 SIMULATIONS OF THE SLICE MODEL, WITH SEASONALITY

6.2.1 *Continuous, weekly and monthly stocking*

In order to investigate the impact of different withdrawal periods on Slice efficacy, simulations were run with different stocking regimes using the seasonal model from chapter four, with a range of different stocking frequencies. Using an average water temperature of 12°C, 500 and 375 degree day withdrawal periods are given by $\tau = 500/12$ and $\tau = 375/12$ respectively.

When fish were stocked continuously, the parasite was unable to survive with no withdrawal period. With a withdrawal period of 375 degree days it survived, though at a low level. Increasing the withdrawal period to 500 degree days noticeably benefited the parasite, as can be seen in figure 6.2, which shows time series of the three withdrawal periods.

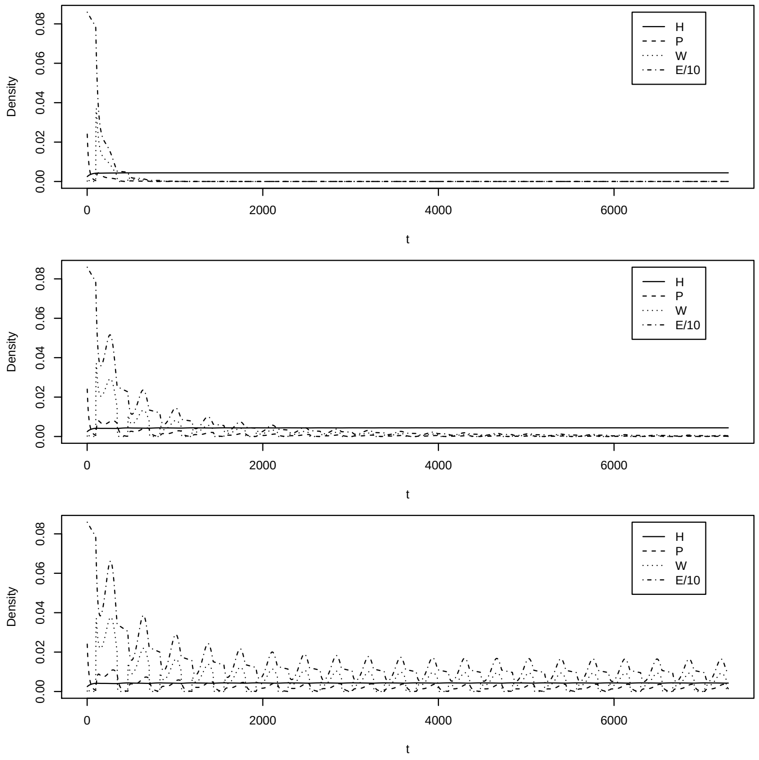


Figure 6.2: Time series plots for different values of the withdrawal period, τ, with continuous stocking. Top, middle and bottom plots show withdrawal periods of $\tau = 0$, $375/12$ and $500/12$ respectively.

Time series plots for weekly and monthly stocking are shown in figures 6.3 and 6.4 for completeness, though the only visible difference between the models with different stocking frequencies are the jumps in the host population caused directly by the stocking frequency itself (i.e. there is no noticeable difference in the parasite population, as was the case in chapter five). Table 6.2 summarises the capture rates, mortalities and parasite burden, and confirms that other than a slight decline in the parasite burden, stocking weekly or monthly has no impact on the efficacy of slice treatment.

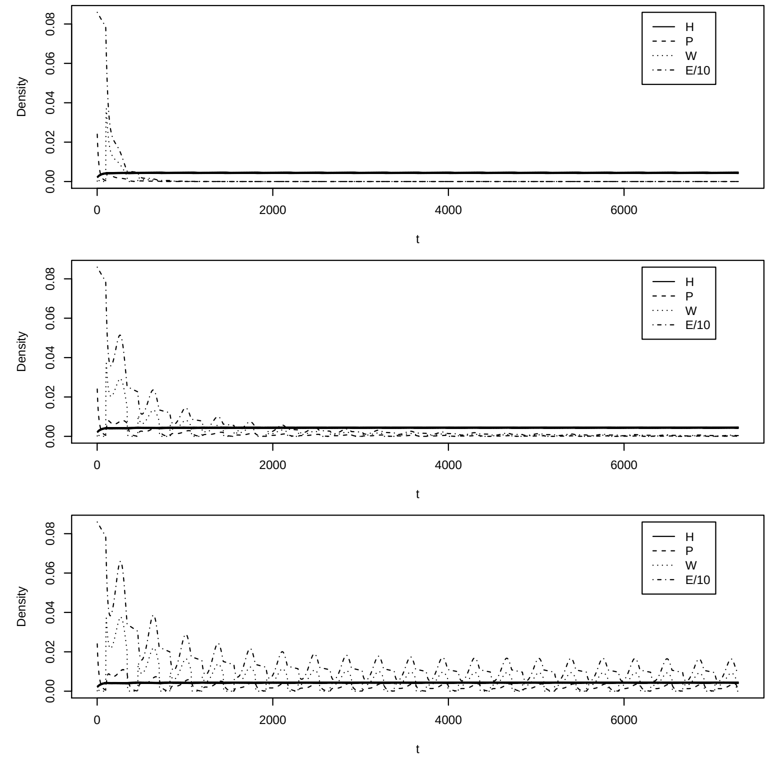


Figure 6.3: Time series plots for different values of the withdrawal period, τ, with weekly stocking. Top, middle and bottom plots show withdrawal periods of $\tau = 0$, 375/12 and 500/12 respectively.

In terms of the impact of the withdrawal period on *A. foliaceus* in a fishery, while the difference between a parasite burden of 0.389, with $\tau = 500/12$, and 0.015, with $\tau = 375/12$ may seem insignificant (especially when compared with the untreated model, where the mean parasite burden was over 5 parasites per host), figure 6.5 shows that, when the value of μ, the mean parasite burden, is changed in this manner in the probability distribution function for the negative binomial distribution (described in chapter two), this could mean that the number of completely uninfected fish could fall from 98.5% to 73.1%. That said, the overall abundance of *A. foliaceus*, and the impact on the fishery, could still be expected to be minimal, and consistent Slice treatment for any of these stocking frequencies still results in capture rates of well over 90%, which compares very well with the untreated rates of capture presented in chapter five of 65-68%. The low level of parasite persistence could mean that a stochastic event, e.g. a period of low stocking, could cause the parasite to go extinct, but on the other hand if treatment with Slice were stopped, then it is likely that the parasite would again have a substantial impact on the fishery.

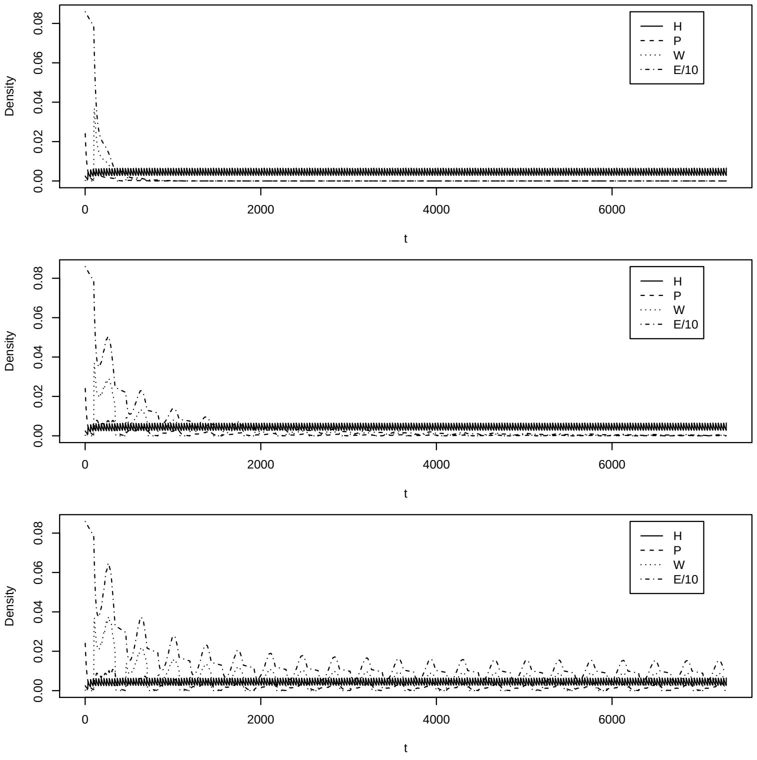


Figure 6.4: Time series plots for different values of the withdrawal period, τ, with monthly stocking. Top, middle and bottom plots show withdrawal periods of $\tau = 0$, 375/12 and 500/12 respectively.

Table 6.2: Table of results for the slice model with continuous, weekly and monthly stocking, with 100% of fish treated and a range of withdrawal periods, τ.

Stocking Frequency	ψ	τ	Mortality (%)	Capture (%)	Mean parasite burden
Continuous	1	0	0	95.3	0.000
	1	375/12	0.1	95.2	0.015
	1	500/12	2.0	93.4	0.389
Weekly	365/52	0	0	95.3	0.000
	365/52	375/12	0.1	95.2	0.015
	365/52	500/12	2.0	93.4	0.387
Monthly	365/12	0	0	95.3	0.000
	365/12	375/12	0.1	95.2	0.013
	365/12	500/12	2.0	93.4	0.362

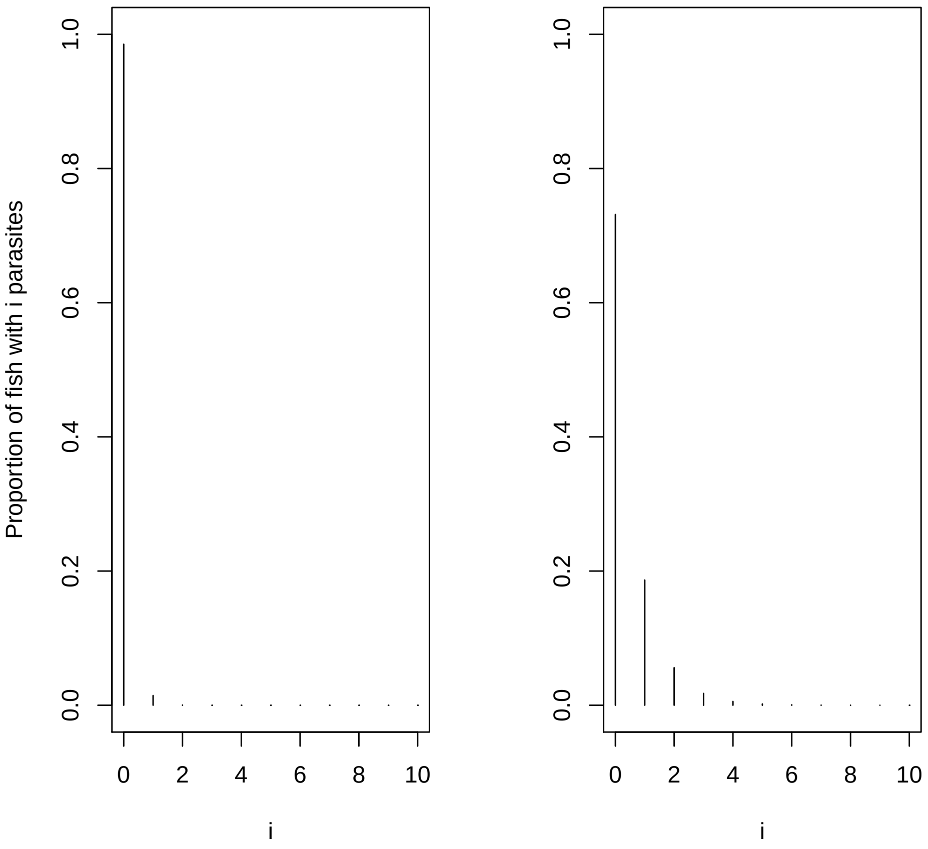


Figure 6.5: Probability distribution for the negative binomial distribution with $k = 0.741$ and $\mu = 0.015$ (left) and $\mu = 0.389$ (right). Each plot shows the proportion of fish with a parasite burden of i

6.2.2 *Annual stocking*

The simulations were then repeated, again with 100% treatment, but this time with yearly stocking, for the full range of offset values. As described in chapter five, the offset is the day of the year on which fish are stocked. The results, with different stocking dates, are presented in figure 6.6. When there is no withdrawal period the treatment is so toxic that the parasite fails to survive regardless of when fish are stocked. With withdrawal periods of $375/12$ and $500/12$ days, perhaps surprisingly, the optimal time to stock with Slice-treated fish is during winter - though this is because, as seen in chapter five, stocking at this time results in too few fish being present in the summer to sustain the infection.

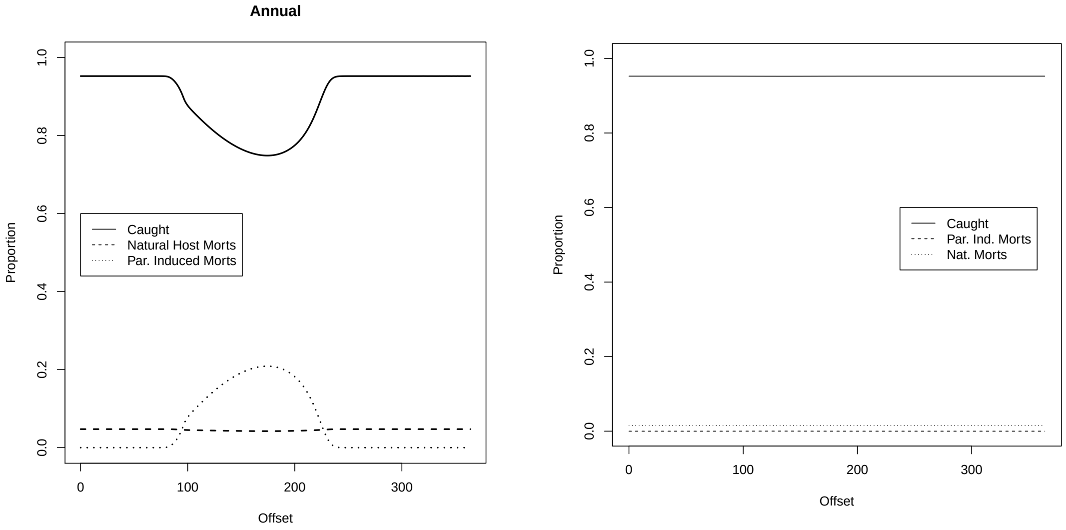
This is clearly more a consequence of the stocking timing than treatment efficacy, as comparison with the untreated model from chapter 5 (reproduced in 6.6) shows. While in the absence of treatment, the capture rate dropped as low as 74.9% with annual stocking, here it remains above 90%. If fish are to be stocked only once per year, then stocking during winter is still best practice, and also renders treatment with Slice relatively useless, as the parasite is already unable to survive. If stocking in summer is necessary for the fishery in order to meet customer expectations, then treating the batch of fish to be stocked with Slice prior to stocking, in this example, improves the capture rate from 74.9% of fish stocked to over 90%, as well as substantially reducing parasite-induced mortalities.

The rod limit described in chapter five was then added back into the model for annual stocking, meaning that a maximum of four fish per angler could be caught per day. In order to achieve this, at each time step the minimum of the sum of the capture rates from both host compartments ($cfH + cH_n$) and 0.0002 was selected and was given the name c_{adj} (adjusted c). The rate of capture within the untreated compartment was then given by $c_{adj}cfH/(cfH + cHn)$, and in the treated compartment by $c_{adj}cfH/(cfH + cHn)$, so that the rate of capture from each compartment remained consistent with the proportion in that compartment.

With the rod limit in place the parasite is now able to survive even when there is no withdrawal period and when fish are stocked during or before the parasite begins to hatch in spring. This can be seen in figure 6.7 which shows the proportion of capture and mortalities for different stocking/treatment offsets. This is again because fish remain in the water for longer - whilst previously fish were stocked and promptly caught prior to the treatment wearing off, with a rod limit in place the fish remain in the water for longer after the treatment has ceased to be effective, and are therefore available for the parasite to attach to. Nevertheless, even in the worst-case scenario when fish are stocked around halfway through the year, the lowest capture rate is around 50% with no withdrawal, 40% with 375 degree days withdrawal and 38% with 500 degree days, which compares favourably with the 21% seen with annual stocking in chapter five in the absence of treatment.

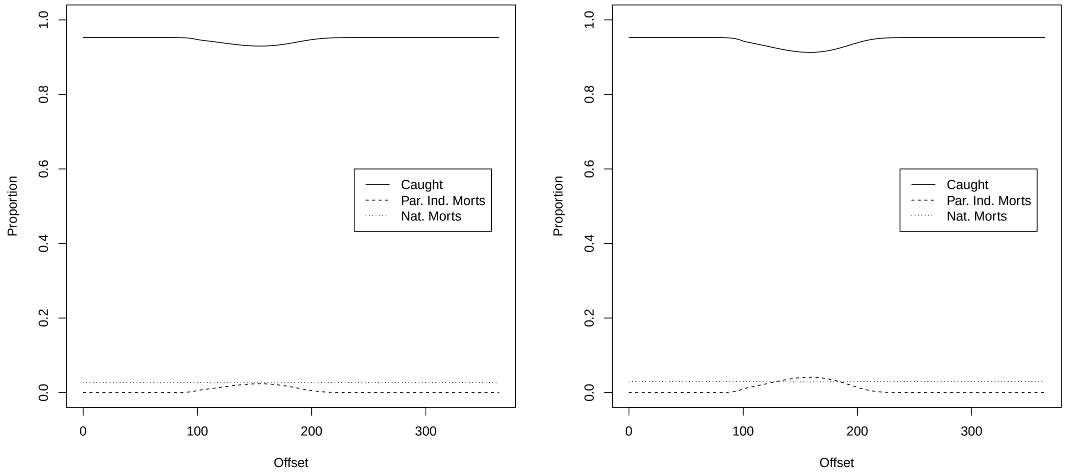
As in chapter five, the inclusion of a rod limit reduces the length of the period during which fish can be safely stocked without allowing the parasite to survive. Relative to the untreated model, however, this period is doubled in length, and fish can now be stocked prior to the beginning of the parasite's overwintering period, as shown in figure 6.7.

Similarly to the results from chapter five, imposing a rod limit on the number of fish caught, or generally stocking fish in such a manner that their residence time is high, is not beneficial when dealing with *A. foliaceus*. If fish are to be stocked in summer then according to this example, under current Cascade guidelines, treatment of these fish with Slice prior to stocking may improve capture rates by 17%, and would increase by a further 3% if the withdrawal period were reduced by 25% to 375 degree days.



(a) Untreated

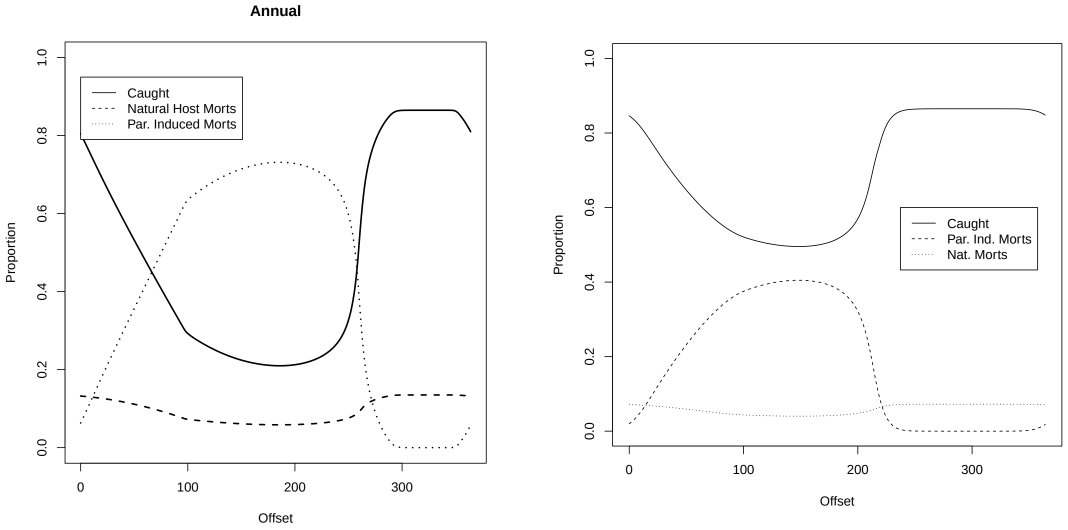
(b) No withdrawal



(c) 375 degree days withdrawal

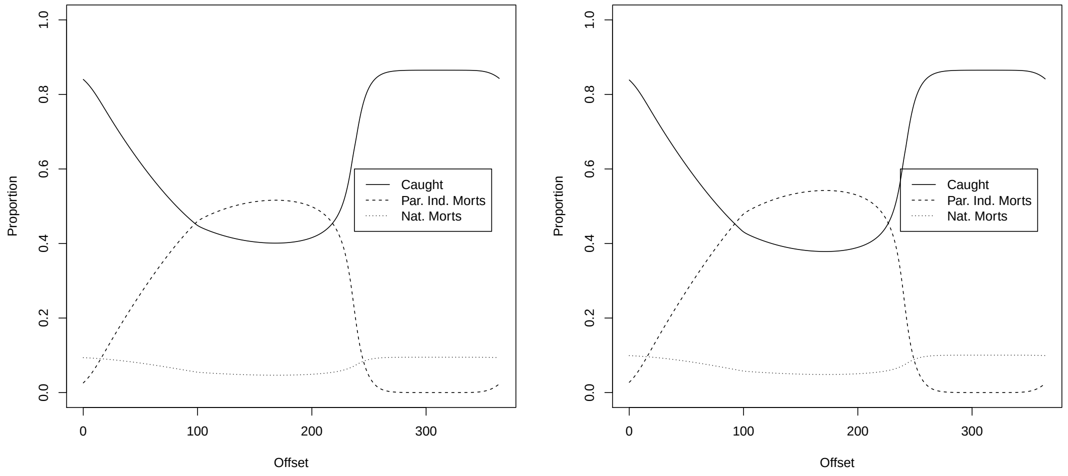
(d) 500 degree days withdrawal

Figure 6.6: Relationship between the stocking/treatment time and the proportion of fish caught, lost to parasite-induced mortality and lost to natural mortality for different withdrawal periods, $\tau = 0$, 375/12, and 500/12, under annual stocking with no rod limit.



(a) Untreated

(b) No withdrawal



(c) 375 degree days withdrawal

(d) 500 degree days withdrawal

Figure 6.7: Relationship between the treatment time and the proportion of fish caught, lost to parasite-induced mortality and lost to natural mortality for different withdrawal periods, $\tau = 0$, 375/12, and 500/12, under annual stocking with a rod limit.

6.2.3 *Optimal Slice treatment time*

As stated in the previous section, persistent treatment with Slice may be costly, and may contribute to resistance build-up. The use of Slice should therefore be minimised by targeting it in the most effective way in order to maximise its impact. This section therefore aims to evaluate the time of year at which the application of Slice is most effective. The model used to do this was as described previously, but this time fish were treated only once per year. In order to implement this in the model, the stocking rate for the two host compartments became:

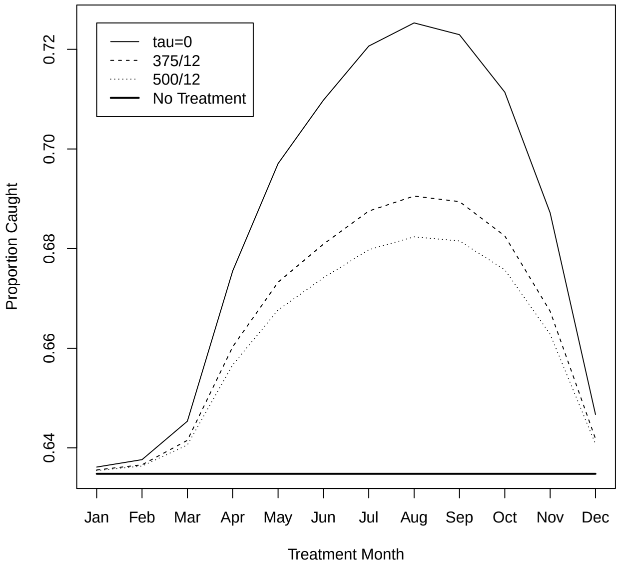
$$s(H_n) = \begin{cases} s(e^{-m\tau}) & \text{if } t = T. \\ \\ 0 & \text{if } t \neq T \end{cases} \tag{6.36}$$

$$s(H) = \begin{cases} s(1 - e^{-m\tau}) & \text{if } t = T. \\ \\ s & \text{if } t \neq T \end{cases} \tag{6.37}$$

where T denotes the time at which treatment was applied, so the total stocking rate was always equal to s. Monthly stocking was used here, as a single daily or weekly treatment would be likely to have a negligible effect, and annual stocking has already been addressed above.

The results are shown in figure 6.8, and demonstrate that the optimal time to stock with Slice-treated fish is at the start of August, and treatment is least effective, as might be expected, when fish are treated at the start of January. This is the optimal treatment time regardless of the withdrawal period. With no treatment the capture rate was around 63.7%, and with the current restriction of 500 degree days, treatment in January improves this by less than 1%. Treatment in August results in 68% of fish stocked being caught, an improvement of just over 4%. This period corresponds with the time at which the parasite is reproducing most quickly. Reducing the withdrawal period by 25% to 375 degree days would improve the capture rate by a further 1%.

Figure 6.9 shows time series of the best and worst treatment times for the model with $\tau = 500/12$. Note that in the treatment months (January and August), the untreated population still grows, due to the reduced efficacy at the time of stocking. With January treatment, its efficacy has largely worn off by the time parasites are searching for hosts in April, and it therefore has little impact on the parasite dynamics. With August treatment the largest monthly recruitment of parasites, which usually occurs post-stocking, is less pronounced, and this impacts egg-laying and hatching throughout the rest of the year. Treatment at this time prevents what would otherwise be the main peak of infection, by reducing the influx of susceptible hosts at a time when the temperature is high and the parasite is reproducing quickly.



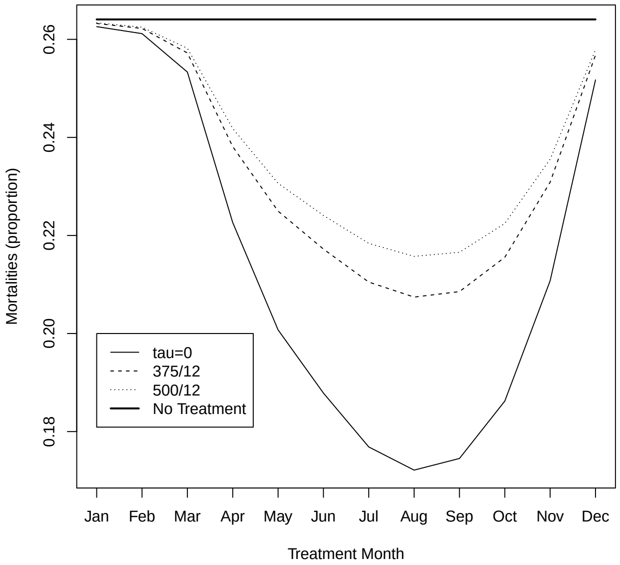


Figure 6.8: Proportion of stocked fish caught (top), proportion of fish lost to parasite-induced mortality (bottom) under monthly stocking. T, on the horizontal axis, represents the time at which the treated fish were stocked. On each plot the solid line denotes $\tau = 0$, the dashed line $\tau = 375/12$, and the dotted line $\tau = 500/12$. The thick line is the model with no treatment.

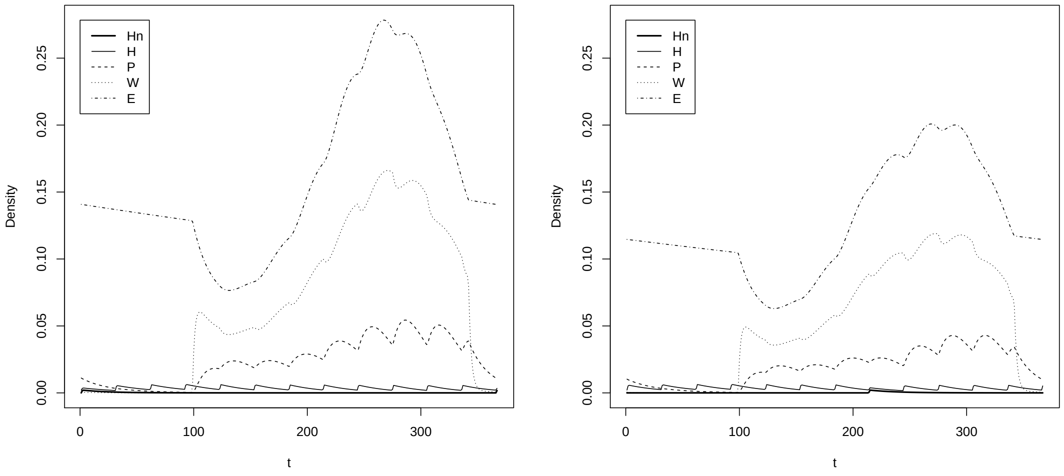


Figure 6.9: Time series plots of the worst (left: January) and best (right: August) times to stock with Slice-treated fish in the model with the current 500 degree day withdrawal period.

6.3 EGG-LAYING BOARDS

Another possible method of control for *Argulus* spp. infections is to suspend boards in the affected water, allow the parasite to lay eggs on them, and then remove and clean the boards at regular intervals. This reduces the number of parasites that successfully hatch and go on to infect fish. The use of these boards in trout fisheries was first proposed over 10 years ago (e.g. [12]), but they are not known to be widely in use. While fairly labour-intensive to maintain, and potentially damaging to the aesthetics of fisheries, they nonetheless provide a potential method of control without the adverse consequences such as resistance which come with chemical interventions like Slice. More recently smaller buoys have been used at several sites to remove eggs and monitor parasite numbers (for example Gartmorn Dam in Clackmannanshire, and Pitfour Fly Fishing Club in Aberdeenshire (`www.pitfourflyfish.co.uk/Documents/Argulus%20Foliaceus%20pamphlet.pdf`)). Karane [22] found that no eggs from a sample that was dessicated (dried out) for a period of two hours hatched within 45 days, while 100% of eggs in a control batch that was continuously submerged at 23°C hatched between 18 and 26 days post-laying. Three different types of egg-laying surface were then designed to be only half submerged in the water at any given time, and then rotated on a weekly basis, which resulted in eggs being dessicated without the need for the removal, cleaning and replacement of the boards. The easiest design to use was shown to be weighted sealed pipes, and more eggs were laid on these than the other designs despite their relatively small surface area. The authors also noted that while eggs were observed on some orange buoys used in the designs, the white buoys were completely free of eggs, and suggest that *A. foliaceus* may have a colour preference in terms of egg-laying sites, and further experiments may further improve the design and attract more egg-laying females [22].

Previously a linear relationship between the proportion of eggs laid on such boards and the growth rate of the parasite population has been found for *A. coregoni* in a farm situation [11], however while this species typically produces one generation per year in these conditions

[15], and hence egg-laying boards need only be removed once per year, *A. foliaceus* are able to produce several generations within a single season [51]. Annual removal of eggs is therefore unlikely to have the same level of success. Accordingly, in addition to the proportion of eggs laid on boards, we will examine the impact of the rate of board removal on the parasite population.

In order to model egg-laying boards, an extra compartment is added to the model, producing the following form:

$$dH/dt = s - \mu_H H - cfH - \alpha P \tag{6.38}$$

$$dP/dt = \beta HW - P(\mu_P + \mu_H + cf + \alpha) - \alpha k \frac{P^2}{H} \tag{6.39}$$

$$dW/dt = h(E + E_B) - \mu_W W - \beta(H + H_n)W + \delta P(\alpha(1 + k\frac{P}{H}) + \mu_H) \tag{6.40}$$

$$dE/dt = (1 - prop)\varepsilon P - hE - \mu_E E \tag{6.41}$$

$$dE_B/dt = prop\varepsilon P - hE_B - \mu_E E_B \tag{6.42}$$

It is assumed that a fixed proportion, *prop*, of eggs are laid on the boards, and that the boards are removed and cleaned at regular intervals. The removal of the boards in the model was achieved using “events" in the deSolve package in R, which allows the user to specify time discrete events using a dataframe containing the relevant time points and multipliers. In this case the dataframe is of the form shown in table 6.3.

Table 6.3: Table of events in R for egg-laying board removal. At $t = 7, 14...$ days, the population named EB is multiplied by 0.

var	time	value	method
EB	7	0	mult
EB	14	0	mult
⋮	⋮	⋮	⋮

6.3.1 *Egg-laying boards - simulation results*

Simulations were run for one year with the same parameters that have been used throughout this section, with continuous stocking of fish; weekly, fortnightly and monthly board removal; and the proportions of eggs laid on the boards were set as 0, 10, 25, 50, 75 and 100%. The results are shown in figure 6.10.

As we would expect, the capture rate increases with the proportion of eggs laid on boards, as the parasite burden and parasite-induced mortalities fall. This has a similar effect to that which would be seen if the parasite's fecundity were reduced. When no eggs are laid on the artificial substrate, the frequency of board removal has no effect, as the far left-hand points in all three plots in figure 6.10 show. Similarly if all eggs are laid on the substrate then the parasite always goes extinct even if the boards are removed four or more times per year. Between these two extremes, the impact of removing boards more frequently is clear, though as eggs typically take over 30 days to hatch, the improvement seen between weekly and monthly removal must largely be attributed to the way in which the model was formulated; specifically, as eggs are being laid and hatching instantaneously, the model allows a proportion of eggs to hatch within a matter of days. While it would be possible to model this by including delays in the egg hatching rate, the results would inevitably show that boards must be removed over a period shorter than the parasite's incubation time. Nevertheless, it is clear that the success of egg-laying boards depends largely on the proportion of eggs laid on them. If 50% of parasites lay on boards then the parasite burden will drop by 50%, and the host capture rate may double as a result, as can be seen in figure 6.10. If, however, the parasite continues to favour natural substrates for egg-laying and only 10% of parasites use the boards, then the 5-10% decrease in parasite burden, and 3-5% increase in fish capture rates is likely to offer a poor cost-benefit ratio. These findings are in agreement with Fenton et al. [11], who found a linear relationship between the proportion of *A. coregoni* eggs laid on egg-traps, and the growth rate of the parasite population. Rather than *A. coregoni*, with which annual board removal would be sufficient, when dealing with *A. foliaceus* the boards should be removed over a period shorter than the parasite's incubation time.

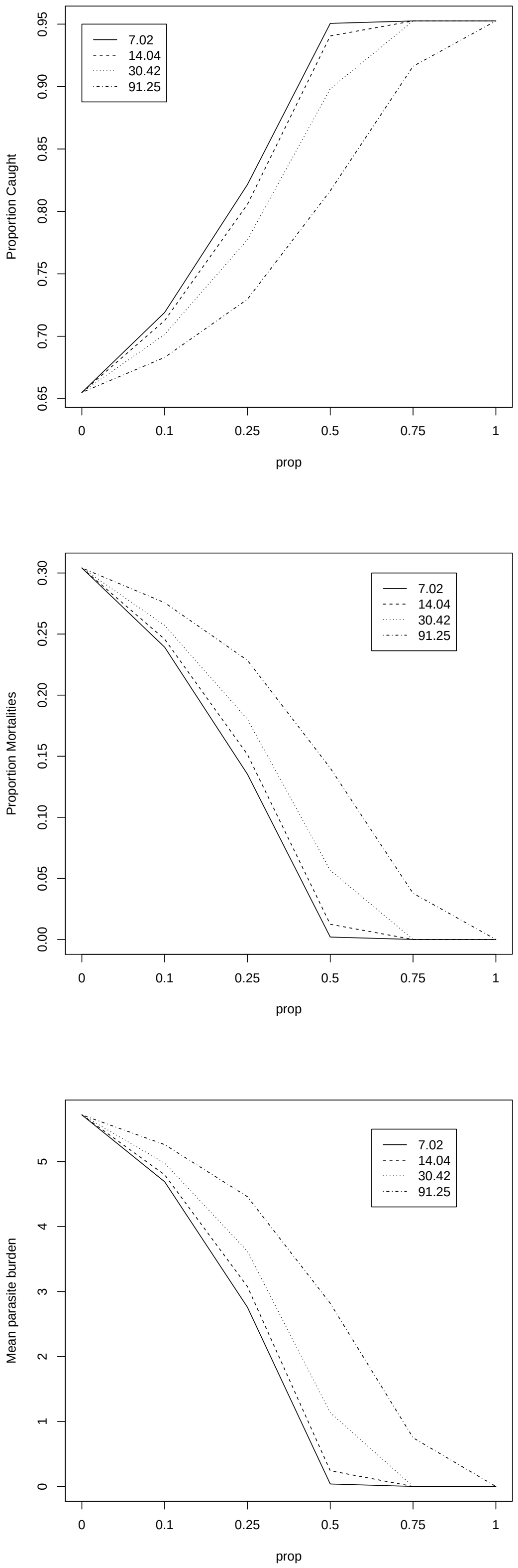


Figure 6.10: Figures showing the proportion of stocked fish (caught), proportion of fish lost due to parasite-induced mortalities (middle) and mean parasite burden (bottom). In each plot the horizontal axis represents the proportion of eggs laid on the removable surfaces. The lines represent weekly (solid), fortnightly (dashed) and monthly (dotted) and quarterly (dot-dashed) removal of the boards.

6.4 CONCLUSIONS

6.4.1 *Slice*

Although fish capture rates may almost be completely restored to their parasite-free levels through the use of Slice with the current withdrawal period of 500 degree days, and further improved under the proposed withdrawal period of 375 days, low levels of parasite persistence means that cessation of treatment would allow the parasite to return to its previous level of abundance. Additionally these few parasites remaining in the system ingesting small ineffective doses of Slice may lead to resistance against the drug in the long term. As mentioned in chapter one, most recreational fisheries have natural populations of coarse fish such as sticklebacks, roach and perch, upon which *Argulus* spp. are able to survive. This means that even if all the trout in a fishery at any given time are treated with Slice, the parasite may continue to survive, and the artificially-stocked fish may once again become infected if and when treatment is stopped.

With annual stocking of Slice-treated fish the parasite was eradicated when there was no withdrawal period, and mortalities and capture rates were improved when the current and proposed withdrawal periods were considered. Even when fish are Slice-treated stocking in summer produces worse capture rates than stocking in winter, as the parasite still benefits from increased host numbers as the treatment wears off. This is a factor of stocking timing than treatment efficacy. Treatment nevertheless produces significant improvements when compared to stocking with untreated fish. In the case of continuous and weekly stocking, the parasite goes extinct when fish do not undergo a withdrawal period after treatment with Slice before being stocked and therefore exposed to the parasite. When withdrawal periods of $\tau = 375/12$ and $\tau = 500/12$ days (i.e. 375 and 500 degree days withdrawal with an average temperature of 12°C) are incorporated, the parasite persists, albeit at a very low level of 0.015 or 0.389 parasites per host. This result is consistent with anecdotal evidence from several fisheries where Slice is regularly administered in order to reduce the impact of *Argulus* spp.

infections, but have been unable to completely eradicate the parasite. While the parasite still persists, these parasite burdens are still very low relative to the untreated mean of 5.7 seen in chapter five.

When the rod limit was included, limiting the number of fish removed by anglers, the impact of the parasite on capture and mortality rates was much worse. The inclusion of a rod limit in the model provides further evidence that a high turnover rate of fish is beneficial when trying to control *A. foliaceus*. In particular making sure that fish are caught quickly relative to the rate at which Slice treatment ceases to be effective is important, and keeps the fish density relatively low, and the proportion of treated fish relative to the total size of the host population high.

While a literature survey has returned no evidence of Slice resistance in *Argulus* spp., this may be partly attributed to the fact that the drug is unlicensed for use in this manner, and has therefore been subject to little research. Evidence does however suggest that Slice efficacy against sea lice has declined in recent years, for example Igboeli [21] estimated that 4 to 26-fold higher concentrations of emamectin benzoate were required to induce the same response in *L. salmonis* in 2011 compared with a similar study conducted between 2002 and 2004. With this in mind, the best options for retaining Slice as an effective treatment against *Argulus* spp. would be 1) to treat aggressively with Slice so that the parasite is eradicated quickly and none remain to develop resistance, and to ensure that fish are caught quickly or 2) to use Slice only when strictly necessary and when it is most effective, in summer. As mentioned above, the first option is non-trivial due to the presence of coarse fish in many fisheries.

Taking the current 500 degree-day withdrawal period into account, one-off treatments with Slice may benefit a fishery during its busiest months, reducing the parasite burden during its most abundant period and improving the fish capture rate. The models show that this method will not eradicate the parasite, and this is unsurprising given that constant Slice treatment still allowed the parasite to persist.

6.4.2 *Egg-laying boards*

Egg-laying boards may provide an effective method of reducing the impact of an *Argulus* spp. infection [12], but this is dependent on how many eggs are actually laid on them, which in turn will depend on the availability of natural egg-laying surfaces within the fishery relative to the density of boards, and appropriate placement of the boards. Their success is widely acknowledged to depend on the removal of hard substrates from the water, which are otherwise favoured by the parasites. This process alone may prove prohibitive for fishery owners considering egg-laying boards as a means of controlling *A. foliaceus*. Board-removal should take place at intervals shorter than the parasite's incubation period, which is typically 30-40 days [51], otherwise the eggs will begin to hatch along with those laid on natural substrates.

Egg-laying boards are labour-intensive to remove and clean, and we are currently unaware of any sites that have used such devices for long enough to ascertain whether they provide an effective long-term method of control. Nevertheless, use of these boards does not carry the same level of risk as chemical treatments such as Slice in terms of resistance development, and with the requisite time and effort they may be of use to some fisheries.

7

DISCUSSION

Argulus foliaceus is a parasite known to cause problems in UK stillwater trout fisheries by reducing the appearance and catchability of fish [52]. The primary aim of this thesis was to formulate a model representative of *Argulus*-trout dynamics, incorporating aspects of seasonality, the phenomenon of the parasite-induced reduction in capture, fish stocking levels and *Argulus*-specific interventions, with the aim of determining how each of these affect parasite abundance and fish capture rates.

In chapter one, the current *Argulus foliaceus* situation in the UK was summarised, along with the information about the parasite's life cycle necessary to formulate and parametrise the model. We then set out to determine the best techniques for managing a stillwater fishery with an infection of *A. foliaceus*.

In chapter two a range of different stocking methods were examined, which reflected the manner in which fisheries are often managed. It was concluded that, while keeping the stocking density low should eradicate the parasite, this may be impractical due to the necessity of maintaining a capture rate high enough to satisfy anglers, or impossible if wild fish populations are present, as *A. foliaceus* is a generalist parasite. When fish were stocked according to the replacement method, whereby fish are only added when others are removed by capture, the parasite effectively killed itself off by slowly reducing the fish density through increased mortality; this may be sufficient to eradicate the parasite in certain circumstances, with the potential to increase the stocking rate after extinction, but it should be noted that this will ultimately fail if reservoir hosts capable of sustaining the parasite are present in the system. The compensatory model was similar to the replacement model, but contained an added term to account for compensation of dead fish, as well as those caught. It was shown that, in what would seem an ideal scenario, successfully maintaining the fish population at a desired level could either be harmless, if this density fell below the parasite survival threshold, or disastrous, as maintaining the host density essentially ensures that the parasite population is adequately provided for, regardless of the damage it does to its own food supply. Reactionary stocking, whereby fish were stocked in such a manner as to maintain a desirable capture rate, was shown to be effective in this regard, but also allowed the parasite burden to become very high, reducing the value obtained from each stocked fish through increased mortality - in other words, each fish stocked was more likely to die, and less likely to be caught. Maintaining the capture rate therefore comes at a high economic cost, and compromises the welfare of the fish. The constant stocking model assumed that a fixed number of fish were stocked continuously, and there was a simple relationship between the number of fish stocked, the fish density, and the resultant parasite burden.

In chapter two the impact of parasite-induced reductions in capture was also investigated. By including a capture function which varied inversely with the parasite burden it was shown that, by preventing the capture of their hosts, *A. foliaceus* was able to survive in an environment with a lower density of fish than was previously required. Biologically this can be explained by the fact that in such cases attached parasites are themselves removed from the water at a slower rate, and also that the residence time of each host in the water is higher, allowing more parasites to successfully attach. While the invasion threshold of the parasite remained at its previous value, once established - or somewhat improbably, if there were a high influx of parasites - the parasite could survive with a lower density of hosts. The exclusion threshold changed, making it harder to get rid of the parasite by manipulation of the fish population density. In other words, the minimum stocking density required for the parasite to successfully establish itself was higher than the density required to sustain it. This is because the capture rate reduction is a function of parasite burden, so will not take effect when only a small number of parasites are added. This hysteresis effect occurred in all of the afore-mentioned stocking models, with the exception of the replacement model, where there was no threshold of which to speak. However, in this model the parasite burden and level of fish mortalities were higher for the duration of the infection.

One of the surprising results which surfaced in this chapter was that deciding whether or not to undertake the seemingly innocuous process of estimating fish mortalities and compensating for them appears to be a process which is potentially harmful to all but the parasite - if the density of fish which the fishery is seeking to maintain is sufficient to sustain the parasite.

There are a great number of ways to choose to stock a fishery, with labour, delivery, flexibility and customer satisfaction all issues of great concern. The models in chapter two demonstrated the importance of stocking methods in controlling *A. foliaceus* in fisheries. It is widely accepted in the industry that encouraging fishery managers to compromise capture rates by reducing stocking densities in order to manage disease is a difficult task. By showing that each of the models were "safe" within various limits, we hope to highlight that guidelines for stocking need not be entirely prescriptive, and that there is a degree of flexibility. As opposed to convincing fishery managers to empty their waters and lose economically disastrous quantities of income, we hope this shows that while this is still the ideal scenario for parasite eradication, small steps can have considerable effects, and a compromise depending on their circumstances is not unreasonable. It is not true to say that all fishery managers strive for the same customers, and consequently the need to maintain a high stocking density may outweigh the issues of quality associated with *Argulus* spp. infections - nevertheless it is necessary for these same fisheries not to suffer mass fish mortalities, as can happen if an infection goes completely unchecked.

In chapter three, a series of alterations were made to the model in order to account for natural host mortalities, parasite reattachment and egg-laying dynamics. While these alterations made quantitative differences to the model, the qualitative results from the second chapter regarding the parasite-induced rate of capture remained consistent. In chapter four seasonality was added to the model by first incorporating temperature dependence into the parasite egg-laying rate. This was shown to result in a cyclic equilibrium, whereby the four population densities fluctuated sinusoidally around the static values found previously, over a period of one year. Over-wintering was then incorporated into the model in such a manner that the parasite was unable to reproduce when the temperature was below 8°C, but eggs benefited from a reduced rate of mortality during this period.

Actual monthly stocking figures were then incorporated into the model to allow parameters to be fit to the model using a mixture of techniques. First a solver in R was used to estimate the parameters α, the rate of parasite-induced fish mortalities and β, the rate at which free-living parasites attach to fish, which have yet to be found experimentally. Due to ethical considerations it is unlikely that α will ever be found empirically, and experiments designed to find β are often unsuccessful due to predation of fish on the parasite. Consequently the value of β found was much higher than the previous estimate inferred from a laboratory-based experiment.

When the same method failed to optimise the parameters ρ and n, the parasite burden required to halve the capture rate and the shape parameter of the reduction function, values were found manually by plotting the same Chi-squared-like function used with the solver in R in parameter space. The values found were $\rho = 15$ and $n = 2$. The fact that the mean parasite burden required to reduce the capture rate by half was low relative to the parasite burden on site, causing a 40% reduction in capture when the parasite burden was at its highest, confirms the notion that the inclusion of this function improves the model fit. That the shape parameter was 2 rather than a lower value confirms the assertion in chapters two and three that a very small parasite burden would have relatively little impact on capture, and validates the move from the exponential reduction in capture to the hill function. The final seasonal model was then compared to the data and shown to provide a good fit to the available data, allowing this model, complete with fitted parameters α, β, ρ and n, to be used in subsequent chapters.

In chapter five it was first shown that stocking fish at increasingly large intervals and in ever-increasing quantities made the timing of stocking events more important. This is a logical result as while stocking on a different day of the week would be expected to have little or no impact on parasite dynamics, when fifty times more fish are being stocked on one day of the year, whether this happens while the parasite is active is likely to be crucial in determining whether or not it will be able to survive. The annual model in particular showed that the parasite was unable to survive at all when fish were stocked during winter (though not too soon before the parasite began to hatch). Generally infrequent stocking appeared to be detrimental to the parasite, but it was hypothesised that this result was due to the extremely high capture rates which followed each stocking event. It is extremely unlikely that any viable fishery would stock and allow capture in such a manner that over half of a year's consignment of fish would be caught within a month, as was the case in the annual stocking model, and so a rod limit was included in the model such that the capture rate was capped at a relatively high four fish per angler (parameterised using footfall data from the same site described in chapter four). This policy is fairly common across artificially-stocked fisheries in the UK, where fisheries want a reasonable return from the fish they stock. Likewise it may be the case that a fishery simply has low angler numbers, which would also restrict the number of fish caught even when the fish density is high. With this rod limit in place the timing of stocking events became even more important as the stocking frequency declined. The parasite was able to survive when fish were stocked at any time of the year, with the exception of mid-November to mid-December, with the rod limit ensuring that the fish density at the beginning of the season was sufficient to allow the parasite to survive. Stocking at this time produced the highest capture rate for the fishery, and also produced the lowest parasite burden and rate of mortalities. It should again be reiterated that this may not necessarily be the case if the fishery is quiet during the winter months. Whereas the model without a rod limit produced the result that stocking annually was better in terms of controlling *Argulus* spp. than stocking monthly or more frequently regardless of timing, with the rod limit annual stocking now also produces the worst case scenario where a large number of fish are stocked in the middle of the year and most remain in the water until the end of the season. In practical terms these results again suggest that keeping the fish density low throughout *A. foliaceus*'s active period is advisable. Furthermore comparisons of the model with and without a rod limit suggest that stocking in large batches may not be detrimental if these fish are likely to be caught quickly, but the rod limit also indicates that stocking in large batches should be undertaken with caution, and the timing of such events should be decided on a per-site basis depending on predicted angler numbers, with an aim to keeping the fish density low over summer when *Argulus* spp. is at its most abundant.

In many fisheries there are few opportunities to stock each year, and while trickle stocking is seen as something of a gold standard, it has been shown here that stocking monthly makes very little difference compared to daily stocking, and indeed by providing the parasite with fluctuating host densities rather than a consistent influx of healthy fish, small improvements may be seen in capture rates - moreso if the timing is such that fish are not added directly before the parasite starts host-searching. Annual stocking may even be undertaken with little risk providing most fish are caught before the start of the parasite's reproductive season. Imposing limits on capture or otherwise stocking large quantities of fish when the residence time is likely to be high and *Argulus* spp. is present is likely to exacerbate the infection by providing a constant source of hosts.

In chapter six treatment with emamectin benzoate was included by adding a compartment, H_n, to the model to represent treated fish. Treatment wore off at a rate, m, and this was represented by hosts moving into the original, untreated host compartment, H. While constant Slice treatment cannot be advocated due to the dangers of resistance development, communications with fishery owners suggest that this practice is likely to continue regardless, and so was a useful scenario to test. Constant treatment of all fish with no withdrawal period from the drug prior to stocking was shown to result in the extinction of the parasite, though if reservoir hosts are present in the fishery then these may be sufficient to sustain the parasite population.

In line with current veterinary cascade guidelines a withdrawal period, τ was added into the model, whereby the drug was less than 100% effective by the time of stocking. Currently the required withdrawal period is 500 degree days, which translates to $\tau = 500/12$ at an average water temperature of 12°C, and in the model this shows that the parasite is still able to survive - albeit at a much lower density than without treatment. This is consistent with personal communications from fishery owners who report that Slice is beneficial in dealing with *Argulus* spp. infections, but continues to persist at a reduced level. Further to this, simulations were run with a shorter proposed withdrawal period of 375 degree days - 25% shorter than the current 500. This was shown to further reduce the impact of the parasite on the fishery, with the parasite still persisting, though at an even lower level. Reducing the withdrawal period by 25%, as is currently being proposed, would improve the efficacy of Slice against *Argulus* spp..

The low level of persistence observed with both withdrawal periods, may translate to significant improvements for the fishery in the short term, but is dangerous in terms of resistance build-up. While this may not be an immediate concern for a fishery using Slice on a regular basis, in the absence of other available chemical treatments, this practice will reduce the efficacy of the drug in the long term, leading eventually to the return of heavy parasite burdens and low capture rates.

As consistent treatment is not advisable for the above reasons, the impact of a single treatment event was then investigated within the monthly stocking framework. The optimal treatment time was found to be the start of August, and unsurprisingly treatment at the start of January was ineffective as there are no parasites attaching to hosts at this time, and the treatment had mostly worn off by the end of the over-wintering period. For maximum benefit Slice treatment should therefore be applied when the parasite is most abundant.

Treatment with egg-laying boards was also investigated, and the efficacy of these was largely dependent on the proportion of eggs laid on the boards, a figure which is not currently known and is likely to be highly variable between sites. While this type of intervention does not carry the risks of chemical treatment with Slice, the benefits may be relatively small for the level of economic, labour and aesthetic cost required for their effective use. More recently-developed pipes suspended in the water and rotated at regular intervals, causing dessication of *A. foliaceus* eggs may provide similar results and require significantly less effort than boards which must be removed, cleaned and replaced. A further avenue for future research would be whether parasites have some genetic disposition for choice of egg-laying surface. This could potentially see the efficacy of egg-laying boards decline over time.

The reduction in capture discussed throughout chapters two and three of this thesis was included phenomenologically in the model, but individual-based models could shed light on the mechanisms driving the negative binomial aggregation of *A. foliaceus* across its hosts, such as morbidity caused by the parasite causing infected fish to have increased exposure times to the parasite.

While the model was shown in chapter four to be representative of the site studied, the drop in parasite numbers between August and September present in the data and not in the model remains unexplained, and could be a result of an undisclosed intervention against *A. foliaceus* at the site, but could also be a consequence of the way in which the model was formulated, as the egg-laying and hatching of the parasite occurs instantaneously. To remedy this a delay for the incubation period of the parasite could be included in the hatching rate within the model, though care would have to be taken when combining this with the over-wintering function in the model. This would also improve the accuracy in the egg-laying board model presented in chapter six, though the findings would inevitably be that the boards would have to be removed over a period shorter than the parasite's incubation period in order to be effective.

The models throughout this thesis have been shown to fit the available data from a UK fishery, and provide the flexibility to model different management methods of stocking and treatments against *A. foliaceus*. Work by Taylor et al. [52] has shown that risk factors including the presence of algal blooms are correlated to the abundance of *A. foliaceus*, and with more data it would be useful to determine the goodness of fit of the model and the parameters estimated in chapter four to other sites. Additionally, data on the rates of capture required by fisheries throughout the year in order for such businesses to remain viable would allow for further optimisation of the model, though this will always vary year-to-year, or day-to-day depending on the number of visiting anglers. While it would have been desirable to provide an optimum stocking and treatment procedure within this thesis, doing so without such knowledge could produce inaccurate results, as it was demonstrated in chapter five that the inclusion of a rod limit in the model could change the optimal timing of stocking events.

While precise recommendations on the number of fish to be stocked at which times are unlikely to be followed without capture rates being taken into a account, the general findings throughout this thesis are fairly comprehensive in that fish should be stocked in large quantities or to high densities with extreme caution, and only if they will be caught quickly, that Slice treatment will be most effective if applied in August, and the efficacy of egg-laying boards depends on the proportion of parasite eggs laid on them. Hysteresis resulting from the parasite-induced reduction in capture may make it harder to eradicate this or any other parasites which cause relatively low rates of host mortality but complicate capture or the harvesting process.

In conclusion, models here have been shown to be representative of the *A. foliaceus*-trout dynamics of a sample fishery in the UK. It has been demonstrated that high fish densities are beneficial to the parasite and detrimental to the fishery in terms of capture rates and the return seen for each stocked fish. Stocking large numbers of fish during the parasite's active period may improve capture rates but will cause the parasite to proliferate and ultimately prove detrimental to both fish welfare and the economic viability of the fishery. There is potential for eradication of the parasite by stocking in such a manner than only caught fish are "replaced", with the caveats that such low host densities may make the fishery unpopular with anglers and hence not economically viable, and natural reservoir populations of fish may still allow the parasite to persist. Batch stocking was shown not to be inherently dangerous in terms of exacerbating *A. foliaceus* infections when fish were caught quickly and the host density was kept low in summer outside of the parasite's over-wintering period. This remains a risky practice, however, as angler numbers and capture rates can be unpredictable, and if fish capture rates are not sufficiently high then the infection may be worsened. Irrespective of this, stocking monthly as opposed to daily, weekly or fortnightly appears to carry little additional risk, and such frequent stocking appears unnecessary for control of *Argulus* spp.- though they may still be necessary in densely-stocked fisheries where high fish densities are required for more demanding (or less skilled) anglers. Consistent treatment with Slice under current veterinary cascade guidelines does not appear to be adequate to eradicate the parasite, and reducing the withdrawal period by 25% as is currently proposed would improve the efficacy of the drug but is still unlikely to result in eradication of the parasite, even with constant treatment. If a single treatment is to be applied then while doing the optimal time for this may intuitively be the start of April when parasites begin to hatch, any parasites surviving this period continue to reproduce and cause heavy parasite lodes later in the year, and for maximum benefit any single treatment with Slice should take place when the water temperature is highest and the parasite is reproducing quickly. Egg-laying boards may provide additional benefit when dealing with *Argulus* spp., but some understanding of the proportion of eggs likely to be laid on these as opposed to any natural substrates would be useful in determining their efficacy. If the proportion is small then the patented boards are likely to require significant outlay for relatively little benefit, but newer less labour-intensive devices potentially provide a method of control less risky than any chemical intervention, with less need to restrict the host density.

Argulus spp. abundance can be reduced stocking carefully, maintaining high rates of fish turnover, careful use of Slice, and egg-laying surfaces; modelling has allowed us to understand the complexities inherent in these methods, and provided a framework for *A. foliaceus* modelling in UK fisheries.

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Part I

APPENDICES

A

APPENDIX A

A.1 PARAMETER ESTIMATION

Typical stocking and capture rates, s and c, were estimated from data collected as part of a survey of over 60 fisheries in England in 2002-2003. The values used in chapter two give the 10th and 90th percentiles, after the removal of outliers.

No estimates for α are currently available, to the best of our knowledge, and are unlikely to become available due to the difficulties of measuring it in the field, and the fact that an experiment to find such a parameter would be unethical. A guess of $\alpha = 0.001$ (assuming fish can survive 20 days with a burden of 50 parasites) was used until chapter four, at which point an optimised value of α was found. The impact of choosing a different value of α is addressed in chapter two, and some sensitivity analysis was conducted in chapter four.

An initial estimate of β was measured by Pasternak et al. [36]. This parameter was found for *Argulus coregoni*, but was used in chapter two as no better data were available for *Argulus foliaceus*. Later, β was calculated with data from Mikheev and Pasternak [31]. At least one parasite attached to each fish within 1-3min. Each tank contained 20 litres of water, 2 fish, and 10 parasites.

βHW = #infection events per unit time (per 1-3 mins)

$\beta * \frac{2}{0.02} * \frac{10}{0.02} = 2$ per 1-3 mins

$\beta = \frac{2 * .02^2}{20} \mathrm{m}^{-3}$

If per minute then multiply by $24 * 60$ if 3 mins $24 * 20$

i.e. β is between$(0.0192 - 0.0576)$ the mean of these two values is $\frac{0.0192 + .0576}{2} = 0.0384$

Along with α, this parameter was optimised in chapter four - details are provided within this chapter.

The best data available for estimating egg mortalities were found in Pasternak et al. [37], where the authors found that eggs had a 76% hatching success rate when kept at room temperature (19-22°C), and took 25-240 days to hatch. From this we infer that the "summer" mortality of *Argulus foliaceus* eggs is given by $\mu_e = \frac{-\ln 0.76}{(25+240)/2}$. Hatching success was reduced to 66% when overwintering was simulated by keeping eggs at 5°C for 5 months. Assuming this is analogous to a mortality rate of $.66 * 100/.76\%$ over a 5 month period, we have an overwintering mortality rate of $\mu_e = \frac{-\ln(0.66/0.76)}{5*365/12}$.

Natural host mortalities, μ_H, are variable depending on the fishery, but is given by $\mu_H = \frac{1}{meanlifespan - ageatstocking}$. The life span of *O. mykiss* can vary from between as little as 4 years to a maximum of 11 years. This is likely to be due to environmental factors such as temperature, population density and temperature. The age at which fish are stocked into a fishery also varies but is typically around 2 years [3].

λ was found by multiplying the mean number of eggs laid by a female argulid (100-150) [7] by the proportion of argulids which are female (0.5) [37], then dividing by the life span of an argulid (this is equivalent to multiplying by the mortality rate μ_H). This gives a lower estimate of

$$100 \times .014 \times .5 = 0.7 \tag{A.1}$$

and an upper estimate of

$$150 \times .031 \times .5 = 2.325 \tag{A.2}$$

At the time of writing chapter two there appeared to be relatively little newer or more precise data on the mean number of eggs laid per female argulid compared to the 100-150 estimate found by bower-shore. A mean of 125 was used, and lambda, in the model without an egg equation, was therefore given by $1/(incubationperiod + timefromhatchingtoegglaying) = 1/(50 + (3 + 40 + 42)/3) * 125/2 \approx 0.713$.

Closer inspection of [37] later provided an estimate of 228 eggs per parasite - found by inspection of a plot showing the number of eggs laid by 10 female argulids.

Parameter Estimates and Definitions

Parameter		Value	Source
s	host stocking rate	0.0051-1.1 m^{-3}day^{-1}	10th and 90th percentiles, unpublished data
c	(optimum) capture rate	0.0036-0.1404 m^{-3} day^{-1}	" "
α	increased host mortality due to infection	0.001 day^{-1} [1]	
β	rate of attachment	0.0384m^{-3}day^{-1}	Mikheev and Pasternak [31]
μ	mortality of attached stages	0.014-0.031 day $^{-1}$	Taylor et al. [52]
d	mortality of free-living stages	0.424-0.476 day^{-1}	Walker [54]
h	hatching rate	0.025-0.033 day $^{-1}$	Taylor et al. [51]
n	average number of eggs laid by a female argulid	100-150	Bower-Shore [7]
k'	inverse degree of aggregation on the host	0.741*	Bandilla et al. [4]
i	parasite incubation period	37.67 days	Taylor et al. [51]
m	time from hatching to egg-laying	50 days	Taylor et al. [51], Schluter [41]
λ	rate of parasite births	$0.713 = (\frac{n}{2(i+m)})$	

B

APPENDIX B

B.1 R CODE

At the start of this project the aim was to use R for modelling throughout this thesis so that the models produced could be used elsewhere. Initially, the available packages did not appear to be capable of producing the results required (though user error cannot be entirely ruled out!) - and so Mathematica was used for the majority of the work. Later R was revisited due to its ease of use when dealing with scripts, and the need to run large numbers of simulations in chapter five. From this point on all code was written in R and is included here in case it proves useful to anyone working on a similar project.

The code was written in Rstudio with R version 3.0.1, but should work with more recent versions of R. Some sections were designed to output spreadsheets and images to a folder on my computer, so file references will definitely need updating.

B.2 CHAPTER FOUR

The following code was used to generate the seasonality plots in chapter 4.

c4-progression.R

```
library(ggplot2)
### Optimise alpha, beta, c, rho, n, and k
library(deSolve) #Old package name?

pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–oldDD.pdf")
plot(t,1/DD,ylab=’Egg–laying rate′,xlab=’Day of year′,type=’l′)
lines(0:365,rep(mean(1/DD),366))
plot(t,DD,ylab=’Egg–laying rate′,xlab=’Day of year′,type=’l′)
lines(0:365,rep(mean(DD),366))
dev.off()

int=1
```

```
base_inits=c(.00422,.00027,.0002,.2,0,0,0,0,0)
x=((365/12)*1:12+1)

time<-seq(int,3650+int,by=int)

ARGY3=function(t,inits,p)
{
  temp=12+8*sin((t-128)*2*pi/(365))
  if(p[10]==1) temp=12 else NULL
  DD=3900/(((.434*temp)+.361)^2)

  #Define Variables
  H=inits[1]   #Rainbow Trout
  AP=inits[2]  #Attached A. foliaceus
  W=inits[3]   #Free-living A. foliaceus
  EG=inits[4]  #A. foliaceus eggs
  SH=inits[5]  #Stocked Fish
  CH=inits[6]  #Caught Fish
  CP=inits[7]  #Caught Pars
  NATH=inits[8]#Nat. H Morts
  PINH=inits[9]#P. ind. H Morts

  c=p[6]
  rho=p[7]
  nn=p[8]
  #  psi=0         #Stocking interval
  #  off=0         #Stocking Offset
  muh=1/(2*365)         #Nat. host mortality

  muw=0.45         #Unattached mortality
  b=p[5]         #A. foliaceus attachment 0.0192-0.0576 #A. foliaceus attachment
  delta=1          #Proportion of pars that survive host death
  #  rodlimit=20      #Maximum number of fish caught per day
  kk=p[9]
  k=(1+kk)/kk  #Parasite aggregation
  OR8=p[2]            #Cut-off temperature

  s3stock=c(1461,840,710,121,350,452,690,1115,1100,600,1324,1308,1461)/(217366*365/12)
  points=seq(365/24,25*365/24,by=365/12)
  s3s=approxfun(points,s3stock)
  stock3=s3s(((t + 15*365/24) %% 365)+365/24) #must define time first

  stock=stock3
  if (p[4]==1) stock=0.000128 else NULL

  catch=c*(rho^nn)/(rho^nn+(AP/H)^nn)
  atop = -log(.76)/((25 + 240)/2) #egg mortality in summer
  blow = -log(.66/.76)/(5*365/12) #egg mortality in winter

  #Temperature dependent parameters
  hatch=ifelse(temp>OR8,0.027,0)
  alpha=p[1]
  mue  =ifelse(temp>OR8,atop,blow)
  beta =ifelse(temp>OR8,b,0.00001)
  mup=1/DD
  egglay=ifelse(temp>OR8,228*.5/DD,0)

  #ODE system
  dH = stock - catch*H - alpha*AP - muh*H
  dAP= beta*H*W - AP*(muh + mup + catch + alpha) - alpha*k*(AP^2)/H
  dW = hatch*EG - muw*W - beta*H*W + delta*(muh*AP + alpha*AP
                                            + alpha*k*(AP^2)/H)
```

```
  dEG= egglay*AP - hatch*EG - mue*EG
  dSH=stock
  dCH=catch*H
  dCP=catch*AP
  dNATH=muh*H
  dPINH=alpha*AP

  list(c(dH,dAP,dW,dEG,dSH,dCH,dCP,dNATH,dPINH)) ### MUST BE IN CORRECT ORDER!!!
}

###Function to minimise
func3=function(par){
  sol=lsoda(base_inits,time,ARGY3,c(par[1],8,1,0,par[2],0.0275,12,3,0.741))
  sols=sol[time>tail(time,1)-366,]
  PH=sols[floor(365/24+(365/12)*0:11),3]/sols[floor(365/24+(365/12)*0:11),2]
  CH=sols[x,7]-sols[x-365/12,7]
  chisqp=sum(((bushy3$ABUN-PH)^2)/PH)/sum(PH)
  chisqc2=sum(((bushy3$CAT-CH)^2)/CH)/sum(CH)
  chisum=chisqp+chisqc2
  return(chisum)
}
beta1=5
alpha1=0.001
beta1=7.12
alpha1=0.0015
c1=0.0275

###No seasonality vs sin
sol=lsoda(base_inits,time,ARGY3,c(alpha1,0,1,1,beta1,c1,15,2,0.741,1,0))
soln=lsoda(base_inits,time,ARGY3,c(alpha1,0,1,1,beta1,c1,15,2,0.741,0,0))
sols=sol[time>tail(time,1)-366,]
solns=soln[time>tail(time,1)-366,]
PH=sols[floor(365/24+(365/12)*0:11),3]/sols[floor(365/24+(365/12)*0:11),2]
PHn=solns[floor(365/24+(365/12)*0:11),3]/solns[floor(365/24+(365/12)*0:11),2]
CH=sols[x,7]-sols[x-365/12,7]
CHn=solns[x,7]-solns[x-365/12,7]

sol=data.frame(sol)
soln=data.frame(soln)
colnames(sol)=colnames(soln)=c("t","H","P","W","E","SH","CH","CP","NATH","PINH")
theme_set(theme_bw())
m <- ggplot(sol, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(sol[1,1],sol[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = ’With no seasonality’) + xlim(min(c(sol[,2],soln[,2])),max(c(sol[,2],soln
      [,2]))) + ylim(0,max(c(sol[,3],soln[,3])))
pdf("C:/Users/nmo2/Dropbox/Thesis/2013–06–29–thesis/images/c4–0–par.pdf")
print(m)
dev.off()
m1 <- ggplot(soln, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(soln[1,1],soln[tail(time,1),1]),
                     low="grey", high="black") +
  labs(title = ’With seasonal egg–laying rates’) + xlim(min(c(sol[,2],soln[,2])),max(c(
      sol[,2],soln[,2]))) +ylim(0,max(c(sol[,3],soln[,3])))
pdf("C:/Users/nmo2/Dropbox/Thesis/2013–06–29–thesis/images/c4–1–par.pdf")
print(m1)
dev.off()

pdf("C:/Users/nmo2/Dropbox/Thesis/2013–06–29–thesis/images/c4–0–ts.pdf")
plot(sol[,1],sol[,2],type=’l’,ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol[,2:5]))
    ,xlab=’t’,ylab=’Density’)
lines(sol[,1],sol[,3],type=’l’,lty=2)
```

```
lines(sol[,1],sol[,4],type='l',lty=3)
lines(sol[,1],sol[,5],type='l',lty=4)
legend(3000,max(soln[,2:5]),c('H','P','W','E'),lty=1:4)
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-1-ts.pdf")
plot(soln[,1],soln[,2],type='l',ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol
     [,2:5])),xlab='t',ylab='Density')
lines(soln[,1],soln[,3],type='l',lty=2)
lines(soln[,1],soln[,4],type='l',lty=3)
lines(soln[,1],soln[,5],type='l',lty=4)
legend(3000,max(soln[,2:5]),c('H','P','W','E'),lty=1:4,bg='white')
dev.off()


##Overwintering
sol=lsoda(base_inits,time,ARGY3,c(alpha1,8,1,1,beta1,c1,15,2,0.741,0,0))
#soln=lsoda(base_inits,time,ARGY3,c(alpha1,0,1,1,beta1,c1,15,2,0.741,0,0))
sols=sol[time>tail(time,1)-366,]
#solns=soln[time>tail(time,1)-366,]
PH=sols[floor(365/24+(365/12)*0:11),3]/sols[floor(365/24+(365/12)*0:11),2]
#PHn=solns[floor(365/24+(365/12)*0:11),3]/solns[floor(365/24+(365/12)*0:11),2]
CH=sols[x,7]-sols[x-365/12,7]
#CHn=solns[x,7]-solns[x-365/12,7]

max(sols[,3]/sols[,2])

sol=data.frame(sol)
#soln=data.frame(soln)
colnames(sol)=colnames(soln)=c("t","H","P","W","E","SH","CH","CP","NATH","PINH")
theme_set(theme_bw())
m <- ggplot(sol, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(sol[1,1],sol[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = 'With no seasonality') + xlim(min(c(sol[,2],soln[,2])),max(c(sol[,2],soln
       [,2]))) + ylim(0,max(c(sol[,3],soln[,3])))
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-2-par.pdf")
print(m)
dev.off()
m1 <- ggplot(soln, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(soln[1,1],soln[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = 'With seasonal egg-laying rates') + xlim(min(c(sol[,2],soln[,2])),max(c(
       sol[,2],soln[,2]))) +ylim(0,max(c(sol[,3],soln[,3])))
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-21-par.pdf")
print(m1)
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-2-ts.pdf")
plot(sol[,1],sol[,2],type='l',ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol[,2:5]))
     ,xlab='t',ylab='Density')
lines(sol[,1],sol[,3],type='l',lty=2)
lines(sol[,1],sol[,4],type='l',lty=3)
lines(sol[,1],sol[,5],type='l',lty=4)
legend(3000,max(soln[,2:5],sol[,2:5]),c('H','P','W','E'),lty=1:4,bg='white')
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-21-ts.pdf")
plot(soln[,1],soln[,2],type='l',ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol
     [,2:5])),xlab='t',ylab='Density')
lines(soln[,1],soln[,3],type='l',lty=2)
lines(soln[,1],soln[,4],type='l',lty=3)
```

```
lines(soln[,1],soln[,5],type='l',lty=4)
legend(3000,max(soln[,2:5],sol[,2:5]),c('H','P','W','E'),lty=1:4,bg='white')
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-2-ts-s.pdf")
plot(0:365,sols[,2],type='l',ylim=c(min(sols[,2:5]),.1*max(sols[,2:5])),xlab='t',
     ylab='Density',xaxt='n')
lines(0:365,sols[,3],type='l',lty=2)
lines(0:365,sols[,4],type='l',lty=3)
lines(0:365,sols[,5]/10,type='l',lty=4)
axis(1,at=seq(365/24,365,by=365/12),labels=month.abb)
legend(3,max(.1*sols[,2:5]),c('H','P','W','E/10'),lty=1:4,bg='white')
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-2-ts-s-pb.pdf")
plot(0:365,sols[,3]/sols[,2],type='l',#ylim=c(min(sols[,2:5]),max(sols[,2:5])),
     xlab='t',ylab='Parasite Burden',xaxt='n')
axis(1,at=seq(365/24,365,by=365/12),labels=month.abb)
dev.off()


##Overwintering WITH VARIABLE STOCKING DATA
soln=lsoda(base_inits,time,ARGY3,c(alpha1,8,1,0,beta1,c1,15,2,0.741,0,0))
solns=soln[time>tail(time,1)-366,]
PHn=solns[floor(365/24+(365/12)*0:11),3]/solns[floor(365/24+(365/12)*0:11),2]
CHn=solns[x,7]-solns[x-365/12,7]

sol=data.frame(sol)
soln=data.frame(soln)
colnames(sol)=colnames(soln)=c("t","H","P","W","E","SH","CH","CP","NATH","PINH")
theme_set(theme_bw())
m <- ggplot(sol, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(sol[1,1],sol[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = 'With no seasonality') + xlim(min(c(sol[,2],soln[,2])),max(c(sol[,2],soln
      [,2]))) + ylim(0,max(c(sol[,3],soln[,3])))
#pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-2-par.pdf")
print(m)
dev.off()
m1 <- ggplot(soln, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(soln[1,1],soln[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = 'With seasonal egg-laying rates') + xlim(min(c(sol[,2],soln[,2])),max(c(
      sol[,2],soln[,2]))) +ylim(0,max(c(sol[,3],soln[,3])))
#pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-21-par.pdf")
print(m1)
dev.off()

#pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-2-ts.pdf")
plot(sol[,1],sol[,2],type='l',ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol[,2:5]))
     ,xlab='t',ylab='Density')
lines(sol[,1],sol[,3],type='l',lty=2)
lines(sol[,1],sol[,4],type='l',lty=3)
lines(sol[,1],sol[,5],type='l',lty=4)
legend(3000,max(soln[,2:5],sol[,2:5]),c('H','P','W','E'),lty=1:4,bg='white')
dev.off()

#pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c4-21-ts.pdf")
plot(soln[,1],soln[,2],type='l',ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol
     [,2:5])),xlab='t',ylab='Density')
lines(soln[,1],soln[,3],type='l',lty=2)
lines(soln[,1],soln[,4],type='l',lty=3)
```

```
lines(soln[,1],soln[,5],type=’l’,lty=4)
legend(3000,max(soln[,2:5],sol[,2:5]),c(’H’,’P’,’W’,’E’),lty=1:4,bg=’white’)
dev.off()
plot(solns[,3]/solns[,2],xaxt=’n’)
axis(1,seq(365/24,365,by=365/12),labels=1:12)


###Run with previous and current set of parameters
#sol=lsoda(base_inits,time,ARGY3,c(0.001,8,1,0,2,0.0275,1,2,0.741,1))
sol=lsoda(base_inits,time,ARGY3,c(alpha1,0,1,1,beta1,c1,15,2,0.741,1))
soln=lsoda(base_inits,time,ARGY3,c(alpha1,0,1,0,beta1,c1,15,2,0.741,1))
sols=sol[time>tail(time,1)-366,]
solns=soln[time>tail(time,1)-366,]
PH=sols[floor(365/24+(365/12)∗0:11),3]/sols[floor(365/24+(365/12)∗0:11),2]
PHn=solns[floor(365/24+(365/12)∗0:11),3]/solns[floor(365/24+(365/12)∗0:11),2]
CH=sols[x,7]-sols[x-365/12,7]
CHn=solns[x,7]-solns[x-365/12,7]
###Plot Old, Fitted and Data
par(mfrow=c(1,1),mar=c(4,4,1,1))
pdf("C:/Users/nm02/Dropbox/Thesis/2013−06−29−thesis/images/c4−prog1−PH.pdf")
plot(bushy3$ABUN,ylim=c(0,max(0,bushy3$ABUN,PH,PHn)),xlim=c(1,12),xaxt=’n’,ylab=’Mean
     parasite burden’,xlab=’Month’,pch=19)
axis(1,at=1:12,labels=month.abb)
lines(PH,col=’grey’)
dev.off()
pdf("C:/Users/nm02/Dropbox/Thesis/2013−06−29−thesis/images/c4−prog1−CH.pdf")
plot(bushy3$CAT,ylim=c(0,max(0,bushy3$CAT,CH,CHn)),pch=19,xaxt=’n’,xlab=’Month’,ylab=’
     Fish caught’)
axis(1,at=1:12,labels=month.abb)
lines(CH,col=’grey’)
#lines(CHn)
#legend(0,max(0,bushy3$CAT,CH,CHn),c(’Before’,’After’),lty=1,col=c(’grey’,’black’))
dev.off()
plot(soln[,3]/soln[,2])

sol=data.frame(sol)
soln=data.frame(soln)

colnames(sol)=colnames(soln)=c("t","H","P","W","E","SH","CH","CP","NATH","PINH")

### Parametric Plots
#library(ggplot2)
sol=data.frame(sol)
soln=data.frame(soln)

colnames(sol)=colnames(soln)=c("t","H","P","W","E","SH","CH","CP","NATH","PINH")
theme_set(theme_bw())
pdf("C:/Users/nm02/Dropbox/Thesis/2013−06−29−thesis/images/c4−progparcon.pdf")
m <- ggplot(sol, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(sol[1,1],sol[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = ’With constant stocking rate’) + xlim(0,max(c(sol[,2],soln[,2]))) + ylim
      (0,max(c(sol[,3],soln[,3])))
print(m)
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013−06−29−thesis/images/c4−progparvar.pdf")
m1 <- ggplot(soln, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(soln[1,1],soln[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = ’With variable stocking rate’) + xlim(0,max(c(sol[,2],soln[,2]))) +ylim(0,
      max(c(sol[,3],soln[,3])))
```

```
print(m1)
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–prog1conts.pdf")
plot(sol[,1],sol[,2],type=’l’,ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol[,2:5]))
     ,xlab=’t’,ylab=’Density’)
lines(sol[,1],sol[,3],type=’l’,lty=2)
lines(sol[,1],sol[,4],type=’l’,lty=3)
lines(sol[,1],sol[,5],type=’l’,lty=4)
legend(3000,max(soln[,2:5]),c(’H’,’P’,’W’,’E’),lty=1:4)
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–prog1varts.pdf")
plot(soln[,1],soln[,2],type=’l’,ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol
     [,2:5])),xlab=’t’,ylab=’Density’)
lines(soln[,1],soln[,3],type=’l’,lty=2)
lines(soln[,1],soln[,4],type=’l’,lty=3)
lines(soln[,1],soln[,5],type=’l’,lty=4)
legend(3000,max(soln[,2:5]),c(’H’,’P’,’W’,’E’),lty=1:4)
dev.off()

###SIN CURVE ADDED - NO OVERWINTERING
###Run with previous and current set of parameters
sol=lsoda(base_inits,time,ARGY3,c(alpha1,0,1,0,beta1,0.0275,15,2,0.741,1))
soln=lsoda(base_inits,time,ARGY3,c(alpha1,0,1,0,beta1,c1,15,2,0.741,0))
#soln=lsoda(base_inits,time,ARGY3,c(OPT$par[1],8,1,0,OPT$par[2],0.0275,1,2,0.741,0))
sols=sol[time>tail(time,1)-366,]
solns=soln[time>tail(time,1)-366,]
PH=sols[floor(365/24+(365/12)*0:11),3]/sols[floor(365/24+(365/12)*0:11),2]
PHn=solns[floor(365/24+(365/12)*0:11),3]/solns[floor(365/24+(365/12)*0:11),2]
CH=sols[x,7]-sols[x-365/12,7]
CHn=solns[x,7]-solns[x-365/12,7]
###Plot Old, Fitted and Data
par(mfrow=c(1,1),mar=c(4,4,1,1))
pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–prog2–PH.pdf")
plot(bushy3$ABUN,ylim=c(0,max(0,bushy3$ABUN,PH,PHn)),xlim=c(1,12),xaxt=’n’,ylab=’Mean
     parasite burden’,xlab=’Month’,pch=19)
axis(1,at=1:12,labels=month.abb)
lines(PH,col=’grey’)
dev.off()
pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–prog2–CH.pdf")
plot(bushy3$CAT,ylim=c(0,max(0,bushy3$CAT,CH,CHn)),pch=19,xaxt=’n’,xlab=’Month’,ylab=’
     Fish caught’)
axis(1,at=1:12,labels=month.abb)
lines(CH,col=’grey’)
#lines(CHn)
#legend(0,max(0,bushy3$CAT,CH,CHn),c(’Before’,’After’),lty=1,col=c(’grey’,’black’))
dev.off()
sol=data.frame(sol)
soln=data.frame(soln)

colnames(sol)=colnames(soln)=c("t","H","P","W","E","SH","CH","CP","NATH","PINH")
theme_set(theme_bw())
m <- ggplot(sol, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(sol[1,1],sol[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = ’With no seasonality’)+xlim(0,max(c(sol[,2],soln[,2]))) +ylim(0,max(c(sol
       [,3],soln[,3])))
pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–progparvar–nosin.pdf")
print(m)
dev.off()
pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–progparvar–sin.pdf")
```

```
m1 <- ggplot(soln, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(soln[1,1],soln[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = ’With temperature−dependent egg−laying’)+xlim(0,max(c(sol[,2],soln[,2])))
      +ylim(0,max(c(sol[,3],soln[,3])))
print(m1)
dev.off()


pdf("C:/Users/nm02/Dropbox/Thesis/2013−06−29−thesis/images/c4−prog2conts.pdf")
plot(sol[,1],sol[,2],type=’l’,ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol[,2:5]))
    ,xlab=’t’,ylab=’Density’)
lines(sol[,1],sol[,3],type=’l’,lty=2)
lines(sol[,1],sol[,4],type=’l’,lty=3)
lines(sol[,1],sol[,5],type=’l’,lty=4)
legend(3000,max(soln[,2:5]),c(’H’,’P’,’W’,’E’),lty=1:4)
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013−06−29−thesis/images/c4−prog2varts.pdf")
plot(soln[,1],soln[,2],type=’l’,ylim=c(min(soln[,2:5],sol[,2:5]),max(soln[,2:5],sol
    [,2:5])),xlab=’t’,ylab=’Density’)
lines(soln[,1],soln[,3],type=’l’,lty=2)
lines(soln[,1],soln[,4],type=’l’,lty=3)
lines(soln[,1],soln[,5],type=’l’,lty=4)
legend(3000,max(soln[,2:5]),c(’H’,’P’,’W’,’E’),lty=1:4)
dev.off()

###SIN CURVE ADDED - NO OVERWINTERING
###Run with previous and current set of parameters
#sol=lsoda(base_inits,time,ARGY3,c(alpha1,0,1,0,beta1,0.0275,15,2,0.741,1))
soln=lsoda(base_inits,time,ARGY3,c(alpha1,0,1,0,beta1,c1,15,2,0.741,0))
solns=soln[time>tail(time,1)-366,]
soln=data.frame(soln)

colnames(soln)=c("t","H","P","W","E","SH","CH","CP","NATH","PINH")
theme_set(theme_bw())
pdf("C:/Users/nm02/Dropbox/Thesis/2013−06−29−thesis/images/c4−sin−const−par.pdf")
m1 <- ggplot(soln, aes(x=H, y=P, color=t))+ geom_point() +
  scale_colour_gradient(limits=c(soln[1,1],soln[tail(time,1),1]),
                        low="grey", high="black") +
  labs(title = ’With temperature−dependent egg−laying’)+xlim(min(soln[,2]),max(soln[,2]))
       +ylim(0,max(c(sol[,3],soln[,3])))
print(m1)
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013−06−29−thesis/images/c4−sin−const−ts.pdf")
plot(soln[,1],soln[,2],type=’l’,ylim=c(min(soln[,2:5]),max(soln[,2:5])),xlab=’t’,ylab=’
    Density’)
lines(soln[,1],soln[,3],type=’l’,lty=2)
lines(soln[,1],soln[,4],type=’l’,lty=3)
lines(soln[,1],soln[,5],type=’l’,lty=4)
legend(3000,max(soln[,2:5]),c(’H’,’P’,’W’,’E’),lty=1:4)
dev.off()


###SIN CURVE ADDED - WITH OVERWINTERING
###Run with previous and current set of parameters
#sol=lsoda(base_inits,time,ARGY3,c(0.001,8,1,0,2,0.0275,1,2,0.741,1))
sol=lsoda(base_inits,time,ARGY3,c(alpha1,8,1,0,beta1,c1,15,2,0.741,0))
#soln=lsoda(base_inits,time,ARGY3,c(OPT$par[1],8,1,0,OPT$par[2],0.0275,1,2,0.741,0))
sols=sol[time>tail(time,1)-366,]
solns=soln[time>tail(time,1)-366,]
```

```
PH=sols[floor(365/24+(365/12)*0:11),3]/sols[floor(365/24+(365/12)*0:11),2]
PHn=solns[floor(365/24+(365/12)*0:11),3]/solns[floor(365/24+(365/12)*0:11),2]
CH=sols[x,7]-sols[x-365/12,7]
CHn=solns[x,7]-solns[x-365/12,7]
###Plot Old, Fitted and Data
par(mfrow=c(1,1),mar=c(4,4,1,1))
pdf("C:/Users/nmo2/Dropbox/Thesis/2013-06-29-thesis/images/c4-prog3-PH.pdf")
plot(bushy3$ABUN,ylim=c(0,max(0,bushy3$ABUN,PH,PHn)),xlim=c(1,12),xaxt='n',ylab='Mean
     parasite burden',xlab='Month',pch=19)
axis(1,at=1:12,labels=month.abb)
lines(PH,col='grey')
dev.off()
pdf("C:/Users/nmo2/Dropbox/Thesis/2013-06-29-thesis/images/c4-prog3-CH.pdf")
plot(bushy3$CAT,ylim=c(0,max(0,bushy3$CAT,CH,CHn)),pch=19,xaxt='n',xlab='Month',ylab='
     Fish caught')
axis(1,at=1:12,labels=month.abb)
lines(CH,col='grey')
#lines(CHn)
#legend(0,max(0,bushy3$CAT,CH,CHn),c('Before','After'),lty=1,col=c('grey','black'))
dev.off()


###SIN CURVE ADDED - WITH OVERWINTERING and fitted parameters
beta1=7.12
alpha1=0.0015
c1=0.0275
###Run with previous and current set of parameters
#sol=lsoda(base_inits,time,ARGY3,c(0.001,8,1,0,2,0.0275,1,2,0.741,1))
sol=lsoda(base_inits,time,ARGY3,c(alpha1,8,1,0,beta1,c1,12,3,0.741,1))
soln=lsoda(base_inits,time,ARGY3,c(OPT$par[1],8,1,0,OPT$par[2],0.0275,1,2,0.741,0))
sols=sol[time>tail(time,1)-366,]
solns=soln[time>tail(time,1)-366,]
PH=sols[floor(365/24+(365/12)*0:11),3]/sols[floor(365/24+(365/12)*0:11),2]
PHn=solns[floor(365/24+(365/12)*0:11),3]/solns[floor(365/24+(365/12)*0:11),2]
CH=sols[x,7]-sols[x-365/12,7]
CHn=solns[x,7]-solns[x-365/12,7]
###Plot Old, Fitted and Data
par(mfrow=c(1,1),mar=c(4,4,1,1))
pdf("C:/Users/nmo2/Dropbox/Thesis/2013-06-29-thesis/images/c4-prog4-PH.pdf")
plot(bushy3$ABUN,ylim=c(0,max(0,bushy3$ABUN,PH,PHn)),xlim=c(1,12),xaxt='n',ylab='Mean
     parasite burden',xlab='Month',pch=19)
axis(1,at=1:12,labels=month.abb)
lines(PH,col='grey')
dev.off()

pdf("C:/Users/nmo2/Dropbox/Thesis/2013-06-29-thesis/images/c4-prog4-CH.pdf")
plot(bushy3$CAT,ylim=c(0,max(0,bushy3$CAT,CH,CHn)),pch=19,xaxt='n',xlab='Month',ylab='
     Fish caught')
axis(1,at=1:12,labels=month.abb)
lines(CH,col='grey')
#lines(CHn)
#legend(0,max(0,bushy3$CAT,CH,CHn),c('Before','After'),lty=1,col=c('grey','black'))
dev.off()


###SIN CURVE ADDED - WITH OVERWINTERING and fitted parameters - including rho and n
beta1=7.12
alpha1=0.0015
c1=0.0275
###Run with previous and current set of parameters
#sol=lsoda(base_inits,time,ARGY3,c(0.001,8,1,0,2,0.0275,1,2,0.741,1))
sol=lsoda(base_inits,time,ARGY3,c(alpha1,8,1,0,beta1,c1,15,2,0.741,1))
```

```
soln=lsoda(base_inits,time,ARGY3,c(OPT$par[1],8,1,0,OPT$par[2],0.0275,1,2,0.741,0))
sols=sol[time>tail(time,1)-366,]
solns=soln[time>tail(time,1)-366,]
PH=sols[floor(365/24+(365/12)*0:11),3]/sols[floor(365/24+(365/12)*0:11),2]
PHn=solns[floor(365/24+(365/12)*0:11),3]/solns[floor(365/24+(365/12)*0:11),2]
CH=sols[x,7]-sols[x-365/12,7]
CHn=solns[x,7]-solns[x-365/12,7]
###Plot Old, Fitted and Data
par(mfrow=c(1,1),mar=c(4,4,1,1))

pdf("C:/Users/nmo2/Dropbox/Thesis/2013-06-29-thesis/images/c4-prog5-PH.pdf")
plot(bushy3$ABUN,ylim=c(0,max(0,bushy3$ABUN,PH,PHn)),xlim=c(1,12),xaxt='n',ylab='Mean
    parasite burden',xlab='Month',pch=19)
axis(1,at=1:12,labels=month.abb)
lines(PH,col='grey')
dev.off()

pdf("C:/Users/nmo2/Dropbox/Thesis/2013-06-29-thesis/images/c4-prog5-CH.pdf")
plot(bushy3$CAT,ylim=c(0,max(0,bushy3$CAT,CH,CHn)),pch=19,xaxt='n',xlab='Month',ylab='
    Fish caught')
axis(1,at=1:12,labels=month.abb)
lines(CH,col='grey')
#lines(CHn)
#legend(0,max(0,bushy3$CAT,CH,CHn),c('Before','After'),lty=1,col=c('grey','black'))
dev.off()

###SIN CURVE ADDED - WITH OVERWINTERING and fitted parameters
###- including rho and n - SECOND OPTIM RUN WITH NEW RHO AND N
#beta1=7.12
##Run with previous and current set of parameters
sol=lsoda(base_inits,time,ARGY3,c(0.001,8,1,0,2,0.0275,1,2,0.741,1))
sol=lsoda(base_inits,time,ARGY3,c(alpha1,8,1,0,beta1,c1,15,2,0.741,1))
soln=lsoda(base_inits,time,ARGY3,c(alpha1,8,1,0,beta1,c1,15,1.9,0.741,0))
sols=sol[time>tail(time,1)-366,]
solns=soln[time>tail(time,1)-366,]
PH=sols[floor(365/24+(365/12)*0:11),3]/sols[floor(365/24+(365/12)*0:11),2]
PHn=solns[floor(365/24+(365/12)*0:11),3]/solns[floor(365/24+(365/12)*0:11),2]
CH=sols[x,7]-sols[x-365/12,7]
CHn=solns[x,7]-solns[x-365/12,7]
##Plot Old, Fitted and Data
par(mfrow=c(1,1),mar=c(4,4,1,1))
pdf("C:/Users/nmo2/Dropbox/Thesis/2013-06-29-thesis/images/c4-prog6-PH.pdf")
plot(bushy3$ABUN,ylim=c(0,max(0,bushy3$ABUN,PH,PHn)),xlim=c(1,12),xaxt='n',ylab='Mean
    parasite burden',xlab='Month',pch=19)
axis(1,at=1:12,labels=month.abb)
lines(PH,col='grey')
dev.off()

###Final Best Fit with error bars

#source(countdat-import.R,chdir=T)
pdf("C:/Users/nmo2/Dropbox/Thesis/2013-06-29-thesis/images/c4-prog6-PH.pdf")
source("C:/Users/nmo2/Desktop/Appendices/countdat-import.R")
lines(PH)
dev.off()
#lines(PHn)



alpha1=0.0015
beta1=7.12

##Run with previous and current set of parameters
```

```
sol=lsoda(base_inits,time,ARGY3,c(alpha1,8,1,1,beta1,0.0275,15,2,0.741,0))
soln=lsoda(base_inits,time,ARGY3,c(alpha1,8,1,0,beta1,0.0275,15,2,0.741,0))
sols=sol[time>tail(time,1)-366,]
solns=soln[time>tail(time,1)-366,]
solns[,1]=sols[,1]=0:365
PH=sols[floor(365/24+(365/12)*0:11),3]/sols[floor(365/24+(365/12)*0:11),2]
PHn=solns[floor(365/24+(365/12)*0:11),3]/solns[floor(365/24+(365/12)*0:11),2]
CH=sols[x,7]-sols[x-365/12,7]
CHn=solns[x,7]-solns[x-365/12,7]
##Plot Old, Fitted and Data

pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–comp1.pdf")
plot(sols[,1],sols[,2],type='l',ylim=c(min(.1*soln[,2:5],.1*sol[,2:5]),max(.1*soln
     [,2:5],.1*sol[,2:5])),xlab='t',ylab='Density')
lines(sols[,1],sols[,3],type='l',lty=2)
lines(sols[,1],sols[,4],type='l',lty=3)
lines(sols[,1],sols[,5]/10,type='l',lty=4)
legend(0,.3,c('H','P','W','E/10'),lty=1:4,bg='white')
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–comp2.pdf")
plot(solns[,1],solns[,2],type='l',ylim=c(.1*min(soln[,2:5],sol[,2:5]),.1*max(soln[,2:5],
     sol[,2:5])),xlab='t',ylab='Density')
lines(solns[,1],solns[,3],type='l',lty=2)
lines(solns[,1],solns[,4],type='l',lty=3)
lines(solns[,1],solns[,5]/10,type='l',lty=4)
legend(0,.3,c('H','P','W','E/10'),lty=1:4,bg='white')
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c4–comp–h.pdf")
plot(solns[,1],solns[,2],type='l',xlab='t',ylab='Density')
lines(sols[,1],sols[,2],type='l',xlab='t',ylab='Density',lty=2)
dev.off()
```

B.3 CHAPTER FIVE

The following code was used to generate the results and plots from chapter five: model-c5.R contains the model, run-offsets.R runs the model for all the possible offsets for a given stocking frequency, and the script runs this repeatedly for all stocking frequencies. File references will need updating, but aside from that placing all three files within the same folder and running script.R will produce all the plots in chapter five (without a rod limit). Apart from the summary plots, for which c5-summary.R was used.

script.R

```
psis=c(1, 365/52, 365/26, 365/12, 365/4, 365/2, 365)
names=c("Continuous", "Weekly", "Fortnightly", "Monthly", "Quarterly", "Biannual", "
     Annual")
path="R/ARGY/c5–Offsets/"
source("R/ARGY/model–c5.R")
```

```
for(i in 1:length(psis)){
  psi=psis[i]
name=names[i]
#set file names for saving plots
file1=paste(path,names[i],"–summary.csv",sep="")
file2=paste(path,names[i],"–all.csv",sep="")
pdfname1=paste(path,names[i],"1.pdf",sep="")
pdfname2=paste(path,names[i],"2.pdf",sep="")
source("R/ARGY/run–offsets.R")
}
```

run-offsets.R

```
### Parameters & Initial Conditions
base_inits=c(2.715423e-03, 2.404820e-02, 1.920324e-04, 8.593183e-01,0,0,0,0,0)
pops=1+length(base_inits)
int=1
time<-seq(int,3650+int,by=int)
tmax=tail(time,1)
soltab=NULL

### Assigns offsets of zero through to psi
base_ptab=NULL
bap=c(0.0015, 8,1,1,7.12, 0.0275, 15,2,0.741)
for(i in 0:psi)  base_ptab=cbind(base_ptab,c(bap,psi,i))

### Mortalities, capture indices
stocked<-seq(6,psi*pops,by=pops)
caught<-seq(7,psi*pops,by=pops)
caughtp<-seq(8,psi*pops,by=pops)
natm<-seq(9,psi*pops,by=pops)
pm<-seq(10,psi*pops,by=pops)

### Offsets range from 0 to psi-1
offs=seq(0,psi-1,by=1)

### Run simulations for different offsets
for( i in 1:psi+1){
  sol=lsoda(base_inits,time,ARGY,base_ptab[,i])
  soltab=cbind(soltab,sol)
}
SWeekly=soltab

#Net figures from last 365 days
stocks=cbind(offs,(soltab[time==tmax,stocked]-soltab[time==(tmax-365),stocked]))
caughts=cbind(offs,(soltab[time==tmax,caught]-soltab[time==(tmax-365),caught]))
caughtpar=cbind(offs,(soltab[time==tmax,caughtp]-soltab[time==(tmax-365),caughtp]))
natmort=cbind(offs,(soltab[time==tmax,natm]-soltab[time==(tmax-365),natm]))
morts=cbind(offs,(soltab[time==tmax,pm]-soltab[time==(tmax-365),pm]))

#Relative to number stocked
caughtsr=caughts[,2]/stocks[,2]
caughtparr=caughtpar[,2]/caughts[,2]
natmortr=natmort[,2]/stocks[,2]
mortsr=morts[,2]/stocks[,2]

pdf(pdfname1)
par(mfrow=c(3,1),mar=c(4,4,1,1))
plot(caughts,ylab="Captures",xlab='',type='l')
plot(morts,ylab="P. Induced Mortalities",xlab='',type='l')
plot(caughtparr,ylab='P. Burden',xlab='Offset',type='l')
```

```
dev.off()

pdf(pdfname2)
par(mfrow=c(1,1),mar=c(4,4,4,4))
plot(offs,caughtsr,ylim=c(0,1),type=’l’,xlab=’Offset’,ylab=’Proportion’,
     main=name,lwd=2)
lines(offs,natmortr,lty=2,lwd=2)
lines(offs,mortsr,lty=3,lwd=2)
legend(0,0.6,c(’Caught’,’Natural Host Morts’,’Par. Induced Morts’),lty=1:3)
dev.off()

### Tidy and save results
results=cbind(rep(psi,psi),offs,caughtsr,mortsr,natmortr,caughtparr)
smin=results[which.min(results[,6]),2]
smax=results[which.max(results[,6]),2]
colnames(results)=c("psi","offset","caught","pmort","natmort","caughtparsperhost")

### Write summary of results to spreadsheet
write.csv(results,file=file1)

### Write last year to spreadsheet
soltab2=soltab[time>(tmax-366),]
write.csv(soltab2,file=file2)

### best and worst parasite burden plots
smin=results[which.min(results[,6]),2]
smax=results[which.max(results[,6]),2]
solmin=soltab2[,10*smin+1:10]
solmax=soltab2[,10*smax+1:10]

pdf(pdfname3)
par(mfrow=c(1,1),mar=c(4,4,1,1))
plot(solmin[,2],type=’l’,xlab=’t’,ylab=’Density’,main=paste(’Offset=’,smin,sep=’’),ylim=c
    (0,max(solmin[,2:5])))
lines(solmin[,3],lty=2)
lines(solmin[,4],lty=3)
lines(solmin[,5],lty=4)
legend(0,max(solmin[,2:5]),c(’H’,’P’,’W’,’E’),lty=1:4)
dev.off()

pdf(pdfname4)
par(mfrow=c(1,1),mar=c(4,4,1,1))
plot(solmax[,2],type=’l’,xlab=’t’,ylab=’Density’,main=paste(’Offset=’,smax,sep=’’),ylim=c
    (0,max(solmax[,2:5])))
lines(solmax[,3],lty=2)
lines(solmax[,4],lty=3)
lines(solmax[,5],lty=4)
legend(0,max(solmax[,2:5]),c(’H’,’P’,’W’,’E’),lty=1:4)
dev.off()

smon=soltab
```

model-c5.R

```
library(deSolve)

ARGY=function(t,inits,p)
{
  temp=12+8*sin((t-128)*2*pi/(365))
  DD=3900/(((.434*temp)+.361)^2)
```

```
  #Define Variables
  H=inits[1]    #Rainbow Trout
  AP=inits[2]   #Attached A. foliaceus
  W=inits[3]    #Free-living A. foliaceus
  EG=inits[4]   #A. foliaceus eggs
  SH=inits[5]   #Stocked Fish
  CH=inits[6]   #Caught Fish
  CP=inits[7]   #Caught Pars
  NATH=inits[8]#Nat. H Morts
  PINH=inits[9]#P. ind. H Morts

  c=p[6]              #capture rate or 1/residence time
  rho=p[7]            # parasite burden required to halve capture rate
  nn=p[8]             #capture reduction shape parameter
  psi=p[10]           #Stocking interval
  off=p[11]           #Stocking Offset
  muh=1/(2*365)       #Nat. host mortality
  muw=0.45            #Unattached mortality
  b=p[5]              #A. foliaceus attachment 0.0192-0.0576 #A. foliaceus attachment
  delta=1             #Proportion of pars that survive host death
  kk=p[9]
  k=(1+kk)/kk         #Parasite aggregation
  OR8=p[2]            #Cut-off temperature

  s=0.000127049
  stock=s*psi*floor((psi-floor((t-off)%%psi))/psi)#stocking function - much more
      efficient than if statements
  catch=c*(rho^nn)/(rho^nn+(AP/H)^nn)            #hill reduction in capture
  atop = -log(.76)/((25 + 240)/2)                #egg mortality in summer
  blow = -log(.66/.76)/(5*365/12)                #egg mortality in winter

  #Temperature dependent parameters
  hatch=ifelse(temp>OR8,0.027,0)
  alpha=p[1]
  mue  =ifelse(temp>OR8,atop,blow)
  beta =ifelse(temp>OR8,b,0.00001)
  mup=1/DD
  egglay=ifelse(temp>OR8,228*.5/DD,0)

  #ODE system
  dH = stock - catch*H - alpha*AP - muh*H
  dAP= beta*H*W - muh*AP-AP*( mup + catch + alpha) - alpha*k*(AP^2)/H
  dW = hatch*EG - muw*W - beta*H*W + delta*(muh*AP + alpha*AP
                                            + alpha*k*(AP^2)/H)
  dEG= egglay*AP - hatch*EG - mue*EG
  dSH=stock
  dCH=catch*H
  dCP=catch*AP
  dNATH=muh*H
  dPINH=alpha*AP

  list(c(dH,dAP,dW,dEG,dSH,dCH,dCP,dNATH,dPINH)) ### MUST BE IN CORRECT ORDER!!!
}
```

c5-summary.R

```
offres=data.frame(psis=c(1, 365/52,365/52, 365/26,365/26,
                  365/12,365/12, 365/4,365/4, 365/2,365/2, 365,365),
           psinames=c("1", "365/52","365/52", "365/26","365/26",
           "365/12","365/12", "365/4","365/4", "365/2","365/2", "365","365"),
           psirefs=c(1,2,2,3,3,4,4,5,5,6,6,7,7),
           offs=c(0,1,5,4,12,8,27,8,66,98,157,0,157),
```

```
           morts=c(31,30.3,30.4,29.9,30.1,28.7,28.2,23.5,14.6,12.1,0.8,0,0.74),
           caps=c(65,65.6,65.6,66,65.8,67.3,67.7,72.3,81.1,83.6,94.5,95.3,74.9),
           pbur=c(5.73,5.7,5.71,5.59,5.64,5.25,5.23,4.18,2.49,2.36,0.16,0,2.52))

offres.rl=data.frame(psis=c(1, 365/52,365/52, 365/26,365/26,
                         365/12,365/12, 365/4,365/4, 365/2,365/2, 365,365),
                  psinames=c("1", "365/52","365/52", "365/26","365/26",
                             "365/12","365/12", "365/4","365/4", "365/2","365/2",
                                 "365","365"),
                  psirefs=c(1,2,2,3,3,4,4,5,5,6,6,7,7),
                  offs=c(0,3,6,3,13,4,8,9,66,89,158,201,328),
                  morts=c(30.5,30.3,30.3,29.9,30.0,28.3,28.7,30.7,21.8,42.6,21.1,72.8,0),
                  caps=c(65,65.6,65.6,66,65.9,67.6,67.3,64.8,73.5,51.6,71.9,21.3,86.5),
                  pbur=c(5.73,5.69,5.7,5.59,5.63,5.19,5.24,5.19,3.39,7.33,2.2,8.85,0))
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c5-nrl-mor.pdf")
plot(offres$psirefs,offres$morts,xaxt=’n’,xlab=’psi’,ylab=’Mortalities (%)’,pch=19)
axis(1,at=1:7,labels=unique(offres$psinames))
dev.off()
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c5-nrl-cap.pdf")
plot(offres$psirefs,offsets.res$caps,xaxt=’n’,xlab=’psi’,ylab=’Captures (%)’,pch=19)
axis(1,at=1:7,labels=unique(offres$psinames))
dev.off()
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c5-nrl-pbur.pdf")
plot(offres$psirefs,offsets.res$pbur,xaxt=’n’,xlab=’psi’,ylab=’Mean parasite burden’,pch
    =19)
axis(1,at=1:7,labels=unique(offres$psinames))
dev.off()
View(offres)

pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c5-rl-mor.pdf")
plot(offres$psirefs,offres.rl$morts,xaxt=’n’,xlab=’psi’,ylab=’Mortalities (%)’,pch=19)
axis(1,at=1:7,labels=unique(offres$psinames))
dev.off()
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c5-rl-cap.pdf")
plot(offres$psirefs,offres.rl$caps,xaxt=’n’,xlab=’psi’,ylab=’Captures (%)’,pch=19)
axis(1,at=1:7,labels=unique(offres$psinames))
dev.off()
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c5-rl-pbur.pdf")
plot(offres$psirefs,offres.rl$pbur,xaxt=’n’,xlab=’psi’,ylab=’Mean parasite burden’,pch
    =19)
axis(1,at=1:7,labels=unique(offres$psinames))
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c5-com-mor.pdf")
plot(offres$psirefs,offres$morts,xaxt=’n’,xlab=’psi’,ylab=’Mortalities (%)’,pch=19,col=’
    grey’,ylim=c(0,100))
lines(offres$psirefs,offres.rl$morts,xaxt=’n’,pch=19,type=’p’)
axis(1,at=1:7,labels=unique(offres$psinames))
legend(1,100,c(’Rod limit’,’No rod limit’),pch=19,col=c(’Black’,’Grey’))
dev.off()
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c5-com-cap.pdf")
plot(offres$psirefs,offres$caps,xaxt=’n’,xlab=’psi’,ylab=’Captures (%)’,pch=19,col=’grey
    ’,ylim=c(0,100))
lines(offres$psirefs,offres.rl$caps,xaxt=’n’,pch=19,type=’p’)
axis(1,at=1:7,labels=unique(offres$psinames))
legend(1,100,c(’Rod limit’,’No rod limit’),pch=19,col=c(’Black’,’Grey’))
dev.off()
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c5-com-pbur.pdf")
plot(offres$psirefs,offres$pbur,xaxt=’n’,xlab=’psi’,ylab=’Mean parasite burden’,pch=19,
    col=’grey’,ylim=c(0,max(offres$pbur,offres.rl$pbur)))
lines(offres$psirefs,offres.rl$pbur,xaxt=’n’,pch=19,type=’p’)
axis(1,at=1:7,labels=unique(offres$psinames))
```

```
legend(1,9,c('Rod limit','No rod limit'),pch=19,col=c('Black','Grey'))
dev.off()
View(offres.rl)
```

B.4 CHAPTER SIX

B.4.1 *Slice models*

Similarly to chapter five, the Slice models were defined in c6-slicemodel.R and run using the scripts c6-slicescript.R and c6-slicescript-opt.R. Additional plots are were produced using the code in c6-efficacy.R and c6-nbinom.R.

c6-slicescript.R

```
## Parameters & Initial Conditions
base_inits=c(0.0025, 2.404820e-02, 1.920324e-04, 8.593183e-01,0,0,0,0,0,0)
pops=1+length(base_inits)
int=1
time<-seq(int,3650*2+int,by=int)
tmax=tail(time,1)
base_ptab=NULL
bap=c(0.0015, 8,1,1,7.12, 0.0275, 15,2,0.741)
psi=1
off=0
m=1/70
tau=0
source("C:/Users/nm02/Desktop/Appendices/c6-slicemodel.R")

####################################
#CONTINUOUS STOCKING
####################################

###No withdrawal
base_ptab=c(bap,psi,off,m,0)
sol=lsoda(base_inits,time,ARGY2,base_ptab)
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c6-slice-001.pdf")
par(mfrow=c(3,1),mar=c(4,4,1,1))
plot(sol[,2]+sol[,11],type='l',xlab='t',ylab='Density',ylim=c(0,max(sol[,2:5]/10)))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5]/10,lty=4)
legend(.85*tmax,max(sol[,2:5]/10),c('H','P','W','E/10'),lty=1:4)
#prop caught and mort and pbur
(sol[tail(time,1),7]-sol[tail(time,1)-365,7])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),10]-sol[tail(time,1)-365,10])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),8]-sol[tail(time,1)-365,8])/(sol[tail(time,1),7]-sol[tail(time,1)
     -365,7])

###375 days
```

```
base_ptab=c(bap,psi,off,m,375/12)
sol=lsoda(base_inits,time,ARGY2,base_ptab)
plot(sol[,2]+sol[,11],type=’l’,xlab=’t’,ylab=’Density’,ylim=c(0,max(sol[,2:5]/10)))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5]/10,lty=4)
legend(.85*tmax,max(sol[,2:5]/10),c(’H’,’P’,’W’,’E/10’),lty=1:4)
#prop caught and mort and pbur
(sol[tail(time,1),7]-sol[tail(time,1)-365,7])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),10]-sol[tail(time,1)-365,10])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),8]-sol[tail(time,1)-365,8])/(sol[tail(time,1),7]-sol[tail(time,1)
     -365,7])

###500 days
base_ptab=c(bap,psi,off,m,500/12)
sol=lsoda(base_inits,time,ARGY2,base_ptab)
plot(sol[,2]+sol[,11],type=’l’,xlab=’t’,ylab=’Density’,ylim=c(0,max(sol[,2:5]/10)))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5]/10,lty=4)
legend(.85*tmax,max(sol[,2:5]/10),c(’H’,’P’,’W’,’E/10’),lty=1:4)
dev.off()
#prop caught and mort and pbur
(sol[tail(time,1),7]-sol[tail(time,1)-365,7])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),10]-sol[tail(time,1)-365,10])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),8]-sol[tail(time,1)-365,8])/(sol[tail(time,1),7]-sol[tail(time,1)
     -365,7])


####################################
#WEEKLY STOCKING
####################################
###No withdrawal
base_ptab=c(bap,365/52,off,m,0)
sol=lsoda(base_inits,time,ARGY2,base_ptab)
pdf("C:/Users/nm02/Dropbox/Thesis/2013−06−29−thesis/images/c6−slice−007.pdf")
par(mfrow=c(3,1),mar=c(4,4,1,1))
plot(sol[,2]+sol[,11],type=’l’,xlab=’t’,ylab=’Density’,ylim=c(0,max(sol[,2:5]/10)))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5]/10,lty=4)
legend(.85*tmax,max(sol[,2:5]/10),c(’H’,’P’,’W’,’E/10’),lty=1:4)
#prop caught and mort and pbur
(sol[tail(time,1),7]-sol[tail(time,1)-365,7])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),10]-sol[tail(time,1)-365,10])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),8]-sol[tail(time,1)-365,8])/(sol[tail(time,1),7]-sol[tail(time,1)
     -365,7])

###375 days
base_ptab=c(bap,365/52,off,m,375/12)
sol=lsoda(base_inits,time,ARGY2,base_ptab)
plot(sol[,2]+sol[,11],type=’l’,xlab=’t’,ylab=’Density’,ylim=c(0,max(sol[,2:5]/10)))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5]/10,lty=4)
legend(.85*tmax,max(sol[,2:5]/10),c(’H’,’P’,’W’,’E/10’),lty=1:4)
```

```
#prop caught and mort and pbur
(sol[tail(time,1),7]-sol[tail(time,1)-365,7])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),10]-sol[tail(time,1)-365,10])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),8]-sol[tail(time,1)-365,8])/(sol[tail(time,1),7]-sol[tail(time,1)
     -365,7])

###500 days
base_ptab=c(bap,365/52,off,m,500/12)
sol=lsoda(base_inits,time,ARGY2,base_ptab)
plot(sol[,2]+sol[,11],type='l',xlab='t',ylab='Density',ylim=c(0,max(sol[,2:5]/10)))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5]/10,lty=4)
legend(.85*tmax,max(sol[,2:5]/10),c('H','P','W','E/10'),lty=1:4)
dev.off()
#prop caught and mort and pbur
(sol[tail(time,1),7]-sol[tail(time,1)-365,7])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),10]-sol[tail(time,1)-365,10])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),8]-sol[tail(time,1)-365,8])/(sol[tail(time,1),7]-sol[tail(time,1)
     -365,7])



####################################
#MonthLY STOCKING
####################################
###No withdrawal
off=0
base_ptab=c(bap,365/12,off,m,0)
sol=lsoda(base_inits,time,ARGY2,base_ptab)
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c6-slice-030.pdf")
par(mfrow=c(3,1),mar=c(4,4,1,1))
plot(sol[,2]+sol[,11],type='l',xlab='t',ylab='Density',ylim=c(0,max(sol[,2:5]/10)))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5]/10,lty=4)
legend(.85*tmax,max(sol[,2:5]/10),c('H','P','W','E/10'),lty=1:4)
#prop caught and mort and pbur
(sol[tail(time,1),7]-sol[tail(time,1)-365,7])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),10]-sol[tail(time,1)-365,10])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),8]-sol[tail(time,1)-365,8])/(sol[tail(time,1),7]-sol[tail(time,1)
     -365,7])

###375 days
base_ptab=c(bap,365/12,off,m,375/12)
sol=lsoda(base_inits,time,ARGY2,base_ptab)
plot(sol[,2]+sol[,11],type='l',xlab='t',ylab='Density',ylim=c(0,max(sol[,2:5]/10)))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5]/10,lty=4)
legend(.85*tmax,max(sol[,2:5]/10),c('H','P','W','E/10'),lty=1:4)
#prop caught and mort and pbur
(sol[tail(time,1),7]-sol[tail(time,1)-365,7])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
(sol[tail(time,1),10]-sol[tail(time,1)-365,10])/(sol[tail(time,1),6]-sol[tail(time,1)
     -365,6])
```

```
(sol[tail(time,1),8]-sol[tail(time,1)-365,8])/(sol[tail(time,1),7]-sol[tail(time,1)
    -365,7])

###500 days
base_ptab=c(bap,365/12,off,m,500/12)
sol=lsoda(base_inits,time,ARGY2,base_ptab)
plot(sol[,2]+sol[,11],type='l',xlab='t',ylab='Density',ylim=c(0,max(sol[,2:5]/10)))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5]/10,lty=4)
legend(.85*tmax,max(sol[,2:5]/10),c('H','P','W','E/10'),lty=1:4)
dev.off()
#prop caught and mort and pbur
(sol[tail(time,1),7]-sol[tail(time,1)-365,7])/(sol[tail(time,1),6]-sol[tail(time,1)
    -365,6])
(sol[tail(time,1),10]-sol[tail(time,1)-365,10])/(sol[tail(time,1),6]-sol[tail(time,1)
    -365,6])
(sol[tail(time,1),8]-sol[tail(time,1)-365,8])/(sol[tail(time,1),7]-sol[tail(time,1)
    -365,7])


####################################
#ANNUAL STOCKING
####################################
###############
#NO Rod Limit
###############
psi=365
time=1:(365*5)
###No withdrawal
soltab=NULL
for(i in 0:psi-1){
base_ptab=c(bap,psi,i,m,0)
sol=rk4(base_inits,time,ARGY2,base_ptab)
soltab=cbind(soltab,sol)}
par(mfrow=c(1,1))
SH=soltab[dim(soltab)[1],11*(0:(psi-1))+6]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+6]
CH=(soltab[dim(soltab)[1],11*(0:(psi-1))+7]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+7])/
    SH
PM=(soltab[dim(soltab)[1],11*(0:(psi-1))+10]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))
    +10])/SH
NM=(soltab[dim(soltab)[1],11*(0:(psi-1))+9]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+9])/
    SH
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c6-slice -365-0.pdf")
plot(0:(psi-1),CH,type='l',ylab='Proportion',xlab='Offset',ylim=c(0,1))
lines(0:(psi-1),PM,lty=2)
lines(0:(psi-1),NM,lty=3)
legend(365*.65,.6,c('Caught','Par. Ind. Morts', 'Nat. Morts'),lty=1:3)
dev.off()

###375 withdrawal
soltab=NULL
for(i in 0:psi-1){
  base_ptab=c(bap,psi,i,m,375/12)
  sol=rk4(base_inits,time,ARGY2,base_ptab)
  soltab=cbind(soltab,sol)}
par(mfrow=c(1,1))
SH=soltab[dim(soltab)[1],11*(0:(psi-1))+6]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+6]
CH=(soltab[dim(soltab)[1],11*(0:(psi-1))+7]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+7])/
    SH
PM=(soltab[dim(soltab)[1],11*(0:(psi-1))+10]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))
    +10])/SH
```

```
NM=(soltab[dim(soltab)[1],11*(0:(psi-1))+9]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+9])/
    SH
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c6-slice-365-375.pdf")
plot(0:(psi-1),CH,type='l',ylab='Proportion',xlab='Offset',ylim=c(0,1))
lines(0:(psi-1),PM,lty=2)
lines(0:(psi-1),NM,lty=3)
legend(365*.65,.6,c('Caught','Par. Ind. Morts', 'Nat. Morts'),lty=1:3)
dev.off()

###500 withdrawal
soltab=NULL
for(i in 0:psi-1){
  base_ptab=c(bap,psi,i,m,500/12)
  sol=rk4(base_inits,time,ARGY2,base_ptab)
  soltab=cbind(soltab,sol)}
par(mfrow=c(1,1))
SH=soltab[dim(soltab)[1],11*(0:(psi-1))+6]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+6]
CH=(soltab[dim(soltab)[1],11*(0:(psi-1))+7]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+7])/
    SH
PM=(soltab[dim(soltab)[1],11*(0:(psi-1))+10]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))
    +10])/SH
NM=(soltab[dim(soltab)[1],11*(0:(psi-1))+9]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+9])/
    SH
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c6-slice-365-500.pdf")
plot(0:(psi-1),CH,type='l',ylab='Proportion',xlab='Offset',ylim=c(0,1))
lines(0:(psi-1),PM,lty=2)
lines(0:(psi-1),NM,lty=3)
legend(365*.65,.6,c('Caught','Par. Ind. Morts', 'Nat. Morts'),lty=1:3)
dev.off()

###############
#WITH Rod Limit
###############
psi=365
time=1:(365*5)
###No withdrawal
soltab=NULL
for(i in 0:psi-1){
  base_ptab=c(bap,psi,i,m,0)
  sol=rk4(base_inits,time,ARGY3,base_ptab)
  soltab=cbind(soltab,sol)}
par(mfrow=c(1,1))
SH=soltab[dim(soltab)[1],11*(0:(psi-1))+6]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+6]
CH=(soltab[dim(soltab)[1],11*(0:(psi-1))+7]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+7])/
    SH
PM=(soltab[dim(soltab)[1],11*(0:(psi-1))+10]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))
    +10])/SH
NM=(soltab[dim(soltab)[1],11*(0:(psi-1))+9]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+9])/
    SH
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c6-slice-365-0-rl.pdf")
plot(0:(psi-1),CH,type='l',ylab='Proportion',xlab='Offset',ylim=c(0,1))
lines(0:(psi-1),PM,lty=2)
lines(0:(psi-1),NM,lty=3)
legend(365*.65,.6,c('Caught','Par. Ind. Morts', 'Nat. Morts'),lty=1:3)
dev.off()

###375 withdrawal
soltab=NULL
for(i in 0:psi-1){
  base_ptab=c(bap,psi,i,m,375/12)
  sol=rk4(base_inits,time,ARGY3,base_ptab)
  soltab=cbind(soltab,sol)}
```

```
par(mfrow=c(1,1))
SH=soltab[dim(soltab)[1],11*(0:(psi-1))+6]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+6]
CH=(soltab[dim(soltab)[1],11*(0:(psi-1))+7]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+7])/
    SH
PM=(soltab[dim(soltab)[1],11*(0:(psi-1))+10]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))
    +10])/SH
NM=(soltab[dim(soltab)[1],11*(0:(psi-1))+9]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+9])/
    SH
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c6-slice-365-375-r1.pdf")
plot(0:(psi-1),CH,type='l',ylab='Proportion',xlab='Offset',ylim=c(0,1))
lines(0:(psi-1),PM,lty=2)
lines(0:(psi-1),NM,lty=3)
legend(365*.65,.6,c('Caught','Par. Ind. Morts', 'Nat. Morts'),lty=1:3)
dev.off()

###500 withdrawal
soltab=NULL
for(i in 0:psi-1){
  base_ptab=c(bap,psi,i,m,500/12)
  sol=rk4(base_inits,time,ARGY3,base_ptab)
  soltab=cbind(soltab,sol)}
par(mfrow=c(1,1))
SH=soltab[dim(soltab)[1],11*(0:(psi-1))+6]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+6]
CH=(soltab[dim(soltab)[1],11*(0:(psi-1))+7]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+7])/
    SH
PM=(soltab[dim(soltab)[1],11*(0:(psi-1))+10]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))
    +10])/SH
NM=(soltab[dim(soltab)[1],11*(0:(psi-1))+9]-soltab[dim(soltab)[1]-365,11*(0:(psi-1))+9])/
    SH
pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c6-slice-365-500-r1.pdf")
plot(0:(psi-1),CH,type='l',ylab='Proportion',xlab='Offset',ylim=c(0,1))
lines(0:(psi-1),PM,lty=2)
lines(0:(psi-1),NM,lty=3)
legend(365*.65,.6,c('Caught','Par. Ind. Morts', 'Nat. Morts'),lty=1:3)
dev.off()

###plot one offset from annual run
off=4
sol=soltab[,off*11+1:11]
plot(sol[,2]+sol[,11],type='l',xlab='t',ylab='Density',ylim=c(0,max(sol[,2:5])))
lines(sol[,3],lty=2)
lines(sol[,4],lty=3)
lines(sol[,5],lty=4)
legend(.85*tmax,max(sol[,2:5]),c('H','P','W','E'),lty=1:4)
```

c6-slicemodel.R

```
library(deSolve)

#Set up the model
ARGY=function(t,inits,p)
{
  temp=12+8*sin((t-128)*2*pi/(365))
  DD=3900/(((.434*temp)+.361)^2)

  #Define Variables
  H=inits[1]   #Rainbow Trout
  AP=inits[2]  #Attached A. foliaceus
  W=inits[3]   #Free-living A. foliaceus
  EG=inits[4]  #A. foliaceus eggs
  SH=inits[5]  #Stocked Fish
```

```
  CH=inits[6]  #Caught Fish
  CP=inits[7]  #Caught Pars
  NATH=inits[8]#Nat. H Morts
  PINH=inits[9]#P. ind. H Morts
  Hn=inits[10]

  ar=p[3]
  c=p[6]
  rho=p[7]
  nn=p[8]
  psi=p[10]         #Stocking interval
  off=p[11]         #Stocking Offset
  m=p[12]
  tau=p[13]
  muh=1/(2*365)         #Nat. host mortality

  muw=0.45         #Unattached mortality
  b=p[5]         #A. foliaceus attachment 0.0192-0.0576 #A. foliaceus attachment
  delta=1          #Proportion of pars that survive host death
  #  rodlimit=20      #Maximum number of fish caught per day
  kk=p[9]
  k=(1+kk)/kk  #Parasite aggregation
  OR8=p[2]            #Cut-off temperature
  s=0.000127049
  stock=s*psi*floor((psi-floor((t-off)%%psi))/psi)
  catch=c*(rho^nn)/(rho^nn+(AP/H)^nn)
  atop = -log(.76)/((25 + 240)/2) #egg mortality in summer
  blow = -log(.66/.76)/(5*365/12) #egg mortality in winter

  #Temperature dependent parameters
  hatch=ifelse(temp>OR8,0.027,0)
  alpha=p[1]
  mue  =ifelse(temp>OR8,atop,blow)
  beta =ifelse(temp>OR8,b,0.00001)
  mup=1/DD
  egglay=ifelse(temp>OR8,228*.5/DD,0)

  #ODE system
  dH = stock*(1-exp(-m*tau))  + m*Hn - muh*H - catch*H -alpha*AP
  dAP= beta*H*W - muh*AP-AP*( mup + catch + alpha) - alpha*k*(AP^2)/H
  dW = hatch*EG - muw*W - beta*(H+Hn)*W + delta*(muh*AP + alpha*AP
                                            + alpha*k*(AP^2)/H)
  dEG= egglay*AP - hatch*EG - mue*EG
  dSH=stock
  dCH=catch*H
  dCP=catch*AP
  dNATH=muh*H
  dPINH=alpha*AP
  dHn= stock*(exp(-m*tau)) -  c*Hn - m*Hn - muh*Hn

  list(c(dH,dAP,dW,dEG,dSH,dCH,dCP,dNATH,dPINH,dHn)) ### MUST BE IN CORRECT ORDER!!!
}

library(deSolve)
ARGY2=function(t,inits,p)
{
  temp=12+8*sin((t-128)*2*pi/(365))
  DD=3900/(((.434*temp)+.361)^2)

  #Define Variables
  H=inits[1]   #Rainbow Trout
  AP=inits[2]  #Attached A. foliaceus
```

```
  W=inits[3]   #Free-living A. foliaceus
  EG=inits[4]  #A. foliaceus eggs
  SH=inits[5]  #Stocked Fish
  CH=inits[6]  #Caught Fish
  CP=inits[7]  #Caught Pars
  NATH=inits[8]#Nat. H Morts
  PINH=inits[9]#P. ind. H Morts
  Hn=inits[10] #Treated fish

  ar=p[3]
  c=p[6]
  rho=p[7]
  nn=p[8]
  psi=p[10]         #Stocking interval
  off=p[11]         #Stocking Offset
  m=p[12]
  tau=p[13]
  muh=1/(2*365)     #Nat. host mortality
  muw=0.45          #Unattached mortality
  b=p[5]            #A. foliaceus attachment 0.0192-0.0576 #A. foliaceus attachment
  delta=1           #Proportion of pars that survive host death
  kk=p[9]
  k=(1+kk)/kk       #Parasite aggregation
  OR8=p[2]          #Cut-off temperature
  s=0.000127049
  stock=s*psi*floor((psi-floor((t-off)%%psi))/psi)
  catch=c*(rho^nn)/(rho^nn+(AP/H)^nn)
  atop = -log(.76)/((25 + 240)/2) #egg mortality in summer
  blow = -log(.66/.76)/(5*365/12) #egg mortality in winter

  #Temperature dependent parameters
  hatch=ifelse(temp>OR8,0.027,0)
  alpha=p[1]
  mue  =ifelse(temp>OR8,atop,blow)
  beta =ifelse(temp>OR8,b,0.00001)
  mup=1/DD
  egglay=ifelse(temp>OR8,228*.5/DD,0)

  #ODE system
  dH = stock*(1-exp(-m*tau)) + m*Hn - muh*H - catch*H - alpha*AP
  dAP= beta*H*W - muh*AP-AP*( mup + catch + alpha) - alpha*k*(AP^2)/H
  dW = hatch*EG - muw*W - beta*(H+Hn)*W + delta*(muh*AP + alpha*AP
                                               + alpha*k*(AP^2)/H)
  dEG= egglay*AP - hatch*EG - mue*EG
  dSH=stock
  dCH=catch*H+c*Hn
  dCP=catch*AP
  dNATH=muh*H
  dPINH=alpha*AP
  dHn= stock*(exp(-m*tau))- c*Hn - m*Hn - muh*Hn

  list(c(dH,dAP,dW,dEG,dSH,dCH,dCP,dNATH,dPINH,dHn)) ### MUST BE IN CORRECT ORDER!!!
}


ARGY3=function(t,inits,p)
{
  temp=12+8*sin((t-128)*2*pi/(365))
  DD=3900/(((.434*temp)+.361)^2)

  #Define Variables
  H=inits[1]   #Rainbow Trout
```

```
  AP=inits[2]  #Attached A. foliaceus
  W=inits[3]   #Free-living A. foliaceus
  EG=inits[4]  #A. foliaceus eggs
  SH=inits[5]  #Stocked Fish
  CH=inits[6]  #Caught Fish
  CP=inits[7]  #Caught Pars
  NATH=inits[8]#Nat. H Morts
  PINH=inits[9]#P. ind. H Morts
  Hn=inits[10] #Treated fish

  ar=p[3]
  c=p[6]
  rho=p[7]
  nn=p[8]
  psi=p[10]         #Stocking interval
  off=p[11]         #Stocking Offset
  m=p[12]
  tau=p[13]
  muh=1/(2*365)     #Nat. host mortality

  muw=0.45          #Unattached mortality
  b=p[5]            #A. foliaceus attachment 0.0192-0.0576 #A. foliaceus attachment
  delta=1           #Proportion of pars that survive host death
  kk=p[9]
  k=(1+kk)/kk       #Parasite aggregation
  OR8=p[2]          #Cut-off temperature
  s=0.000127049

  stock=s*psi*floor((psi-floor((t-off)%%psi))/psi)
  catch=c*(rho^nn)/(rho^nn+(AP/H)^nn)

  cat=min(catch*H+c*Hn,0.0002)    #rod limit
  atop = -log(.76)/((25 + 240)/2) #egg mortality in summer
  blow = -log(.66/.76)/(5*365/12) #egg mortality in winter

  #Temperature dependent parameters
  hatch=ifelse(temp>OR8,0.027,0)
  alpha=p[1]
  mue  =ifelse(temp>OR8,atop,blow)
  beta =ifelse(temp>OR8,b,0.00001)
  mup=1/DD
  egglay=ifelse(temp>OR8,228*.5/DD,0)

  #ODE system
  dH = stock*(1-exp(-m*tau)) + m*Hn - muh*H - cat*catch*H/(catch*H+c*Hn) - alpha*AP
  dAP= beta*H*W - muh*AP-AP*( mup + catch + alpha) - alpha*k*(AP^2)/H
  dW = hatch*EG - muw*W - beta*(H+Hn)*W + delta*(muh*AP + alpha*AP
                                              + alpha*k*(AP^2)/H)
  dEG= egglay*AP - hatch*EG - mue*EG
  dSH=stock
  dCH=cat
  dCP=catch*AP
  dNATH=muh*H
  dPINH=alpha*AP
  dHn= stock*(exp(-m*tau))- cat*c*Hn/(catch*H+c*Hn) - m*Hn - muh*Hn

  list(c(dH,dAP,dW,dEG,dSH,dCH,dCP,dNATH,dPINH,dHn)) ### MUST BE IN CORRECT ORDER!!!
}

ARGY4=function(t,inits,p)
{
  temp=12+8*sin((t-128)*2*pi/(365))
```

```
DD=3900/(((.434*temp)+.361)^2)

#Define Variables
H=inits[1]   #Rainbow Trout
AP=inits[2]  #Attached A. foliaceus
W=inits[3]   #Free-living A. foliaceus
EG=inits[4]  #A. foliaceus eggs
SH=inits[5]  #Stocked Fish
CH=inits[6]  #Caught Fish
CP=inits[7]  #Caught Pars
NATH=inits[8]#Nat. H Morts
PINH=inits[9]#P. ind. H Morts
Hn=inits[10]

ar=p[3]
c=p[6]
rho=p[7]
nn=p[8]
psi=p[10]         #Stocking interval
off=p[11]         #Stocking Offset
m=p[12]
tau=p[13]
tt=p[14]          #treatment time
muh=1/(2*365)     #Nat. host mortality

muw=0.45          #Unattached mortality
b=p[5]            #A. foliaceus attachment 0.0192-0.0576 #A. foliaceus attachment
delta=1           #Proportion of pars that survive host death
kk=p[9]
k=(1+kk)/kk       #Parasite aggregation
OR8=p[2]          #Cut-off temperature
s=0.000127049
stock=s*psi*floor((psi-floor((t-off)%%psi))/psi)

#define vector - ones where treatment occurs
vec=rep(0,365)
vec[(1:(floor(psi)))+floor(psi)*tt]=rep(1,floor(psi))

catch=c*(rho^nn)/(rho^nn+(AP/H)^nn)
cat=min(catch*H+c*Hn,0.0002)
atop = -log(.76)/((25 + 240)/2) #egg mortality in summer
blow = -log(.66/.76)/(5*365/12) #egg mortality in winter

#Temperature dependent parameters
hatch=ifelse(temp>OR8,0.027,0)
alpha=p[1]
mue  =ifelse(temp>OR8,atop,blow)
beta =ifelse(temp>OR8,b,0.00001)
mup=1/DD
egglay=ifelse(temp>OR8,228*.5/DD,0)

#ODE system
dH = stock*(1-vec[(t%%365)+1])+(vec[(t%%365)+1])*stock*(1-exp(-m*tau)) + m*Hn - muh*H -
      cat*catch*H/(catch*H+c*Hn) - alpha*AP
dAP= beta*H*W - muh*AP-AP*( mup + catch + alpha) - alpha*k*(AP^2)/H
dW = hatch*EG - muw*W - beta*(H+Hn)*W + delta*(muh*AP + alpha*AP
                                                + alpha*k*(AP^2)/H)
dEG= egglay*AP - hatch*EG - mue*EG
dSH=stock
dCH=cat
dCP=catch*AP
dNATH=muh*(H+Hn)
```

```
  dPINH=alpha*AP
  dHn= vec[(t%%365)+1]*stock*(exp(-m*tau))- cat*c*Hn/(catch*H+c*Hn) - m*Hn - muh*Hn

  list(c(dH,dAP,dW,dEG,dSH,dCH,dCP,dNATH,dPINH,dHn)) ### MUST BE IN CORRECT ORDER!!!
}

ARGY5=function(t,inits,p)
{
  temp=12+8*sin((t-128)*2*pi/(365))
  DD=3900/(((.434*temp)+.361)^2)

  #Define Variables
  H=inits[1]   #Rainbow Trout
  AP=inits[2]  #Attached A. foliaceus
  W=inits[3]   #Free-living A. foliaceus
  EG=inits[4]  #A. foliaceus eggs
  SH=inits[5]  #Stocked Fish
  CH=inits[6]  #Caught Fish
  CP=inits[7]  #Caught Pars
  NATH=inits[8]#Nat. H Morts
  PINH=inits[9]#P. ind. H Morts
  Hn=inits[10] #Treated fish

  ar=p[3]
  c=p[6]
  rho=p[7]
  nn=p[8]
  psi=p[10]         #Stocking interval
  off=p[11]         #Stocking Offset
  m=p[12]
  tau=p[13]
  tt=p[14]          #treatment time
  muh=1/(2*365)     #Nat. host mortality

  muw=0.45          #Unattached mortality
  b=p[5]            #A. foliaceus attachment 0.0192-0.0576 #A. foliaceus attachment
  delta=1           #Proportion of pars that survive host death
  kk=p[9]
  k=(1+kk)/kk       #Parasite aggregation
  OR8=p[2]          #Cut-off temperature
  s=0.000127049
  stock=s*psi*floor((psi-floor((t-off)%%psi))/psi)
  vec=rep(0,365)
  catch=c*(rho^nn)/(rho^nn+(AP/H)^nn)
  cat=min(catch*H+c*Hn,0.0002)
  atop = -log(.76)/((25 + 240)/2) #egg mortality in summer
  blow = -log(.66/.76)/(5*365/12) #egg mortality in winter

  #Temperature dependent parameters
  hatch=ifelse(temp>OR8,0.027,0)
  alpha=p[1]
  mue  =ifelse(temp>OR8,atop,blow)
  beta =ifelse(temp>OR8,b,0.00001)
  mup=1/DD
  egglay=ifelse(temp>OR8,228*.5/DD,0)

  #ODE system
  dH = stock*(1-vec[(t%%365)+1])+(vec[(t%%365)+1])*stock*(1-exp(-m*tau)) + m*Hn - muh*H -
       cat*catch*H/(catch*H+c*Hn) - alpha*AP
  dAP= beta*H*W - muh*AP-AP*( mup + catch + alpha) - alpha*k*(AP^2)/H
  dW = hatch*EG - muw*W - beta*(H+Hn)*W + delta*(muh*AP + alpha*AP
                                                 + alpha*k*(AP^2)/H)
```

```
  dEG= egglay*AP - hatch*EG - mue*EG
  dSH=stock
  dCH=cat
  dCP=catch*AP
  dNATH=muh*(H+Hn)
  dPINH=alpha*AP
  dHn= vec[(t%%365)+1]*stock*(exp(-m*tau))- cat*c*Hn/(catch*H+c*Hn) - m*Hn - muh*Hn

  list(c(dH,dAP,dW,dEG,dSH,dCH,dCP,dNATH,dPINH,dHn)) ### MUST BE IN CORRECT ORDER!!!
}
```

c6-nbinom.R

```
#y values on plot are frequencies
#c1 parasite count per host
#mu average p/h
#size=k
c1<-seq(0,10,by=1)
pdf("C:/Users/nmo2/Dropbox/Thesis/2013–06–29–thesis/images/c6–nbinom.pdf")
par(mfrow=c(1,2))
size=0.741
plot(c1,dnbinom(c1, mu = 0.015, size = size),type=’h’,pty=1,ylim=c(0,1),xlab=’i’,ylab=’
    Proportion of fish with i parasites’)
plot(c1,dnbinom(c1, mu = 0.389, size = size),type=’h’,pch=2,ylim=c(0,1),xlab=’i’,ylab=’’)
dev.off()
```

c6-efficacy.R

```
efficacy=function(t){
  exp(-t/70)
}
t=0:100
pdf("C:/Users/nmo2/Dropbox/Thesis/2013–06–29–thesis/images/c6–efficacy1.pdf")
plot(t,efficacy(t),ylab=’Efficacy’,xlab=’Time after treatment’,type=’l’,ylim=c(0,1))
tau=20
lines(tau+t,exp(-tau/70)*efficacy(t),lwd=2)
lines(0:20,rep(0,21),lwd=2)
lines(c(20,20),c(0,exp(-tau/70)),lwd=2)
legend(60,1,c(’No withdrawal’,’20 days withdrawal’),lwd=1:2)
dev.off()

withdrawal=function(t,tau){
  exp(-tau/70)*exp(-t/70)
}
t=0:100
pdf("C:/Users/nmo2/Dropbox/Thesis/2013–06–29–thesis/images/c6–efficacy2.pdf")
plot(t,withdrawal(t,0),ylab=’Efficacy’,xlab=’Time after stocking’,type=’l’,ylim=c(0,1))
lines(t,withdrawal(t,20),lwd=2)
legend(60,1,c(’No withdrawal’,’20 days withdrawal’),lwd=1:2)
dev.off()
```

B.4.2 *Egg-laying board models*

c6-ELBmodel.R

```
library(deSolve)
ARGY=function(t,inits,p)
{
  temp=12+8*sin((t-128)*2*pi/(365))
  DD=3900/(((.434*temp)+.361)^2)

  #Define Variables
  H=inits[1]   #Rainbow Trout
  AP=inits[2]  #Attached A. foliaceus
  W=inits[3]   #Free-living A. foliaceus
  EG=inits[4]  #A. foliaceus eggs
  SH=inits[5]  #Stocked Fish
  CH=inits[6]  #Caught Fish
  CP=inits[7]  #Caught Pars
  NATH=inits[8]#Nat. H Morts
  PINH=inits[9]#P. ind. H Morts
  EB=inits[10] #Eggs laid on boards

  c=p[6]      #capture rate/residence time in the absence of infection
  rho=p[7]    #parasite burden required to halve the capture rate
  nn=p[8]     #shape parameter for capture reduction
  psi=p[10]   #Stocking interval
  off=p[11]   #Stocking Offset
  muh=1/(2*365)         #Nat. host mortality
  muw=0.45     #Unattached mortality
  b=p[5]       #A. foliaceus attachment 0.0192-0.0576 #A. foliaceus attachment
  delta=1      #Proportion of pars that survive host death
  kk=p[9]
  k=(1+kk)/kk   #Parasite aggregation
  OR8=p[2]      #Cut-off temperature below which overwintering occurs
  prop=p[12]    #proportion of eggs laid on boards
  rem=p[13]     #board removal (not actually used)
  s=0.000127049 # constant stocking rate
  stock=s*psi*floor((psi-floor((t-off)%%psi))/psi)
  catch=c*(rho^nn)/(rho^nn+(AP/H)^nn)
  atop = -log(.76)/((25 + 240)/2) #egg mortality in summer
  blow = -log(.66/.76)/(5*365/12) #egg mortality in winter

  #Temperature dependent parameters
  hatch=ifelse(temp>OR8,0.027,0)
  alpha=p[1]
  mue  =ifelse(temp>OR8,atop,blow)
  beta =ifelse(temp>OR8,b,0.00001)
  mup=1/DD
  egglay=ifelse(temp>OR8,228*.5/DD,0)

  #ODE system
  dH = stock - catch*H - alpha*AP - muh*H
  dAP= beta*H*W - muh*AP-AP*( mup + catch + alpha) - alpha*k*(AP^2)/H
  dW = hatch*(EG+EB) - muw*W - beta*H*W + delta*(muh*AP + alpha*AP
                                            + alpha*k*(AP^2)/H)
  dEG= (1-prop)*egglay*AP - hatch*EG - mue*EG
  dSH=stock
  dCH=catch*H
  dCP=catch*AP
  dNATH=muh*H
  dPINH=alpha*AP
  dEB= prop*egglay*AP - hatch*EB - mue*EB #board removal via events

  list(c(dH,dAP,dW,dEG,dSH,dCH,dCP,dNATH,dPINH,dEB)) ### MUST BE IN CORRECT ORDER!!!
}
```

c6-ELBscript.R

```
#load model from other file
source("C:/Users/nm02/Desktop/Appendices/c6–ELBmodel.R")

## Parameters & Initial Conditions
base_inits=c(H=2.715423e-03, AP=2.404820e-02, W=1.920324e-04, EG=8.593183e-01,SH=0,CH=0,
    CP=0,NATH=0,PINH=0,EB=0)
int=1
time<-seq(int,3650+int,by=int)
tmax=tail(time,1)
base_ptab=NULL
bap=c(0.0015, 8,1,1,7.12, 0.0275, 15,2,0.741)

#range of values used for the proportion of eggs laid on boards
prop=c(0,0.1,0.25,0.5,0.75,1)

#board removal periods
remt=c(365/52,365/26,365/12,365/4)

j=NULL
i=NULL
#create empty matrix to output results
ebtab=NULL
#runs the model for the range of parameters specified above and outputs results to a
    matrix
  for(j in 1:length(remt)){
  rem=remt[j]
  #define time points for the event functionality in the ode solver
  tims=subset(time,time%%floor(rem)+1==1)
  #produce compatible data frame: sets population EB (eggs laid on board) equal to zero
  #at regular intervals to represent the removal and cleaning of the boards.
  eventdat <- data.frame(var = c(rep(’EB’,length(tims))), time = tims,
    value = c(rep(0,length(tims))), method = c(rep("mult",length(tims))))
  for(i in 1:length(prop)){
        base_ptab=c(bap,1,0,prop[i],rem)
  #run the model
        sol<- lsoda(func=ARGY, y=base_inits, time, base_ptab, events=list(data = eventdat
            ))
  #output results to matrix
        ebtab=cbind(ebtab,sol)}}

#Plot generation
pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c6–elb–cap.pdf")
par(mfrow=c(1,1))
ebtab=ebtab[(tmax-366):tmax,]
teb=11*(0:(length(prop)-1))
plot(res[teb+7]/res[teb+6],ylab=’Proportion Caught’,type=’l’,xlab=’prop’,xaxt=’n’)
lines(res[teb+7+66]/res[teb+6+66],lty=2)
lines(res[teb+7+66+66]/res[teb+6+66+66],lty=3)
lines(res[teb+7+66+66+66]/res[teb+6+66+66+66],lty=4)
axis(1,1:length(prop),labels=prop)
legend(1,0.95,round(remt,2),lty=1:4)
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013–06–29–thesis/images/c6–elb–mor.pdf")
par(mfrow=c(1,1))
res=ebtab[3650,]-ebtab[3650-366,]
teb=11*(0:(length(prop)-1))
plot(res[teb+10]/res[teb+6],ylab=’Proportion Mortalities’,type=’l’,xlab=’prop’,xaxt=’n’)
lines(res[teb+10+66]/res[teb+6+66],lty=2)
```

```
lines(res[teb+10+66+66]/res[teb+6+66+66],lty=3)
lines(res[teb+10+66+66+66]/res[teb+6+66+66+66],lty=4)
axis(1,1:length(prop),labels=prop)
legend(4.5,0.3,round(remt,2),lty=1:4)
dev.off()

pdf("C:/Users/nm02/Dropbox/Thesis/2013-06-29-thesis/images/c6-elb-pbur.pdf")
par(mfrow=c(1,1))
res=ebtab[3650,]-ebtab[3650-366,]
teb=11*(0:(length(prop)-1))
plot(res[teb+8]/res[teb+7],ylab='Mean parasite burden',type='l',xlab='prop',xaxt='n')
lines(res[teb+8+66]/res[teb+7+66],lty=2)
lines(res[teb+8+66+66]/res[teb+7+66+66],lty=3)
lines(res[teb+8+66+66+66]/res[teb+7+66+66+66],lty=4)
axis(1,1:length(prop),labels=prop)
legend(4.5,5.5,round(remt,2),lty=1:4)
dev.off()
```