A PRELIMINARY INVESTIGATION OF THE POSSIBLE EFFECTS OF RHIZOCEPHALAN PARASITISM ON THE MANAGEMENT OF THE CRAB FISHERY AROUND SOUTH GEORGIA

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Abstract

Relatively high levels of infection by a rhizocephalan barnacle have been found in the population of the crab *Paralomis spinosissima*, which has been harvested by a new fishery around South Georgia (Subarea 48.3) since 1992. One of the main effects of the parasite is to render infected animals sterile. Parasitism can therefore reduce the effective spawning stock biomass, and this clearly has implications for stock management.

The possible implications of parasitism for management are investigated by considering a population model that captures the main characteristics of the system. An age-based host-parasite model is constructed, incorporating two scenarios for the stock-recruit relationship of the host: (i) resilience; and (ii) sensitivity to declines in spawning stock. The effects of harvesting both healthy and infected animals are contrasted with the effects of harvesting healthy animals only. Equilibrium and transition dynamics of the models are explored for ranges of parameter values.

Results indicate a need to harvest or remove infected animals from the population. The need is stronger when the population is sensitive to declines in spawning stock. Results highlight the importance of incorporating parasitism in the design of a management strategy for this crab population. The main data requirements for improving on this preliminary study are identified.

Résumé

La population de crabes *Paralomis spinosissima* exploitée par une nouvelle pêcherie autour de la Géorgie du Sud (sous-zone 48.3) depuis 1992 manifeste des niveaux relativement élevés d'infestation par une balane rhizocéphale. Ce parasite a pour effet, entre autres, de provoquer la stérilité des individus infestés. De ce fait, le parasitisme peut réduire la biomasse réelle du stock reproducteur, d'où des implications évidentes sur la gestion des stocks.

Les implications possibles du parasitisme en matière de gestion sont étudiées par l'examen d'un modèle de population qui englobe les principales caractéristiques du système. Il a donc été conçu un modèle hôte-parasite selon l'âge, considérant la relation stock-recrutement de l'hôte sur la base de : (i) la résistance; et (ii) la sensibilité au déclin du stock reproducteur. Les effets de l'exploitation d'individus sains et d'individus infestés sont comparés à ceux de l'exploitation d'individus sains uniquement. La dynamique d'équilibre et de transition des modèles est explorée pour diverses valeurs paramétriques.

Les résultats indiquent qu'il conviendrait de pêcher ou d'éliminer les individus infestés de la population. Cet impératif doit être respecté encore plus strictement lorsque la population est sensible à la baisse du stock reproducteur. Les résultats mettent en évidence l'importance de la prise en considération du parasitisme dans la conception d'une stratégie de gestion de cette population de crabes. Les principales données nécessaires pour approfondir cette étude préliminaire sont identifiées dans ce document.

Резюме

В популяции краба *Paralomis spinosissima*, промысел которого начат в районе Южной Георгии (Подрайон 48.3) с 1992 г., обнаружены относительно высокие

уровни заражения усоногими ризоцефалановыми раками. Одним из главных результатов заражения этим паразитом является стерилизация инфицированных особей. Паразитизм может, таким образом, уменьшить размер фактической биомассы нерестующей части запаса, и это, очевидно, будет иметь значение для управления промыслом.

Изучается возможное значение паразитизма для управления путем рассмотрения популяционной модели, которая включает в себя основные характеристики системы. Построена основанная на возрасте модель "хозяин/паразит", включающая две потенциальные ситуации, описывающие соотношение "запас/пополнение" у организма-хозяина: (i) устойчивость и (ii) чувствительность по отношению к изменению биомассы нерестующей части запаса. Сравниваются последствия облова как здоровых, так и инфицированных особей, а также последствия облова только здоровых особей. Изучается равновесная и переходная динамика моделей для ряда величин параметров.

Полученные результаты указывают на необходимость облова или намеренного изъятия из популяции инфицированных крабов. Это в особенности необходимо, когда популяция чувствительна к спадам нерестующей части запаса. Результаты подчеркивают важность того, что при разработке стратегии управления этой популяцией краба надо принимать в расчет паразитизм. Перечислены основные данные, сбор которых требуется для продолжения настоящего исследования.

Resumen

Se ha registrado un nivel relativamente alto de infección de cirrípodos rizocéfalos en la población de *Paralomis spinosissima*, que ha sido explotada por una nueva pesquería llevada a cabo en la zona de Georgia del Sur (subárea 48.3) desde 1992. Uno de los efectos principales del parásito es la esterilidad de los animales infectados. Por lo tanto, el parasitismo puede reducir la biomasa reproductora efectiva del stock, repercutiendo así en la gestión del stock.

Se investigan las posibles repercusiones del parasitismo en la gestión mediante un modelo de la población que toma en cuenta las características principales del sistema. Se ha diseñado un modelo, basado en la edad, que considera la relación huésped-parásito, e incorpora dos hipótesis para la relación stock-recluta del huésped: (i) resistencia y (ii) susceptibilidad a la disminución del stock reproductor. Los efectos de explotar animales infectados y sanos se contrastan con los efectos de explotar animales sanos solamente. Se explora la dinámica de equilibrio y transicional del modelo para distintos valores de los parámetros.

Los resultados indican que es necesario capturar y eliminar los animales infectados de la población. Esta necesidad es de mayor importancia cuando la población es susceptible a las disminuciones del stock reproductor. Estos resultados subrayan la importancia de incorporar el parasitismo en el diseño de una estrategia de gestión para esta población de centollas. Se identifican los datos principales necesarios para mejorar este estudio preliminar.

INTRODUCTION

The first fishing trip targeting crabs in Subarea 48.3, by the FV *Pro Surveyor*, presented in Otto and MacIntosh (1992), revealed relatively high levels of infection by a rhizocephalan barnacle (*Briarosaccus callosus*) in the population of *Paralomis spinosissima*. This parasite also infects lithodid crab species in Alaskan waters. One of the main effects of the parasite is that infected crabs become castrated and are therefore no longer part of the spawning stock (Hawkes *et al.*, 1986a; Hoggarth, 1990). It is also highly likely that growth is affected (Hawkes *et al.*, 1986a; Otto and MacIntosh, 1992), and mortality of infected animals may be higher than for healthy animals. These factors are clearly of relevance to stock management.

One of the standard fisheries theories for harvesting parasitised populations is that the

percentage of infected animals (also called the prevalence) should decrease with increasing fishing mortality. This generally includes the very important assumption that both healthy and infected individuals are harvested. In the case of the crab fishery around South Georgia, it seems that only healthy males will be harvested. The size frequency data, albeit from limited information and only a single fishing trip, indicate that very few infected animals are found above the minimum 'commercial' size of 102 mm carapace width (CW). This implies that if only males above this size limit are retained, there would be no fishing mortality on infected animals. If we further assume that the discards do indeed survive, the harvest would only include healthy males. If the infected discards are destroyed or die in the process, the situation would be similar to that in which both healthy and infected animals are harvested, even if the fishing mortalities on the two categories are not identical.

Kuris and Lafferty (1992) consider a wide range of parasites, including parasitic castrators such as *B. callosus*, and nemertean worms which feed on embryos of decapod crustaceans. They note that the parasites may be protected by management practices that protect females because these parasites commonly either affect only females or feminise males. The authors use a general host-parasite model to investigate the effects of parasites on management strategies under various hypotheses about the recruitment dynamics of host and parasite.

In this paper I consider a model more specifically aimed at capturing the main characteristics of the system under consideration: the fishery for *P. spinosissima* infected by *B. callosus*. The possible effects of harvesting only healthy animals on the spawning stock and the prevalence are investigated using this hypothetical host-parasite model. I stress the word hypothetical because, although I have attempted to capture the characteristics of the system, the parameters used here are largely arbitrary. Very little is known about both the host and parasite in this fishery, and the model is therefore necessarily simple with many assumptions. The general patterns and messages emerging from the results are important, although the absolute numbers cannot be used as guidelines. The results also highlight the importance of undertaking more studies on crab growth, demographic parameters of healthy and infected animals, and the population dynamics of and interactions between the host and parasite populations.

A summary review of current knowledge is given in the next section. The basics of the host-parasite model are presented here under the headings 'A Hypothetical Host-Parasite Model' and 'Results'. First, a general picture of the likely interactions and characteristics of the system is built on the basis of current knowledge and ecological generalisations. Second, details of the model and the different assumptions and scenarios are discussed. All equations and parameter values used in the analyses have been relegated to the appendix.

INFORMATION RELEVANT TO
THE HOST-PARASITE MODEL

It is necessary to turn to studies of other crab species to gain more information about rhizocephalan parasitism and its effect on the hosts. All lithodids show some levels of prevalence, including *Lithodes antarcticus* in the waters around Chile, Argentina and the Falkland Islands. Crab species that are infected with *B. callosus* in north Pacific waters include the red, blue and golden (or brown) king crabs. The information summarised here pertains mainly to studies of these crab populations.

The Parasite

A general description of the life history of the rhizocephala can be found in, for example, Hoggarth (1990), and I summarise from this reference here. Parasitism begins with the attachment of a female cyprid larva to the host. The larva grows, effectively into its host, absorbing nutrients directly from the host. This stage is known as the interna. Sexual development involves the eruption of 'externa'. Some related species of rhizocephala are known to require at least 9 to 12 months to reach reproductive maturity and develop externa (Hawkes *et al.*, 1986a). The time required for *B. callosus* may be similar. Clutches of eggs hatch within the externa and are later released, usually at the nauplius stage. Generally, a host carries a single parasite, but small numbers of crabs with two or more externa have been found (Hoggarth, 1990).

I have not found any reference to suggest what the life-span of the parasite is likely to be, but at the one extreme a parasite could live until its host dies. Crabs are frequently reported with scars of *B. callosus* infections where the externa have been

lost (Sloan, 1984). This suggests that, at least in some cases, the parasite may die before the host does. There is, of course, a possibility that the externa are merely seasonally shed. Hoggarth (1990) notes that limited attention has been paid to the biology of post-parasitised crabs. In his study of the false king crab, *Paralomis granulosa*, which, around the Falkland Islands, is also infected by *B. callosus*, all scarred females were non-ovigerous and scarred males were not (morphometrically) mature. Hoggarth suggests that they probably remain sterile.

Growth and Mortality of the Host

The effects of parasitism that are most relevant to stock management are those relating to growth and reproductive capability.

Many studies suggest that the presence of *B. callosus* does not completely inhibit moulting of its host (Hoggarth, 1990). A decrease in parasite prevalence with increasing size for males has been found in blue and golden king crabs (Sloan, 1984; Hawkes *et al.*, 1986a), the false king crab (Hoggarth, 1990) and also *P. spinosissima* around South Georgia (Otto and MacIntosh, 1992). Although various mechanisms and factors could lead to this pattern of prevalence, it is thought that one of the main causes is the reduction in growth rate and feminisation of male hosts (Hawkes *et al.*, 1986a and 1987). This would imply that animals are most susceptible while still relatively small, and that the large crabs are the ones that have escaped parasitism.

The size frequency distributions in Figure 1 of Otto and MacIntosh (1992) show that a very small proportion of commercially-sized crabs (i.e., above 102 mm CW) are parasitised. This suggests that retaining only males above this size would effectively involve harvesting healthy animals only. The discards did, however, contain relatively large numbers of infected animals. The choice of the legal size of 102 mm CW for *P. spinosissima* is intended to allow at least one breeding season for males, and I shall assume that this is the case for the purposes of this study (see 'A Hypothetical Host-Parasite Model' and 'Results'). The validity of this assumption depends on whether the size at morphometrical maturity can be assumed to be similar to the size at functional maturity (Basson and Hoggarth, 1994). Here, functional maturity means that an animal is capable of breeding successfully, whereas morphological maturity means that the animal is in the size range where the chela has started growing at the higher adult growth rate.

Data for both *P. granulosa* and *Lithodes aequispina* further suggest that animals are infected with the parasite early in life (Hoggarth, 1990). This would imply that only part of the healthy population (those below a certain size, for example) is susceptible at any time.

There is no conclusive evidence to show how host mortality is affected by the presence of a parasite. Although host mortality may not be greatly affected, a small increase due to parasitism is a possibility.

With respect to *P. spinosissima*, very little is currently known about its growth patterns (moult increment and moult frequency by size and sex), and there is a clear need to improve our knowledge in this regard. It is also important to consider normal (or healthy), parasitised and scarred animals separately when studying their life history and biology.

Reproduction

Mature-sized parasitised female crabs have always been found to be non-ovigerous, and it is generally accepted that *B. callosus* is responsible for the sterilisation of female lithodids (Hoggarth, 1990). Male crabs are also generally castrated, though some specimens with spermatophores containing sperm of normal appearance have been found (Sparks and Morado, 1986). For the purposes of this study, it seems reasonable to assume that parasitised crabs of either sex do not form part of the spawning stock, and that post-parasitised crabs do not rejoin the spawning stock but remain sterile.

Prevalence

The only information on the prevalence of *B. callosus* in the *P. spinosissima* population around South Georgia is from Otto and MacIntosh (1992, Table 2), where sample sizes for normal animals and those infected with rhizocephala are given. I have excluded the small samples of animals infected with microsporidians and calculated the prevalence as the ratio of numbers infected to total numbers (Table 1).

Comparisons with prevalence from other studies, summarised from Hoggarth (1990) and given in Table 2 below, suggest that the level at South Georgia is moderately high. At Shag Rocks the prevalence is on the high side of low. The true prevalence may be much higher, but it would be difficult to estimate without knowledge of the growth and mortality of infected and uninfected animals. The sample prevalence only includes animals with visible externa, and therefore does not take account of animals in earlier stages of infection (i.e., before the development of the externa). The true prevalence may, of course, also be lower than the sample prevalence if there is, for example, a very patchy distribution of prevalence over the whole area. Current information on prevalence from Subarea 48.3 is based on a single trip covering a small area (less than 220 n miles²) and there is no spatial information to indicate either sample location or the likely spatial variability of the prevalence. It does, however, seem fair to conclude that the level of prevalence, as estimated from the initial data, is high enough to warrant closer investigation and attention.

may also be that crabs were taken from a more open habitat at Shag Rocks than at South Georgia. According to Otto and MacIntosh (1992), fishing in submarine canyons was not particularly productive, so offshore areas were explored. It would be useful and informative to estimate prevalence by habitat-type (e.g., submarine canyon or open, offshore) from the data for Subarea 48.3.

Clearly, further information on prevalence in *P. spinosissima* around South Georgia (including Shag Rocks, of course) is required, and in this regard it is essential that animals below the commercial size (<102 mm CW) are also sampled. It is relatively easy to observe the externa on a parasitised crab. Infected males can be recognised at a glance, and infected females can be recognised by pulling open the abdomen, which is part of the standard sampling procedure of egg stages. An internal investigation would therefore not be essential, although the prevalence would be underestimated without it because parasitised crabs which have not yet developed externa would not be recognised.

Table 1: Sample prevalence of the rhizocephalan *B. callosus* (in %) with total sample size in brackets, obtained from Table 2 in Otto and MacIntosh (1992) and excluding animals with microsporidians.

	South Georgia	Shag Rocks
Males	22% (2 257)	6% (502)
Females	13% (2 687)	7% (426)

Table 2: Prevalence (in %) of *B. callosus* from other studies, summarised from Hoggarth (1990). Note that these estimates are based on samples (as for Table 1 above) and may not reflect the prevalence in the population as a whole.

Species	Location	% Prevalence
Paralithodes camtschatica (red king crab)	North Pacific	1-2%
Paralithodes platypus (blue king crab)	North Pacific	Unparasitised*
	Alaskan fjord system	76%
Lithodes aequispina (golden king crab)	Alaskan fjord system	20%
	Canadian fjord system	40%
Lithodes murrayi	SW Indian Ocean	3%
Lithodes couesi	SW Indian Ocean	<1%
Paralomis granulosa (false king crab)	Chilean waters	2%
	Falkland Island waters	<1%

* Large areas of open sea in North Pacific

There is some evidence that prevalence is higher in relatively closed systems, such as canyons or fjords, than in areas of open ocean. Various explanations have been put forward as to why this may be the case (see e.g., Sloan, 1984; Hawkes *et al.*, 1986b). The difference in prevalence at Shag Rocks and South Georgia Island may be due to sampling variability, but it

A HYPOTHETICAL
HOST-PARASITE MODEL

The Basic Structure
of the Model

The information under the heading 'Information Relevant to the Host-Parasite Model'

allows us to make some reasonable assumptions about the parasite dynamics in a host-parasite model. Many questions remain, but it is possible to construct a relatively simple model, and to start investigating the likely effects of harvesting on the prevalence of parasitism and on the abundance of the spawning stock. One possible picture of the structure of the system may be as follows:

- Crabs are susceptible to parasitism over some period of their life-span before becoming sexually mature.

- Parasitised crabs are sterile and do not form part of the spawning stock.

- Parasitised crabs suffer a slightly higher level of (constant) natural mortality than uninfected crabs.

- In each year the number of newly-infected crabs is proportional to the number of susceptible crabs and to the number of parasite larvae.

- In each year the number of parasite larvae ('recruits') is proportional to the number of infected crabs in the previous year.

- Once a crab is infected it remains infected.

- Male crabs are harvested at a size/age one year after having attained sexual maturity, so that they have one opportunity to breed before being vulnerable to harvesting.

- If discarded crabs survive, then the harvest of male crabs above 102 mm CW implies that fishing mortality operates only on healthy crabs, because a very small number of parasitised crabs are of commercial size.

- If parasitised crabs are destroyed during the process of harvesting, then fishing mortality operates on both healthy and parasitised crabs.

Clearly, these assumptions are simplifications, but they are based on a reasonable knowledge of *B. callosus* and a mixture of knowledge and analogy regarding the host population. In some cases it would be easy to suggest more realistic assumptions. For example, it is unlikely that natural mortality is constant over the entire lifespan of a crab; it is more likely to decrease at older ages when moult frequency is reduced. However, given the paucity of data it makes more sense to try and construct a simple model and investigate the broad patterns of response.

A size- or stage-structured model is likely to be more appropriate than an age-based model. In general, it is easier to obtain estimates of some parameters in terms of size (e.g., size-at-first-capture, size-at-maturity and distributions of numbers-by-size) than in terms of age. A size-based model would require some information on the growth pattern: for example, distributions of moult increment and moult frequency by size. At this stage, however, very little is known about the growth pattern of this crab population, and I have therefore used an age-based model. One obvious advantage of an age-based model is that the time of transition from one age class to the next is fixed and known. The disadvantage is that we do not know how age relates to parameters such as size at maturity and first capture. The age-related parameters used in this study are therefore largely arbitrary, and should be seen as relative age rather than absolute 'real crab' age! The advantages of an age- or size-structured model over a simpler model that ignores age are that age-at-maturity and age-at-first-capture can be incorporated, and the number of spawners in the population can be more accurately modelled.

I should comment on the assumption that the number of parasite larvae is proportional to the number of infected animals in the previous time-period. The time lag allows a year for newly-infected hosts to develop sexually mature externa. The parasite population, however, consists of a mixture of juveniles and adults. It is therefore arguable that the number of larvae should be proportional to the number of infected hosts in the same year rather than the previous year, but excluding newly-infected animals. I also considered a version of the model where this alternative hypothesis applies. The results from the two models are very similar, although there are numerical differences. Results presented in this paper are for the model which includes a one-year time lag. This problem can be avoided by explicitly modelling the parasite population in terms of juveniles and adults.

Details of the Basic Host-Parasite Model and Scenarios Considered

The basics of the model are as follows. The model is deterministic. Once the characteristics of the system are better known, stochasticity can be incorporated. Only males are considered at this stage because only males are being harvested. Females should be included at a later stage since

they are also subject to parasitism and hence a source of infection. Females may also be a more crucial component of the spawning stock than males. The model is constructed in terms of numbers of animals in each age class, with two categories for each age class: healthy animals and infected animals. Natural mortality is assumed to be constant over all age classes, and somewhat higher for infected than for healthy animals. Recruitment to the host population is assumed to relate to the spawning stock via the relationship illustrated in Figure 1 and given in the appendix. The same asymptotic value (R in the appendix) is used throughout, but two values for the parameter that describes the steepness of the curve (r in the appendix) are used. A high value of this parameter corresponds to a very steep curve that reaches the asymptote at very low levels of spawning stock. This implies a stock with a high level of resilience to changes in the spawning stock biomass and is called the resilient stock-recruit scenario. A low value corresponds to a slowly increasing curve and a population that is sensitive to changes in the spawning stock (the sensitive stock-recruit scenario). There are, of course, other possible stock-recruit relationships that could be considered later.

$-\blacksquare-$ r=10 $-\vartriangle-$ r=0.01 $-\circ-$ r=0.02
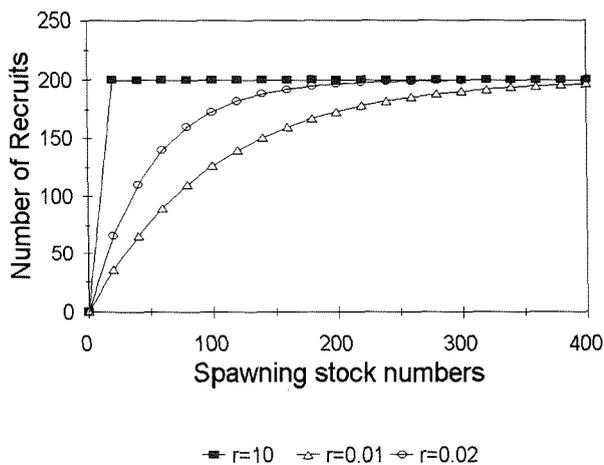
Figure 1:
Hypothetical stock-recruit relationships (see appendix). The two scenarios used in the models are given by: r = 1 (resilient) and r = 0.01 (sensitive).

In each year the number of newly-infected animals in each susceptible age class is proportional to the total number of infective parasite larvae, and to the number of healthy animals (i.e., susceptibles) in that age class. The coefficient of proportionality (or infection rate) is assumed to be constant, both with age and time,

and only animals between a given range of ages are susceptible. The number of parasite larvae in each year is assumed to be proportional to the total number of adult parasites in the previous year, again with a constant coefficient of proportionality. There is also an implicit assumption that each infected animal carries only one parasite. This leads to a one-to-one relationship between the number of parasites and the number of infected animals. I also assume that infected animals do not recover, or lose the parasite. Although this is not entirely realistic, it should mainly affect the magnitude of prevalence rather than the patterns of change in prevalence under different harvesting scenarios.

Two harvesting scenarios are considered. The first involves harvesting healthy animals from the age-at-first-capture and older. This scenario implicitly assumes that no, or very small numbers of commercially-sized crabs are infected, and that all discarded animals survive. The second involves harvesting healthy and infected animals from the age-at-first-capture and older. Selectivity is assumed to be knife-edge in both cases.

Two important points with respect to the crab fishery in Subarea 48.3 should be noted here. First, in practical terms, the scenario in which healthy and infected animals are harvested does not imply a change in the minimum legal size. It does, however, implicitly assume that infected crabs appear in the catch as part of the discards, and that these infected crabs are destroyed rather than returned. Second, both scenarios assume that healthy sub-legal sized crabs are returned and survive.

The difference equations that describe the population-dynamics-at-age are given in the appendix, together with the parameters used in this hypothetical model. These parameters, particularly the infection rate, the larval production rate, host mortality and recruitment, affect the prevalence. Three sets of parameters were used, leading to three (arbitrary) levels of prevalence in the unexploited equilibrium stock: low (10%), medium (35%) and high (65%).

I initially run the model with no harvest to obtain the equilibrium prevalence and spawning stock numbers for the unexploited stock. Starting the system at the unexploited equilibrium solution, the model is then run with non-zero fishing mortality. This leads first to a transition period and then to a new equilibrium solution. It

is possible to obtain analytical solutions for the equilibrium population sizes, but the algebra is tedious because of the age-structured nature of the model, so all calculations are done numerically.

RESULTS

The principal outputs are the changes in the prevalence and in the spawning numbers as a function of fishing mortality. Again, the actual numbers should not be interpreted as pertaining to the crab population in Subarea 48.3 because the parameters used are almost certainly not appropriate. However, the general patterns that emerge are relevant since the model has been structured to reflect the basic characteristics of the system.

Equilibrium Solutions for the Unexploited Stock

To begin with, the spawning numbers are affected by the prevalence even when there is no harvest. For example, Figure 2 shows how the spawning numbers decline as the prevalence increases for the two assumptions about recruitment. Note that the spawning numbers are expressed as a percentage of the spawning numbers of the unexploited, zero-prevalence population ($N^{ss}(F = 0, p = 0)$, where F = fishing mortality and p = prevalence). The main reason is that infected animals do not form part of the spawning stock. The point is that given a non-zero level of infection, the spawning stock is already below its maximum level, even without any harvesting.
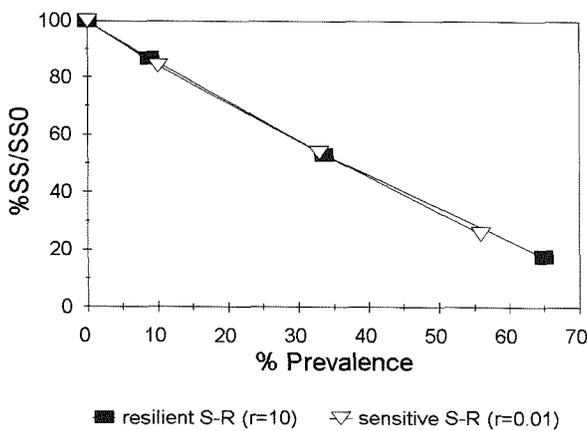
Figure 2:
Ratios (in %) of spawning stock numbers at different prevalences to the spawning stock numbers with zero prevalence and zero fishing mortality.

It is unclear how or whether such a reduction in spawning stock would affect recruitment and production of the crab population around South Georgia. It is, however, an important point with regard to the interpretation of Article II of the Convention. For example, should the spawning stock be considered relative to the unexploited infected population or relative to some measure of the unexploited uninfected population? The results below will further illustrate why this question is relevant.

Equilibrium Solutions at Different Levels of Exploitation and Infection

Consider the results for the resilient stock-recruit scenario (see Figure 1, $r = 10$), medium level of infection and the two harvesting strategies. Figure 3a illustrates how the prevalence changes as fishing mortality increases. When only healthy animals are harvested the percentage of infected animals in the population increases. This is because the susceptible part of the population that leads to newly-infected animals is not being harvested, since they are below the age-/size-at-first-capture. The absolute number of infected animals therefore stays the same, as does the population size of the parasites. Also note that this happens because recruitment is generally constant over a large range of spawning stock values. When both infected and healthy animals are harvested, the percentage of infected animals declines as fishing mortality increases. In this model there is no mechanism for reinfection of the population once all infected animals have been removed, but in reality this may not be the case. If, for example, other crab species are infected by the same parasite, then there is plenty of scope for reinfection of P. spinosissima.

Figure 3b illustrates the changes in the ratio between the numbers of spawners in the exploited and the unexploited (with non-zero prevalence) populations as fishing mortality increases for the two harvesting scenarios. When only healthy males are harvested, the spawning stock ratio decreases as fishing mortality increases. Such a decline would also be exhibited by a population with zero prevalence. In contrast, the other scenario shows a small increase in exploited spawning stock over unexploited at low values of fishing mortality. At higher levels of fishing mortality the ratio decreases to below 100%. The increase in numbers of spawners at low fishing mortality is a result of the decrease in the number of infected animals, which leads
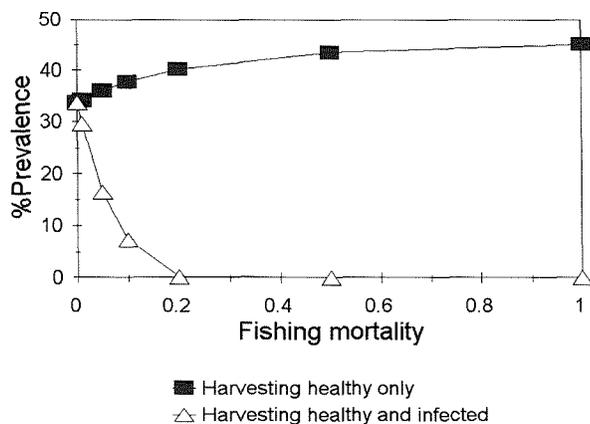
Figure 3a:
Prevalence (in %) for a range of fishing mortalities. Prevalence in the unexploited stock is 34%; the resilient stock-recruit scenario was used.
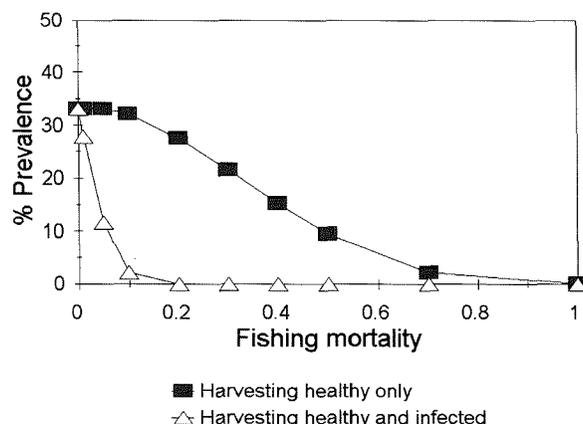

Figure 4a:
Prevalence (in %) for a range of fishing mortalities. The sensitive stock-recruit scenario was used; the unexploited prevalence is 34%.
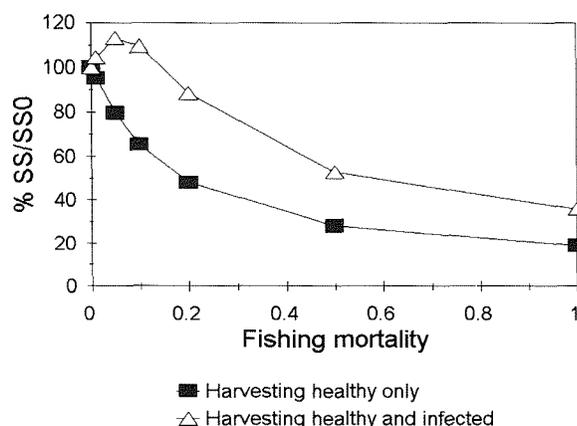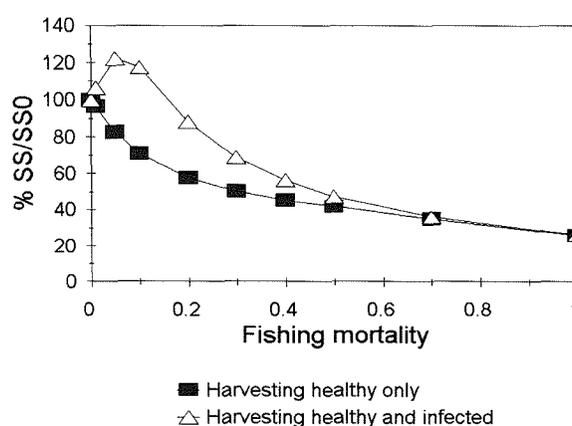

Figure 3b:
Ratios of exploited to unexploited (infected) spawning stock numbers for a range of fishing mortalities. Prevalence in the unexploited stock is 34%; the resilient stock-recruit scenario was used.

Figure 4b:
Ratios of exploited to unexploited (infected) spawning stock numbers for a range of fishing mortalities. The sensitive stock-recruit scenario was used; the unexploited prevalence is 34%.

to a decrease in the parasite population. This in turn leads to a decrease in the number of newly-infected animals. The decline in new infections implies a larger number of sexually mature healthy animals and, if fishing mortality is low enough, there is a net increase in the number of healthy animals. Also recall that there is at least one year (i.e., age class) in which mature animals are not yet harvested. This pattern of spawning stock ratios for the case where healthy and infected animals are harvested is, however, dependent on the initial prevalence, i.e., the prevalence in the unexploited population (see below). Note that in Figure 3b the spawning stock numbers have been scaled to the unexploited spawning stock numbers from the population with non-zero prevalence, $N^{ss}(F = 0, p = 34\%)$.

The same graphs for the sensitive stock-recruitment relationship (see Figure 1, $r = 0.01$) are shown in Figures 4a and b. Here the prevalence declines with increasing fishing mortality when only healthy animals are harvested, though the decline is far less rapid than when both infected and healthy animals are harvested (Figure 4a). The patterns of changes in spawning stock (Figure 4b) are quite similar to those shown in Figure 3b.

In this scenario, with the sensitive stock-recruit relationship, the prevalence declines when only healthy animals are harvested because of the very strong relationship between stock and recruitment (compare Figures 3a and 4a). For an intermediate value of r (e.g., $r = 0.02$, see Figure 1), there is an initial increase in prevalence

as fishing mortality F increases, and only at levels of F close to 1 does the prevalence start to decline.

So far I have taken a single example, one level of initial prevalence, and examined the effect of harvesting only healthy, or both healthy and infected animals. I shall now consider other levels of prevalence. Figures 5 and 6 illustrate the patterns of change in spawning stock ratios for different levels of initial prevalence and fishing mortality. The resilient stock-recruitment relationship is used in all cases. Spawning stock numbers are expressed as percentages of the unexploited, zero-prevalence spawning stock (i.e., $N^{ss}(F = 0, p = 0)$) for the two harvesting scenarios: healthy animals only (Figure 5), and both healthy and infected animals (Figure 6).

One of the important points that emerges from these two figures is the difference between spawner ratios at high fishing mortality for the two harvesting strategies. In the case where healthy and infected animals are harvested, the spawner ratios converge at high fishing mortality. This is not surprising, since the prevalence drops to zero at high fishing mortality. When only healthy animals are harvested the spawning stock always decreases. The examples shown here are for a high value of 'r', i.e., a population resilient to changes in spawning stock, but the similarity between Figures 3b and 4b suggests that the patterns would be similar for a low value of 'r', i.e., a population sensitive to changes in spawning stock.

Some Examples of the Dynamics of the Harvested Population

The above results are for the equilibrium solutions. In some cases the transition from the unexploited to the exploited equilibrium solutions is smooth and relatively rapid (Figure 7). In Figures 7, 8 and 9, the changes in spawning stock ratios are given both in terms of the unexploited zero-prevalence spawners ($N^{ss}(F = 0, p = 0)$, curve b), and in terms of the unexploited but non-zero-prevalence population (e.g., $N^{ss}(F = 0, p = 63\%)$, curve a). Harvesting starts in year 10 on an unexploited equilibrium population, and the same fishing mortality is applied in each year until a new exploited equilibrium is obtained.

In other cases, however, the transition dynamics can be more complicated. This is particularly true when recruitment is sensitive to changes in spawning stock. Figure 8 illustrates
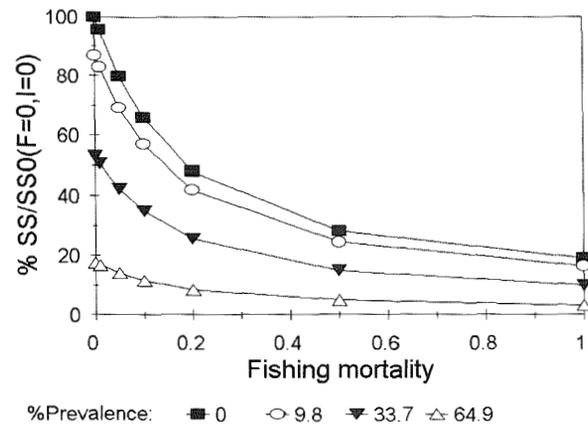
Figure 5:
Harvesting healthy animals only: spawning stock numbers at a range of fishing mortalities and prevalences, expressed as a percentage of the unexploited spawning stock when prevalence is 0. The resilient stock-recruit relationship was used.
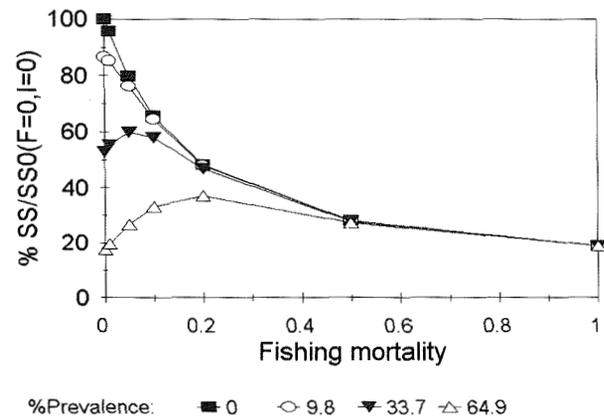

Figure 6:
Harvesting healthy and infected animals: spawning stock numbers at a range of fishing mortalities and prevalences, expressed as a percentage of the unexploited spawning stock when prevalence is 0. The resilient stock-recruit scenario was used.

the transition dynamics for the sensitive stock-recruit scenario ($r = 0.01$), harvesting only healthy animals with an initial prevalence of 56%. Here curve (a) is based on $N^{ss}(F = 0, p = 56\%)$.

The main point of interest is the rapid drop in the spawning ratio after harvesting has commenced, and the subsequent rise and fall in the ratio. Starting from 100% (curve a), the ratio drops as low as 40% before finally reaching an equilibrium at around 80%. Similar dynamics are also observed when both healthy and infected animals are harvested, and for both assumptions about recruitment (see e.g., Figure 9).
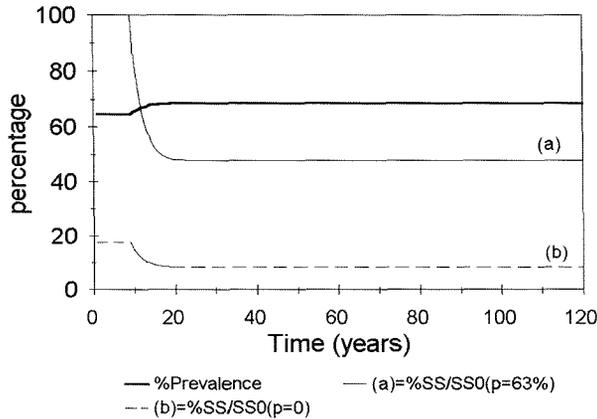
Figure 7:
Prevalence and spawning stock ratios over time for a fishing mortality of $F = 0.2$ starting in year 10 and harvesting healthy animals only. The resilient stock-recruit relationship was used.
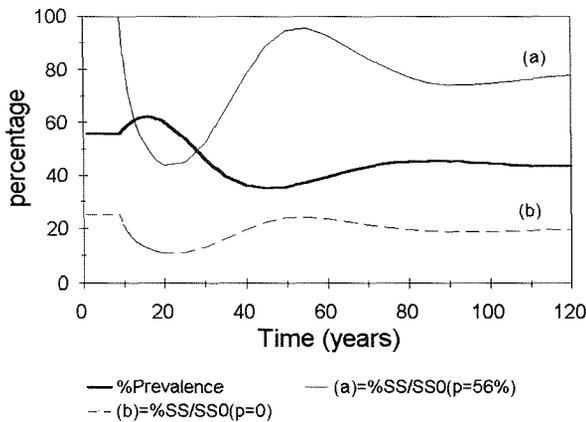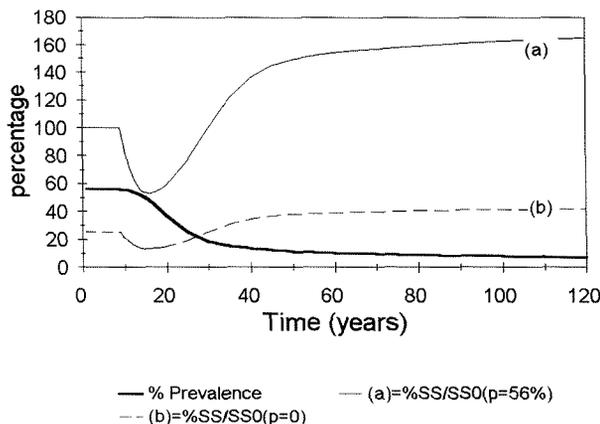

Figure 8:
Prevalence and spawning stock ratios over time for a fishing mortality of $F = 0.2$ starting in year 10 and harvesting healthy animals only. The sensitive stock-recruit relationship was used.

Figure 9:
Prevalence and spawning stock ratios over time for a fishing mortality of $F = 0.2$ starting in year 10 and harvesting healthy and infected animals. The resilient stock-recruit relationship was used.

The prevalence, the fishing mortality and the degree of interaction between the different components of the system (the parasite population, susceptible hosts and infected individuals) all affect the transition dynamics. The present lack of information on the crab-rhizocephalan system makes it impossible to say whether the dynamics illustrated in Figures 8 and 9 really would be exhibited by this stock.

DISCUSSION

The results just presented illustrate three important points. The first is that the spawning stock of an unexploited population with non-zero prevalence of *B. callosus* is likely to be below that of an unexploited population with zero prevalence. This may or may not affect recruitment, depending on the relationship between spawners and recruits. In practical terms, an assessment would provide an estimate of the spawning stock associated with a given non-zero prevalence in the population. It may be impossible to obtain an estimate of the spawning stock associated with zero prevalence.

Secondly, for the two stock-recruit relationships considered here, the spawning stock ratio decreases as fishing mortality increases when only healthy animals are harvested. When healthy and parasitised animals are harvested, the spawning stock ratio decreases less rapidly than it does when only healthy animals are harvested. In some cases, there may be an increase in the spawning stock at relatively low levels of fishing mortality. One may argue that if the stock-recruit relationship is resilient, then the spawning stock ratio may be allowed to drop to very low levels before there would be any effect on recruitment. This is true in theory, but in practice the problem is that the nature of any relationship between stock and recruitment is often unknown, particularly at the start of a new fishery.

The third point relates to the possible dynamics of the system in the period of transition between the unexploited and exploited equilibria. In some cases, the spawning stock may drop to very low levels during the transition phase, even if the exploited equilibrium level is not much lower than the unexploited level. The transition dynamics are controlled by the model structure and choice of parameters, which may not be realistic. Results, however, illustrate the importance of considering both equilibrium and dynamic properties of these types of models.

All the above points are of relevance with respect to the interpretation and implementation of Article II of the CCAMLR Convention. In particular, sub-paragraph 3(a) sets out one of the objectives as the:

'prevention of decrease in the size of any harvested population to levels below those which ensure its stable recruitment. For this purpose its size should not be allowed to fall below a level close to that which ensures the greatest net annual increment.'

There are, of course, many caveats and questions associated with the model used and the results presented here. For example, what is the most likely shape of the relationship between stock and recruitment? When are the hosts most susceptible to parasitism? Are there likely to be sub-populations of crabs in unfished areas that could lead to reinfection of sub-populations that have been harvested, and have a reduced prevalence?

Although the structure of the model is based on a reasonable amount of information from studies of other crab species that are also infected by *B. callosus*, the parameters used are largely arbitrary. This may not matter a great deal, provided the relative magnitudes of parameters are realistic. For example, age-at-first-capture is greater than age-at-maturity, and age-of-greatest-susceptibility is less than both of these.

CONCLUSIONS AND FURTHER WORK

This very preliminary study has shown that parasitism may be an important factor in the management of the crab fishery in Subarea 48.3. The type of response would depend on the recruitment dynamics of the host and the parasite. In general, there is likely to be some merit in destroying parasitised animals that appear in the catch. In all the cases considered here, the prevalence decreases more rapidly when infected crabs are also harvested than when only healthy crabs are harvested. Such a strategy would not require a reduction in the current minimum legal size requirement (102 mm CW), but it would require selection of parasitised animals from the discards in the catch. This will not be impossible in practice, since animals with externa, males in particular, are easily recognised. It may, however, be a somewhat time-consuming process, and the feasibility of such a strategy would have to be investigated.

The conclusions from this study are entirely in line with those from Kuris and Lafferty (1992). The more general model considered in that study also suggests that management strategies should vary, based on the recruitment dynamics of both host and parasite, and that the common practice of releasing infected animals is not advantageous to the host population.

At this stage, one of the most important tasks is the collection and provision of more data, particularly with respect to the following:

1. Prevalence on an appropriate spatial scale: this would enable us to investigate how 'patchy' parasitism is, and whether the overall level is high enough to cause concern.

2. Information on growth of healthy and infected animals: ideally this should include information on moult frequency and moult increment to enable us to construct a size-based model which could then take estimates of size-at-maturity and at-first-capture directly into account. Information on growth is of course essential for management, even in the absence of parasitism.

There is also a great deal of scope for improving and extending the modelling work. For example, estimates of model parameters appropriate for *P. spinosissima* in Subarea 48.3 should be considered. A size-based model may be more appropriate than an age-based model. Such an approach should consider size classes keyed to critical life history events. Females should be included in the model because, even if they are not commercially harvested, they are also a source of infection and a key component in the stock-recruitment dynamics. It may also be useful to do more extensive sensitivity analyses of the models to determine which parameters are most important. The model used in this study is based on assumptions about the functional forms for the stock-recruitment and host-parasite relationships. It would be prudent to consider the effects of other possible relationships.

ACKNOWLEDGEMENTS

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Tableau 1: Fréquence de la présence, dans un échantillon, du rhizocéphale *B. callosus* (en %), la taille totale de l'échantillon étant indiquée entre parenthèses, selon le Tableau 2 de Otto et MacIntosh (1992) exception faite des individus porteurs de microsporidies.

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EQUATIONS

The different equations used in the hypothetical host-parasite model are given below. The total population N consists of healthy H and infected I animals in each age class where a refers to age and t to time (year in this case):

$$N_{a,t} = H_{a,t} + I_{a,t} \quad \text{for all ages}$$

Recruitment to the first age class ($a = 1$) is as follows:

$$H_{1,t} = R_t \quad \text{and} \quad I_{1,t} = 0$$

where R_t is the number of recruits in year t, given by the stock-recruit relationship:

$$R_t = R\left(1 - e^{-rN_t^{ss}}\right)$$

N_t^{ss} is the number of spawners in year t and is the sum of all healthy animals in age classes from age-at-maturity, a_{mature}, and above. The parameter R determines the asymptotic level of recruitment and r determines how steep the increase in R_t is as N_t^{ss} increases (see Figure 1).

Healthy animals are assumed to be susceptible only between certain ages, referred to as the lower and upper age of susceptibility, a_{low} and a_{up} respectively. Also note that it is assumed that the age-at-first-capture is larger than the age-at-maturity. It is unknown where the upper age-at-susceptibility falls with regard to the age-at-maturity or age-at-first-capture, and I assume that:

$$1 \leq a_{low} < a_{up} < a_{mature} < a_{capture}$$

The equations for the healthy and infected parts of the population when $a_{low} \leq a \leq a_{up}$ (i.e., susceptible age classes) are:

$$H_{a+1,t+1} = H_{a,t} \, S_H \left(1 - q\, P_t\right)$$

$$I_{a+1,t+1} = I_{a,t} \, S_I + q\, P_t \, H_{a,t} \, S_H$$

where q is the rate of infection and P_t is the number of parasites (larvae) available to infect healthy animals. Note that double infections are ignored. The terms S_H and S_I are the survival terms for the healthy and infected categories respectively. For $a_{up} < a < a_{capture}$ the equations are:

$$H_{a+1,t+1} = H_{a,t} \, S_H \quad \text{and} \quad I_{a+1,t+1} = I_{a,t} \, S_I$$

and for $a \geq a_{capture}$ the equations are:

$$H_{a+1,t+1} = H_{a,t} \, S_H \, e^{-F} \quad \text{and} \quad I_{a+1,t+1} = I_{a,t} \, S_I \, e^{-d}$$

Note that the values of the fishing mortality terms are as follows for the different scenarios:

(a)   No harvest: $F = 0, d = 0$
(b)   Harvesting healthy animals only: $F > 0, d = 0$
(c)   Harvesting healthy and infected animals: $F > 0, d = F$

The equation that determines the number of parasite larvae in each year is given by:

$$P_{t+1} = kI_t$$

where k is the proportionality constant, also called the larval production rate, and I_t is the total number of parasitised individuals (summed over all age classes). This equation is effectively a stock-recruitment relationship for the parasite because each infected animal is assumed to carry one parasite and the time-lag between recruits P_{t+1} and 'spawning parasites', I_t, allows one year for development of externa and the sexual maturation of the parasite.

H_t is the total number of healthy individuals (summed over all age classes) in year t, and the total population is given by:

$$N_t = H_t + I_t$$

The spawning stock numbers in year t, N_t^{ss} is calculated as the sum of healthy animals in age classes from the age-at-first maturity and above in year t. The prevalence is calculated as the ratio of infected crabs to total population:

$$\text{Prevalence in year } t = \frac{I_t}{N_t}$$

PARAMETERS

The parameter values used in the analyses are summarised here for completeness. I emphasise that values are largely arbitrary and do not (necessarily) relate to any real crab population. Parameters were partly chosen to provide three levels of prevalence in the equilibrium, unexploited population (see text).

Table A1: Parameter-values used in the analyses.

Recruitment	Infection Rates
$R = 200$ a) $r = 10$ - resilient S-R b) $r = 0.1$ - sensitive S-R relationship	a) $q = 0.009$ b) $q = 0.010$ c) $q = 0.012$
Relevant Age-parameters $a_{low} = 1$ $a_{up} = 2$ $a_{mature} = 5$ $a_{capture} = 6$	Larval Production Rate $k = 0.05$
Annual Survival Rates $(\exp(-m))$ $s_H = \exp(-0.1)$ $s_I = \exp(-0.15)$	Fishing Mortality $0 \leq F \leq 1.0$ $0 \leq d \leq 1.0$