

Modelling Crustacean Fisheries: Effects of Parasites on Management Strategies

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The reproductive performance of commercially important crustaceans may be considerably affected by symbiotic nemertean egg predators and parasitic castrators. Because these parasites commonly affect only females or feminize males, they may be protected by management practices that protect females. To manage a parasitized stock, we suggest that strategies should vary depending on the recruitment dynamics of both host and parasite. For a certain spatial scale, recruitment to a population may be "open" or "closed" depending on the behavior of planktonic larvae, the duration of these planktonic stages, and the flush rate of the environment of the adult host. Both hosts and parasites may have open or closed larval recruitment. We developed mathematical models to investigate the impact of protection of females on a hypothetical fishery for different combinations of host and parasite recruitment dynamics. The models suggest that the common practice of releasing females is not advantageous when a fishery is affected by a parasite. Retaining females in the catch is preferable in most cases. Treating or culling infected females may be advisable when host recruitment is closed.

Le succès de la reproduction d'espèces de crustacés d'importance commerciale peut être fortement compromis par des németéens symbiotes prédateurs des oeufs et des «castrateurs» parasites. Étant donné que ces parasites n'attaquent ordinairement que les femelles et féminisent les mâles, ils peuvent être protégés par les mesures de gestion visant la protection des femelles. Les auteurs recommandent que les stratégies de gestion de stocks parasités devraient être adaptées à la dynamique du recrutement de l'hôte et du parasite. À une certaine échelle spatiale, le recrutement à une population peut être «ouvert» ou «fermé» selon le comportement des larves planctoniques, la durée de ces stades planctoniques et le taux d'élimination de l'environnement de l'hôte adulte. Les hôtes et les parasites peuvent aussi avoir un recrutement de larves ouvert ou fermé. Les auteurs ont élaboré des modèles mathématiques pour étudier l'impact de la protection des femelles sur une pêcherie hypothétique en fonction de diverses combinaisons de la dynamique du recrutement des hôtes et des parasites. Les modèles portent à croire que la pratique commune de remettre les femelles à l'eau n'est pas avantageuse lorsqu'une pêcherie est compromise par un parasite. Ils sont d'avis que ces femelles ne devraient pas être remises à l'eau dans la plupart des cas. Le traitement ou la destruction sélective des femelles infectées peut être indiqué lorsque le recrutement de l'hôte est fermé.

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Infectious organisms may affect growth (Overstreet 1979; Lester 1978b; Sloan 1984), reproduction (Sloan 1984; Lester 1978a; Hicks 1982), egg survival (Wickham 1979; Kuris and Wickham 1987; Campbell and Bratney 1986; Shields et al. 1990a; Kuris 1992), longevity (Meyers et al. 1989), and marketability (Meyers et al. 1989; Sparks and Hibbits 1979) of commercially important Crustacea. In some cases, the infectious agents are abundant and may significantly affect host populations (Botsford and Wickham 1978; Botsford 1986; Hobbs and Botsford 1989; Shields et al. 1990b; Kuris et al. 1991). In other situations, insufficient data are available to conclude that host population dynamics are affected, but the infectious organisms are sufficiently prevalent to suggest so (Sloan 1984; Sparks 1982).

Several distinctive host–parasite interactions may be important to fisheries. Microbial diseases, which generally reproduce to high intensities within a host, include bacteria (e.g. Stewart et al. 1966), fungi (e.g. Sparks 1982), protozoans (e.g. Newman and Ward 1973; Meyers et al. 1989; Skurdal et al. 1990), and viruses (e.g. Couch et al. 1975; Johnson 1983). The population dynamics of such "microparasites" (sensu Anderson

and May 1979) have been extensively investigated (Anderson and May 1979, 1981; May 1985) with some consideration given to finfish fisheries (Dobson and May 1987).

Parasitic castrators, such as rhizocephalan barnacles and eucaridean isopods, block the reproductive output of their host (Kuris 1974). Male hosts are frequently feminized morphologically and behaviorally (e.g. Veillet 1945; Reinhard 1956; Rasmussen 1959; Phillips and Cannon 1978). Unlike microparasites, the pathological effects of parasitic castrators are not additive; an individual castrator completely prevents host reproduction (Kuris 1974).

Nemertean worms feed on embryos of decapod crustaceans (Humes 1942; Kuris 1978; Wickham 1979; Aiken et al. 1985; Wickham et al. 1985, Shields et al. 1989; Shields and Kuris 1990). These have been termed symbiotic egg predators (Kuris 1971, 1992; Kuris and Wickham 1987). At high intensities, nemerteans can kill more than half the eggs produced by host populations (Wickham 1979, 1986; Shields and Kuris 1988; Kuris et al. 1991). They have been included in models of the cyclic dynamics of the Dungeness crab, *Cancer magister*, fish-

ery in California (Botsford and Wickham 1978; Botsford 1986; Hobbs and Botsford 1989).

Standard management practices on commercial crustacean species, including restrictions on catch (number of individuals), size (minimum length or width), sex (males only), effort (number of fishing days), location, seasons (usually nonbreeding), and gear, are usually ad hoc measures aimed at protecting the reproductive output of the stock (Botsford 1992). Each of these practices may increase the overall impact of parasites on future yield if fishing increases the relative abundance of parasitized hosts. This may occur when parasitized individuals grow more slowly (Hicks 1982), females are not fished but the infectious agent occurs predominantly on females (e.g. Lester 1978a; Wickham et al. 1985; Shields et al. 1990b; Kuris et al. 1991), changed behavior of parasitized individuals reduces their rate of entry to traps (Crothers 1968; Sloan 1984; Skurdal et al. 1990), heavily parasitized geographic locations are less exploited by fishermen (Hicks 1982), or infected individuals are released following shipboard culling because they are unmarketable (Petrushevski and Schulman 1958).

Management is essential for conservation and perpetuation of crustacean fisheries. We argue that infectious organisms substantially impact some important crustacean fisheries and that they should be considered in management strategies. Our argument is based on a simple fisheries model in which we incorporate parasites and then vary management practices and recruitment dynamics of both host and parasite.

Recruitment Dynamics

To manage a parasitized stock, we propose that fishing practices should vary depending on the recruitment dynamics of both the host and parasite. Recruitment to a stock may be conceived as comparatively "open" or "closed" (sensu Caswell 1978) based on the relative spatial scales of the fishery compared with host and parasite population dynamics. For the host, this depends on the behavior of planktonic larvae, duration of larval stages, and the flush rate of the water mass of the adult habitat. In open recruitment systems, larval dispersal is widespread and postlarval settlement is not dependent on productivity of adults from that location. In closed systems, larval dispersal is relatively confined and settlement is dependent on productivity of the adults from that location. Larval duration is probably the most useful and available clue for appropriate classification of the spatial scale of host recruitment dynamics.

For the parasites, the mode of transmission and infection dynamics are the principal determinants of the scale of parasite recruitment. Closed recruitment will likely result if the infectious organism is transmitted by contact between infected and uninfected hosts (including cannibalism), the free-living infectious stage is short lived or limited in its mobility, or the movement of larvae between water masses is restricted geographically (e.g. Sloan 1985).

The scale of recruitment patterns has attracted increasing attention with respect to theory (Roughgarden et al. 1988; Warner and Hughes 1988; Underwood and Fairweather 1989; Possingham and Roughgarden 1990) and its application to fisheries (Dadswell 1979; Harding et al. 1983; Ennis 1986). As most benthic crustaceans important to fisheries have long-lived larvae, it is generally assumed that the source of larvae for recruitment is not locally based (Jamieson 1986). However, for the American lobster, *Homarus americanus*, the crustacean for which there are the most data on geographic abundance and

movement of larvae, the nature of recruitment patterns continues to be actively debated (e.g. Ennis 1986).

Classical population theory is based on the assumption of a closed system, and Dobson and May (1987) modelled the effects of parasites on fisheries in this context. However, the likelihood that the scale of parasite recruitment may differ from that of the host introduces unexpected complexity to host-parasite recruitment dynamics. Figure 1 illustrates the 2×2 contingency matrix for open versus closed recruitment of hosts and parasites. We speculate that parasite recruitment will often be closed relative to the recruitment pattern of the host. Comparatively few parasites of crustaceans appear to have long-lived, widely dispersing transmissive stages. For example, the rhizocephalans, an important group of parasitic castrators (Kuris 1974), have free-living transmissive stages (nauplii, cypris) that are nonfeeding and usually competent to infect a new host in a few days (Høeg and Lützen 1985).

A likely example of a parasite closed – host open recruitment system is the interaction between the nemertean egg predator, *Carcinonemertes regicides*, and its host, the red king crab, *Paralithodes camtschaticus*, in the Kodiak Archipelago and in southeastern Alaska (Fig. 1). Parasite abundance varies greatly on a small geographic scale and, although transmission has not been directly studied, the temporal pattern of rapid increase on infected hosts indicates that the free-living stage is so brief that autoinfection has been postulated (Kuris et al. 1991). In contrast with the parasite, the host's larvae develop over a 3- to 4-mo period (Weber 1967), and substantial larval transport over considerable distances appears probable for some areas (Haynes 1974).

A system in which recruitment of both host and parasite is closed is the golden king crab, *Lithodes aequispina*, and the rhizocephalan, *Briarosaccus callosus*, in British Columbia (Fig. 1). Some populations are confined in isolated fjords where sills near the mouths restrict water movement (Sloan 1984, 1985). Host larval behavior (e.g. hatching at depth) enhances the likelihood of retention. Parasite larvae are released in the same habitat (Sloan 1985). Their retention is further enhanced by a relatively short larval duration (Hawkes et al. 1985). Another closed–closed system occurs with crayfish, *Astacus astacus*, and a microsporidian. Crayfish lack a planktonic larval stage and the microsporidian, *Thelohania*, is transmitted by cannibalism (Skurdal et al. 1990).

An example of open host and parasite recruitment is the Dungeness crab fishery in northern California which is heavily infested with *Carcinonemertes errans* (Wickham 1986) (Fig. 1). Larval development of Dungeness crabs is long (3-4 mo, Reilly 1983), and exposure to strong currents prevents the separation of distinct populations (Soulé and Tasto 1983). Although larval settlement of *C. errans* has not been achieved in laboratory studies, preliminary evidence indicates a lengthy larval period of more than 50 d (Roe 1979).

Examples of host closed – parasite open recruitment patterns might be expected in situations where crustaceans act as intermediate hosts and definitive hosts disperse parasite eggs widely (Kuris 1990). This may occur with the Chinese lung fluke, *Paragonimus westermani*, a serious human parasite, that uses the Chinese mitten crab, *Eriocheir japonicus*, and other freshwater crustaceans as intermediate hosts. Humans and other vertebrates become infected by eating raw crabs that may be parasitized at a prevalence (the proportion of hosts infected, Margolis et al. 1982) of 70% (Yokogawa 1953). These larval trematodes are "typical parasites" (sensu Kuris 1974).

	Host closed	Host open
Parasite closed	<p><i>Lithodes aequispina</i> <i>Briarosaccus callosus</i></p> <p><i>Astacus astacus</i> <i>Thelohania contejeani</i></p>	<p><i>Paralithodes camtschaticus</i> <i>Carcinonemertes regicides</i></p>
Parasite open	<p><i>Eriocheir japonicus</i> <i>Paragonimus westermani</i></p>	<p><i>Cancer magister</i> <i>Carcinonemertes errans</i></p>

FIG. 1. Interaction between the scale of host and parasite recruitment dynamics presented as a 2×2 contingency table. Examples of fisheries in these categories are provided.

Although there may be potential for these parasites to affect crabs, control of lung flukes is directed at reducing transmission to humans. Our general recommendations do not address this sort of public health issue.

Table 1 presents a list of important crustacean fisheries for which there is substantial evidence that infectious diseases may significantly affect the yield or reproductive output of at least some stocks. Unfortunately, the relative scales of recruitment for host and parasite are not known for most of the examples and they cannot, therefore, be placed in the recruitment categories of Fig. 1.

We emphasize that open and closed recruitment are relative terms, although we treat them in an absolute sense for modelling purposes. The most readily recognizable systems are those in which the recruitment pattern of the host strongly contrasts with transmission dynamics of the parasite (host open – parasite closed, host closed – parasite open). The distinction between host open – parasite open and host closed – parasite closed depends on the scale of recruitment relative to that of the fishery. For example, a fishery that exploits a small geographic region of a closed host population might be best managed as an open system if recruits to the fished area were independent of the parent stock in that area.

The Model

Efforts to diminish the impact of a parasite on a fishery may benefit from the incorporation of epidemiological theory in fisheries models. The idea that a reduction in host abundance below a certain threshold will eliminate a parasite was first argued analytically by Kermack and McKendrick (1927). Dobson and May (1987) proposed the same mechanism for finfish fisheries.

Here, we present a model that compares the effects of various management strategies on a hypothetical crustacean fishery that is parasitized by a parasitic castrator. The model is developed for the four recruitment patterns of host and parasite depicted in Fig. 1; we have not attempted to simulate a specific system.

We employed difference equations to subdivide a crustacean host stock into five life history stages (larvae, juveniles, males, uninfected females, and infected females). Our comparisons

are based on stock sizes and fishery yields at equilibrium levels. For this reason, the models were deterministic and deliberately stabilized by density-dependent natural mortality.

Assumptions

To specifically investigate crustacean fisheries, we assumed that the host reproduces seasonally and the parasite impacts reproduction (not mortality) and we distinguish fishing mortality for both male and female hosts.

We assumed that per capita natural mortality of infected and uninfected hosts (adults and juveniles) was dependent on the density of hosts (with juveniles using one half the resources of adults). Per capita larval mortality and fishing mortality, on the other hand, were assumed to be density independent.

The parasite population was represented by the prevalence of infected hosts. In the model, parasites (actually parasitic castrators) eliminated the fecundity of infected females (although we believe that egg predators and microparasites will have similar effects, these parasites cause only partial reduction in host fecundity and, for egg predators, induce intensity-dependent pathology and have an aggregated distribution). Parasite mortality occurred only when infected hosts died or were treated. If the parasite affects both marketability and reproduction, its impact on the fishery will be greater than we calculate. This would be especially true for cases where host recruitment is open.

The parasite was assumed to be host specific. If the parasite is not host specific, fishing the target species would have a lessened effect on prevalence. Petrushevski and Schulman (1958) suggested, in this case, that efforts should be made to harvest alternative hosts as well.

We assumed that fertilization rates for females were independent of sex ratio and that the sex ratio of recruits was 1:1. Recruitment of host or parasite was defined as either open or closed. Where host recruitment was closed, larval density was a linear function of the density of adult, uninfected females. Where the recruitment of the host was defined as open, larval density was constant (in nature this would be a stochastic parameter). Where parasite recruitment was closed, parasite transmission was a linear function of the product of infected

TABLE 1. Some infectious agents for which there is evidence that recruitment, yield, or marketability of commercially important crustacean hosts was substantially affected. Prevalences reported are peak values.

Fishery	Region	Parasite	Interaction	Prevalence (%)	Reference(s)	Remarks
<i>Lithodes aequispina</i>	British Columbia	<i>Briarosaccus callosus</i> (Rhizocephala)	Parasitic castrator	40	Sloan 1984, 1985	Parasitized hosts behaved like postspawned female hosts. Host and parasite are continuous spawners; had reduced growth
<i>Paralithodes camtschaticus</i>	Alaska	<i>Carcinonemertes regicides</i> (Nemertea)	Symbiotic egg predator	100	Kuris et al. 1991	1983-85 caused brood failure in Cook Inlet, around Kodiak I., and in southeastern Alaska; autoinfection
<i>Portunus pelagicus</i>	Queensland	<i>Sacculina granifera</i> (Rhizocephala)	Parasitic castrator	12-50+	Lester 1978a; Bishop and Cannon 1979	Parasitized crabs did not molt; behaved like females
<i>Callinectes sapidus</i>	Gulf of Mexico	<i>Loxothylacus texanus</i> (Rhizocephala)	Parasitic castrator	?	Overstreet 1978	Affects growth, epizootics in 1965 and 1977
	Virginia	<i>Paramoeba perniciososa</i> (Sarcodina)	Microparasite	57	Newman and Ward 1973; Johnson 1977; Couch 1983	"Grey crab disease" always fatal; seasonal epizootics are a frequent cause of mass mortalities
<i>Carcinus maenas</i>	Eastern Atlantic, Mediterranean	<i>Sacculina carcini</i> (Rhizocephala)	Parasitic castrator	25-100	Crothers 1968; Høeg and Lützen 1985	Parasitized crabs behave like reproductive females
<i>Cancer magister</i>	California	<i>Carcinonemertes errans</i> (Nemertea)	Symbiotic egg predator	100	Wickham 1979, 1986	Can cause brood failure at high intensities
<i>Chionoecetes bairdi</i>	Alaska	cf. <i>Haemotodinium</i> sp. (Dinoflagellida)	Microparasite	?	Meyers et al. 1989	"Bitter crab disease"; infected crabs not marketable; fatal
		<i>Trichomaris invadens</i> (fungi)	Microparasite	75	Sparks and Hibbits 1979; Sparks 1982; Hicks 1982	"Black mat disease"; affects population dynamics, growth reproduction, and marketability
<i>Homarus americanus</i>	North Atlantic	<i>Aerococcus viridans</i> (bacteria)	Microparasite	40	Stewart et al. 1966; Stewart 1975	"Gaffkemia"; epizootics reported; infection via damaged cuticles; mortality in shipping
<i>Penaeus duorarum</i>	Gulf of Mexico	<i>Baculovirus penaei</i> (virus)	Microparasite	80	Couch and Courtney 1977; Couch et al. 1975	Mortality increases with pollutant stress; transmission postulated via cannibalism

female density and uninfected female density. Finally, where parasite recruitment was open, parasite transmission was a linear function of the density of adult, uninfected females.

Per capita fishing mortality, defined as the proportion of adults fished (juveniles were not caught), was independent of density. The yield of the fishery was, therefore, the product of the fishing mortality and the size of the fished population.

Model Structure (see Fig. 2)

(1) If both host and parasite recruitment are closed, the life history stages of the host are represented as

$$(1a) L_{t+1} = sbF_t$$

where L_{t+1} is the number of larvae at time $t + 1$, s is the proportion of larvae that survive to settlement, b is the number of larvae produced per uninfected female, and F_t is the number of uninfected females at time t ,

$$(1b) J_{t+1} = (1 - d_t)L_t$$

where J_{t+1} is the number of juveniles at time $t + 1$ and d_t is the density-dependent per capita natural mortality at time t ,

$$(1c) M_{t+1} = (1 - d_t)(1 - f_m)(M_t + J_t/2)$$

where M_{t+1} is the number of males at time $t + 1$ and f_m is the proportion of the males taken by the fishery,

$$(1d) F_{t+1} = (1 - d_t)(1 - f_f)(F_t + J_t/2 - (\beta_1 L_t)(F_t + J_t/2))$$

where f_f is the proportion of the females taken by the fishery, β_1 is the number of uninfected hosts that become infected by the presence of one infected host from t to $t + 1$ (transmission efficiency), and I_t is the number of infected females at time t , and finally,

$$(1e) I_{t+1} = (1 - d_t)(1 - f_p)(I_t + (\beta_1 I_t)(F_t + J_t/2)).$$

The yield to the fishery is presented in three parts, $Y_{M_{t+1}}$, $Y_{F_{t+1}}$, and $Y_{I_{t+1}}$ where Y_{t+1} is the yield at time $t + 1$ (specified by life history stage):

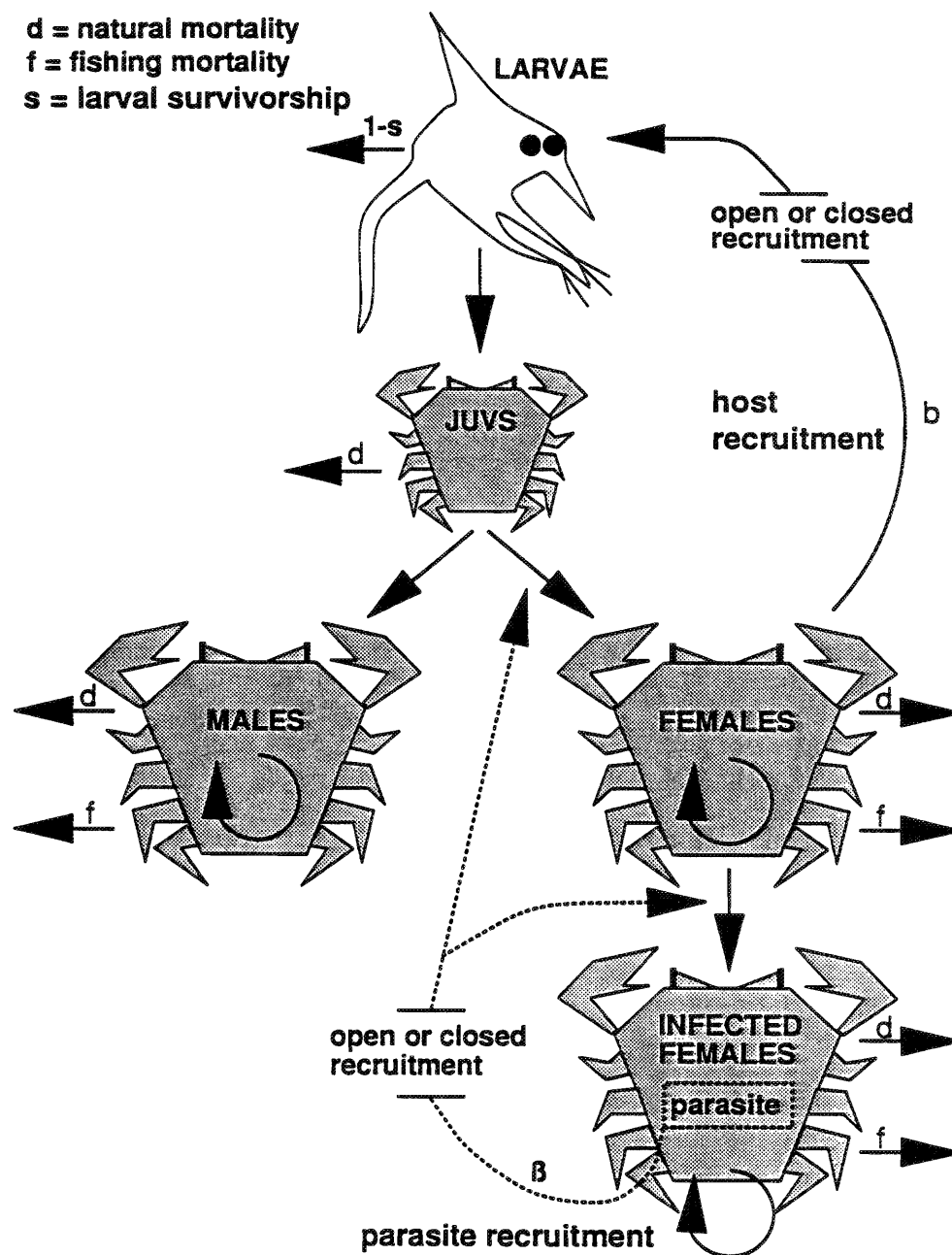


FIG. 2. Flowchart representation of the life history stages – infectious dynamics model. Boxes represent abundances of five life history stages of a crustacean host. Solid arrows represent the movement of individuals into and out of these stages. Broken arrows represent the effect of parasites on the infection status of females and juveniles. Infected females do not reproduce.

$$(1f) \quad Y_{Mt+1} = (M_t + J_t/2)f_m(1 - d_t)$$

$$(1g) \quad Y_{Ft+1} = (1 - \beta_1 I_t)(F_t + J_t/2)f_f(1 - d_t)$$

$$(1h) \quad Y_{It+1} = (I_t + \beta_1 I_t(F_t + J_t/2))f_f(1 - d_t)$$

Natural mortality is a function of stock size such that

$$(1i) \quad d_t = (M_t + F_t + I_t + J_t/2)/K$$

where K is a constant that is proportional to the carrying capacity.

(2) If parasite recruitment is open and host recruitment is closed, all the equations in part 1 apply except that

$$(2a) \quad F_{t+1} = (1 - d_t)(1 - f_f)(1 - \beta_2)(F_t + J_t/2)$$

where β_2 is the proportion of uninfected hosts that become infected over time t . Furthermore,

$$(2b) \quad I_{t+1} = (1 - d_t)(1 - f_f)(I_t + \beta_2(F_t + J_t/2))$$

$$(2c) \quad Y_{Ft+1} = (1 - \beta_2)(F_t + J_t/2)f_f(1 - d_t)$$

$$(2d) \quad Y_{It+1} = (I_t + \beta_2(F_t + J_t/2))f_f(1 - d_t)$$

(3) If host recruitment is open and parasite recruitment is closed, all the equations in part 1 apply except that

$$(3) \quad L_{t+1} = L_t$$

(4) If both host and parasite recruitment are open, all of the equations in part 1 apply except those modifications made in parts 2 and 3.

Management Strategies

We investigated the following four management strategies: (1) all adult individuals were kept by the fishery ("keep females"), (2) only adult males were kept by the fishery ("release females"), (3) only adult males were kept by the fishery and infected females were not released ("cull infected females"), and (4) only adult males were kept by the fishery and infected females were treated before they were released ("treat infected females"). These were integrated into the model with the following modifications: keep females, $f_f = f_m$; release females, $f_f = 0$; cull infected females, $f_f = f_m$, $F_{t+1}^* = F_{t+1} + (1 - d_f/2)YF_{t+1}$; and treat infected females, $f_f = f_m$, $F_{t+1}^* = F_{t+1} + (1 - d_f/2)(YF_{t+1} + YI_{t+1})$.

The carrying capacity of the host in the absence of parasites was set to equal 1000 individuals. Simulations were run using an initial equilibrium of 100, 200, or 500 infected females (figures show 200). fishing mortality was then varied from 0 to 1 and yield and the abundance of males, uninfected females, and infected females were recorded for the four management strategies described above.

Results

The effects of management strategies or fishing tactics on yield (in number of marketable individuals), stock size, sex ratio, and parasite prevalences are presented in Fig. 3 and 4. The outcomes are varied and suggest that strong interactions between management, recruitment, and parasites are likely to occur.

No Parasites

To allow a comparison with other published models and clearly demonstrate the effect of parasites, we first present the behavior of the model in the absence of parasites.

Closed host recruitment

Keeping females produced dynamics similar to classic surplus production models (Ricker 1954). This tactic generated a comparatively higher yield at low fishing mortality than did releasing females, due, primarily, to the inclusion of both sexes in the catch (Fig. 3A). The reduction in stock size, however, was more dramatic because recruitment was lower. Maximum sustainable yield, MSY, occurred at an intermediate level of fish mortality where stock size is reduced to half the carrying capacity. With high fishing mortality, both stock and yield declined to zero (sex ratio remained equal).

There was a positive correlation between fishing mortality and yield when females were released (Fig. 3A). This caused a marked decrease in the proportion of males and a slight drop in stock size. If we had assumed that fertilization rate decreased as sex ratio became strongly biased towards females, yield would have declined at sufficiently high fishing mortality.

Open host recruitment

Abundance decreased with increasing fishing mortality, but fishing did not affect the availability of new recruits. For this reason, yield increased with fishing mortality whether females were kept or released (Fig. 3C and 3D). Yield was over twice as high if females were kept than if they were released because both sexes were included in the catch and the productivity of the stock increased at low population densities.

Parasites present

Closed host recruitment

If host recruitment was closed, parasites reduced stock abundance. The percent reduction in host abundance was equal to the percent of individuals that were castrated. This is analogous to results of analytical models of parasitic castrators (Lafferty 1991). Under these conditions, releasing females returned a consistently low yield, even if fishing mortality was high (Fig. 4B and 4F). This was caused by an increase in the abundance of infected females and a subsequent decrease in the abundance of uninfected females. Keeping females, on the other hand, reduced the prevalence of the parasite.

If parasite recruitment was closed, at intermediate levels of fishing mortality, prevalence fell to zero and the system reverted to the hump-shaped trajectory for the yield curve in the absence of parasites (Fig. 4A and 4E). Both culling or treating infected females reduced prevalence to zero at an intermediate fishing mortality. The system then followed the trajectory for releasing females in the absence of parasites (Fig. 3B and 3D).

Open parasite recruitment (Fig. 4E–4H) produced the lowest yields because no fishing strategy can completely eliminate the parasite, and recruitment to the stock is dependent on uninfected female host abundance. Keeping females drove host stock size and yield to zero at moderate fishing mortality. Releasing females provided yields that increased slowly with increasing fishing mortality. Culling infected females generated a higher yield than did releasing females because more resources were made available to the stock. Treating infected females produced the highest yield due to the corresponding increase in reproductive output.

Open host recruitment

If host recruitment was open, parasitism had no effect on the yield of the stock (Fig. 4I–4P). Culling infected females generated a slightly higher yield than either treating infected females or releasing females due to the small increase in productivity associated with lowered stock size.

Fishing affected parasite prevalence. If parasite recruitment was closed, keeping females reduced parasite prevalence as fishing mortality increased, ultimately eliminating the parasite from the stock. Releasing females, under the same conditions, had the opposite effect; this led to greater than 50% prevalence at high fishing mortality. In contrast, if parasite recruitment was open, releasing females led to a slight increase in parasite prevalence, while keeping females did not affect prevalence.

Discussion

For closed systems, Dobson and May (1987) suggested that increasing fishing mortality could eliminate a parasite without causing the collapse of the fishery if the transmission threshold was above the MSY. This assumes that a fishery takes all individuals with equal probability. Parasites of crustaceans, however, often affect only females (e.g. nemertean egg predators) or feminize male hosts (e.g. Rhizocephala). Such hosts may be protected by ad hoc management practices (especially if reproductive output declines). In this case, our model indicates that increased fishing mortality will increase the impact of a parasite. For fishing pressures to reduce parasitism, parasitized individuals must be kept, culled, or treated and released. Which strategy will be most effective depends partially on the recruitment dynamics of the host and parasite. These same arguments apply in any case where a fishery takes a disproportionately

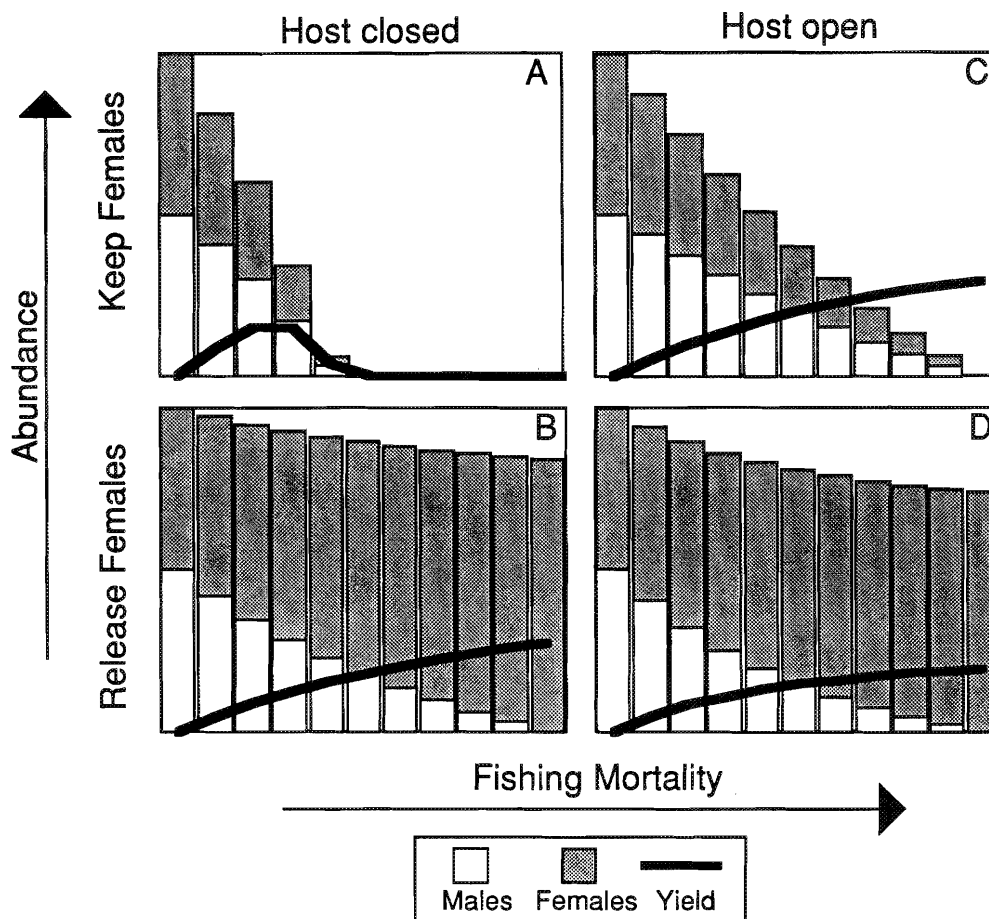


FIG. 3. Fishery yield (solid lines) and the abundance of males (open bars) and females (shaded bars) as a function of fishing mortality for closed and open recruitment when the fishery releases or keeps females.

large percentage of uninfected hosts due to size limits, altered behavior, etc.

Our model limits its investigation of parasitism to female castration. If males are also castrated, the impact of parasitism on the fishery would be higher if infected males were normally released by the fishery, fertilization were dependent on uninfected male density, or if castrated males copulated unproductively with uninfected females. In these cases, the strategy that we suggest for dealing with infected females should also be applied to infected males.

Because stocks may be linked by an exchange of larvae, our modelling of stocks as isolated entities is oversimplified. For example, although parasites will not affect recruitment if host recruitment is open, they may indirectly impact distantly connected stocks that are dependent on a shared source of recruits. This calls for careful evaluation of associated stocks prior to the initiation of a management strategy. A series of connected open systems might be best managed as a single closed system. If variation in parasite prevalence exists between these systems, an adaptive management approach might be most appropriate. In this case, regions with high prevalence of the parasite might be fished with removal of infected hosts. If recruitment of the parasite is locally closed, it may be possible to reduce the impacts of the parasite without significantly reducing the larval pool shared by the connected host stocks. If parasite recruitment is open (within a stock), fishing infected hosts will reduce the export of parasites into other connected stocks.

We note that certain crustacean fisheries are suitable for experimental manipulations to test theoretical predictions and improve yield or recruitment. Many crab and lobster fisheries protect reproductive capacity by releasing females or, at least, ovigerous females, and undersized individuals. Most modern fisheries are sufficiently intensive that a very high proportion of the annual recruits that exceed the fishable size threshold are caught in each fishing season (e.g. Ennis 1986; Jamieson 1986). Consequently, a considerable proportion of the females and small males in these fisheries are also briefly handled and released each season. This is a unique feature of these fisheries that enables experimental intervention.

The Alaskan red king crab fishery is infested with nemertean egg predators in the Kodiak, Cook Inlet, and Southeastern Management Areas, and certain fisheries experience substantial parasitization by rhizocephalans (Table 1). These cases may be suitable for a large-scale manipulation. Experiments could test the hypothesis that diseases affecting reproductive output are an important determinant of subsequent recruitment to the fishery. In practical terms, such an experimental probe may determine whether local stocks can recover. Preconditions for experimentation include classification of the scale of recruitment for both host and parasite as relatively open or closed, determination of the geographic boundaries of closed cells, and cooperation of the commercial fishing industry. Knowledge of the dispersion pattern of parasites among the host populations, of

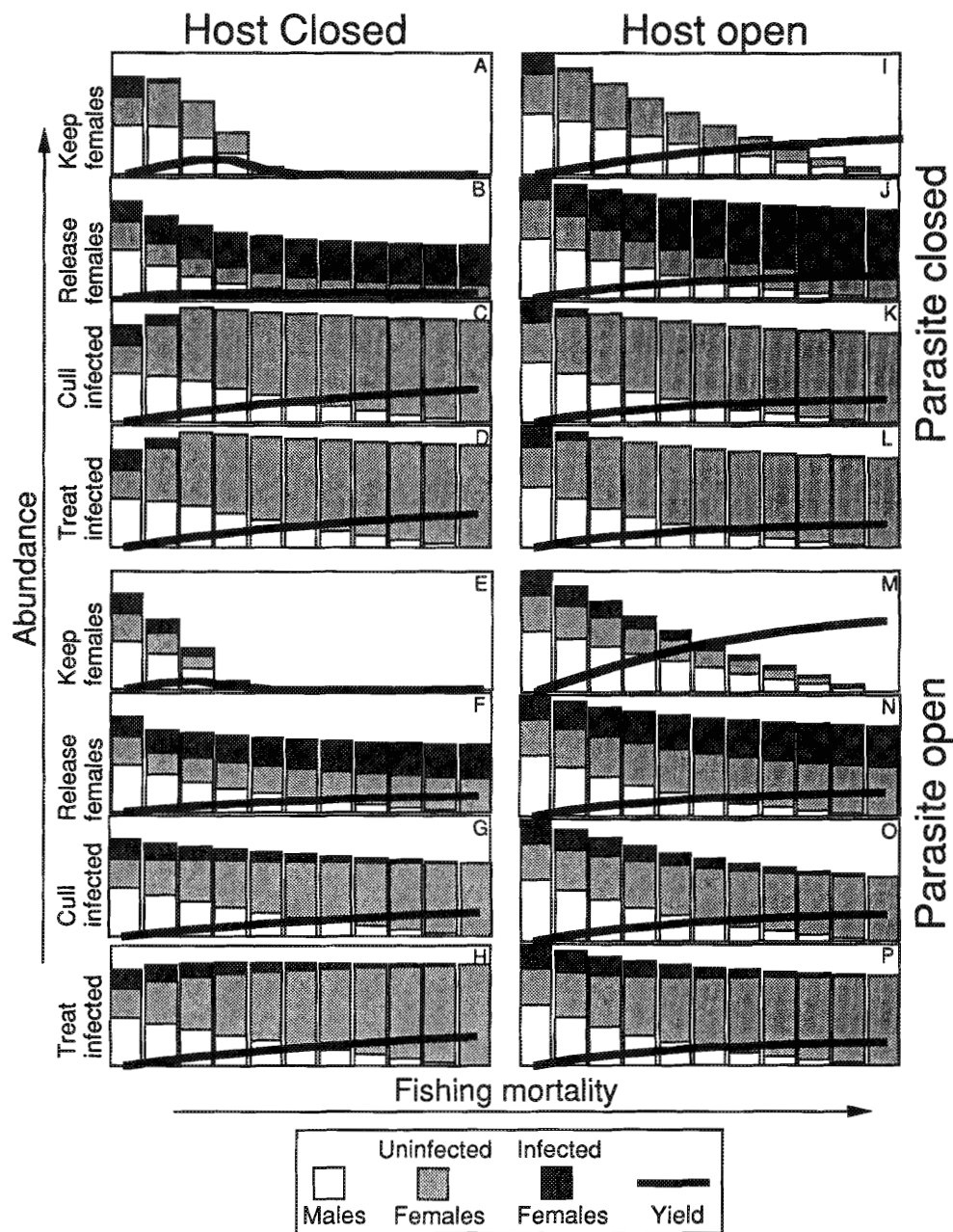


FIG. 4. Fishery yield (solid lines) and the abundance of males (open bars), uninfected females (light shaded bars), and infected females (dark shaded bars) as a function of fishing mortality when the fishery releases females, keeps females, culls infected females, or treats infected females. Yields are indicated for closed and open recruitment of host and parasite.

the use of alternative host species by the parasite, and of seasonality of parasite transmission would aid implementation.

For the Alaskan red king crab, the complex geography of the Alaskan coastline provides an appropriate setting to attempt the substantial reduction of nemertean infestations. Extensive long-term observations by the Alaska Department of Fish and Game and U.S. National Marine Fisheries biologists provide a historic background for catch statistics and reproductive performance in local areas (Blau 1983, 1986, unpublished information), and data are now available for nemertean abundance in these areas (Shields et al. 1990b; Kuris et al. 1991). As this appears to be a host open – parasite closed recruitment system (Fig. 1), our model suggests that retaining females in the catch

in locations such as Uganik Bay, Kachemak Bay, Excursion Inlet, or Port Frederick should reduce the abundance of *C. regicides*. The survey of nemertean abundance by Kuris et al. (1991) and Shields et al. (1990b) indicates that there are sufficient areas to replicate treatments. Representatives of commercial fishermen's associations see this as an opportunity to actively improve the depressed red king crab fishery and have expressed a willingness to cooperate with this sort of large-scale experiment.

Fisheries with a high prevalence of rhizocephalan parasitic castrators also provide circumstances suitable for experimentation. For golden king crabs, isolated in fjords of British Columbia and Alaska, a suitable experiment would be to cull

parasitized crabs. A more extensive survey of rhizocephalan distribution and abundance would be needed to provide enough locations for replication.

Reviewing the other fisheries in Table 1, it is evident that more basic research on the epidemiology of these parasites is needed to define the scale of parasite recruitment. This need is greatest for the microparasites, as we are unable to characterize recruitment for most of these infectious agents. Further work on parasite systematics (using molecular techniques) and experimental transfer studies will improve our knowledge of host specificity. Field experiments with model systems, perhaps using intertidal invertebrates, might help test experimental methodologies and prove easier to estimate productivity, recruitment, and other population parameters (Shields and Kuris 1988; Lafferty 1991). Improved understanding of the relationships between host reproductive output, larval abundance, larval behavior, and settlement will also aid the recognition of the relative geographic scale of host and parasite recruitment.

In summary, our model suggests that management strategies should vary based on the recruitment dynamics of host and parasite. Females should be fished if host recruitment is open, or both host and parasite recruitment are closed and fishing effort is moderate, or parasites are unimportant, fishing effort being moderate. Parasitized females should be culled if both host and parasite recruitment are closed and fishing effort is high. Parasitized females should be treated (assuming this is possible) if host recruitment is closed and parasite recruitment is open. Finally, females should be released when parasites are unimportant, fishing effort is high, and host recruitment is closed.

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