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Freshwater mussels (Unionoidea) and their hosts: patterns and models of parasitism

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Summary

1. In Nearctic and temperate habitats, bradytictic reproductive seasons allow mussels to parasitize hosts before their tachytictic coinhabitants. Because hosts may develop acquired immunity to glochidial infestation, bradytictic reproduction may be a means of competing with tachytictic mussels.

2. Reproduction by specialists, those having few potential hosts, result in low population sizes. Often, this renders specialists more susceptible to extirpation and extinction. Conversely, generalists may exist in great numbers given the right conditions. Generalists are opportunistic, and have evolved to cope with random fluctuations in their population size. Specialists have evolved to cope with fluctuating host numbers.

3. Simulations indicate that stable populations are very sensitive to host numbers and, to a lesser degree, the amount of natural immunity in the host population. Stable population sizes are less sensitive to initial mussel population sizes. Threshold levels of host numbers exist below which mussel populations will become extirpated. Therefore, extirpation may result from a decrease of host numbers, although hosts are still available.

4. Mussel population sizes and incidence of recruitment may fluctuate because of purely stochastic events. Average population sizes of mussels are therefore difficult to assess without long-term monitoring. Populations having a temporary low population size may be very susceptible to extirpation.

5. Introduction of immune exotic hosts may drive both specialists and generalists to extirpation. Introduction of exotic mussels capable of parasitizing any host will result in the extirpation of generalists, but specialists may coexist.

Introduction

Members of the freshwater bivalve group Unionoidea have a larval stage that obligately parasitizes vertebrate hosts. A few are known to parasitize amphibians (Howard, 1915; Seshaiya, 1941), and at least one species metamorphoses without a parasitic stage (Kondo, 1990). Most use fishes as their hosts. Three types of larvae are recognized: the glochidium of the Unionidae, Margaritiferidae, and Hyriidae; the lasidium of the Mycetopodidae; and the haustorial larva of the Mutellidae. Very little is known about the lasidium and haustorial larva, and this study is limited to those species with a glochidium.

Glochidia, depending on the species, attach themselves to the fins, skin, or gills of fishes. Here they ingest host tissue and resorb much of their own, eventually metamorphosing and dropping off the fish. Freshwater mussels have evolved a variety of mechanisms to disperse these larvae, or to lure potential hosts to them. The least specialized mussels simply broadcast their glochidia into the water, relying on chance to bring parasite and host together. Other species package glochidia into mucous matrices called conglutinates and superconglutinates. These structures often resemble fish food items such as worms, insects, or other fishes. Glochidia are transferred when the conglutinates are eaten (Fuller, 1971; Kat, 1984). A few species have specialized adult mantle structures that act as lures to attract hosts. Glochidia are expelled when these flaps are disturbed (Kraemer, 1970). Glochidiosis may be lethal to the host under very high intensities of infestation. These cases are known from hatchery and other conditions in which large numbers of fishes occur in close contact with large numbers of mussels (Davis, 1934; Murphy, 1942). The prevalence of this mortality under normal conditions is not known.

There is no consensus concerning whether mussels are generalists or specialists in terms of host use. Some species have a high degree of host specificity (Zale & Neves, 1982; Neves, Weaver & Zale, 1985; Yeager & Neves 1986a,b). Others use a great variety of hosts (Trdan & Hoeh, 1982). In this study, a specialist is defined as a mussel for which, at any given time, only a small number of suitable hosts is available. A generalist is a mussel with a large number of hosts. This differs slightly from the stricter definitions these terms have in parasitology in that here a mussel using a single, but abundant host, is classified as a generalist. It is known that freshwater mussel diversity is strongly related to fish diversity (Watters, 1992), but whether this relationship is caused by stenotypic parasitism is unknown.

Specialists generally have sophisticated lures or conglutinates that increase the efficiency of contacting a host. Because these items are not universally appealing to all fishes, it is hypothesized that specialists utilize a smaller number of host species than do generalists. This translates into an absolute fewer number of available hosts in most circumstances. Generalists, on the other hand, are hypothesized as broadcast reproducers that use a much wider range of hosts, implying an absolute greater number of hosts than that available to a specialist. The compromise may be glochidial efficiency: specialist individuals have fewer potential hosts but are more efficient at contacting them; generalist individuals have low efficiency in contacting individual hosts, but compensate by releasing great numbers of glochidia that may parasitize a broad range of hosts.

Under normal environmental conditions, freshwater mussels probably do not compete for food or space. There is a growing awareness that they may compete for hosts (Rashleigh, 1995). This is particularly true if hosts may carry only a finite number of glochidia. Fishes develop an acquired immunity to repeated glochidial parasitization. There is some evidence that immunity to one species may impart immunity to all (Reuling, 1919). Therefore, opportunities to infest a host may be on a first come basis. If the number of available hosts is low, then mussels would be competing for these fishes (Trdan & Hoeh, 1982). Strategies that enable glochidia to contact hosts first would be selected under such conditions. Such strategies could involve lures, reproductive timing, and glochidial mechanical efficiency in acquiring a host (Hoggarth & Gaunt, 1988). Freshwater mussels have developed several reproductive strategies for completing their life-cycles.

Glochidial infections are not generally thought of as a disease, but they are in every respect. In this regard they are not unlike other parasites that have been studied. As such their population dynamics may be investigated using epidemiological models for species that have parasitic larval stages, while being free-living as adults. Individual-based models of host-parasite interactions also are useful tools for examining this phenomenon. The probability of a glochidium encountering a host, successfully parasitizing it, and imparting immunity are stochastic processes. These can be modeled into simulations using parameters derived from field observations. One or more parameters may be varied to study the effect of that change on the course of the simulation.

The effects of the introduction of exotic hosts and /or mussels on native mussels have not been investigated. Many fish species have been purposefully or accidentally introduced into temperate and subtropical areas, where they have flourished (Courtenay *et al.*, 1986). Although some of these apparently may be parasitized by native mussels, most do not appear to be suitable hosts. It has been suggested that the introduction of unsuitable hosts may overwhelm and diminish normal glochidial efficiency by "diluting" host numbers (Howells, 1994). This phenomenon may be simulated with the models presented here.

The introduction of exotic unionids has not been a problem in North America, but is becoming so elsewhere. The Asian *Anodonta woodiana* (Lea, 1834) was reported as an exotic in Europe and Indonesia. This species was introduced from Taiwan into Java, Sumatra, Sulawesi, Nusa Tenggara Islands, and Moluccas (Djajasasmita, 1982; Dharma, 1992). Initial invasions of these islands were the result of the introduction of parasitized Nile tilapia (*Oreochromis niloticus* [Linné, 1758]) and silver carp (*Hypophthalmichthys molitrix* [Cuvier & Valenciennes, 1839]) as food fishes. Similarly, it was introduced into Hungary (Kiss & Petro, 1992), France (Girardi & Ledoux, 1989), and Romania (Sarkany-Kiss, 1986) on food and foraging fishes. It is now present in the Dominican Republic (Watters & Kohl, 1995). This mussel may be using native fish species as hosts in these areas. Based upon previous invasions, *Anodonta woodiana* is a prolific breeder and may become abundant (Dudgeon & Morton, 1983). It is not known what effect such an invasion has on native mussel species. This effect is simulated with models in this study.

The purpose of this study was to determine if epidemiological models (or, more precisely, epizootological models) and simulations could explain the different strategies seen in unionoidean reproduction. In particular, what kinds of predictions could such models make about generalists and specialists, and how populations react to perturbations in their reproductive cycles from changes in host numbers and the introduction of exotics.

Methods and Materials

Host specificity

The associations of hosts and mussels are derived from the listing in Watters (1994a). Mussels were divided into the Margaritiferidae, Anodontinae, Pleurobemini, Amblemini, and Lampsilini. These were further divided into bradytictic and tachytictic breeders. Bradytictic breeders spawn in the summer and carry the glochidia within the marsupia overwinter, releasing them the following spring. Tachytictic breeders spawn in the spring and release glochidia that summer. Fish hosts were included from the Lepisosteidae, Clupeidae, Salmonidae, Cyprinidae, Catastomidae, Ictaluridae, Cottidae, Centrarchidae, and Percidae. Although other fish families have been recorded as hosts, most hosts belong to the previous nine families. It has been suspected that many of these relationships are spurious, particularly those determined at the turn of the century (Hoggarth, 1992). This view is overly critical of the data. Interest in host identifications necessarily waned during the World Wars, and it was not until the 1970's that more rigorous studies were published. Therefore, if we take 1950 as a conservative, but arbitrary, starting date for "good" relationships, we find that 68% of the associations (total=472) were made on or after that time. Although most of the older relationships have not been retested, thirty subsequent host identifications have confirmed the original observations. Our knowledge of these associations is better than is generally believed. However, it must be emphasized that these associations represent potential host-parasite relationships based on compatibility. Although over half of these associations are based on field observations, to what degree the remaining associations occur in nature is unknown.

The reproductive periods (spawning, gravid) are taken from Ortmann's (1919) monograph on Pennsylvania mussels. These careful observations represent the best comprehensive data available on unionacean reproductive timing. The initiation of Nearctic and temperate mussel reproduction depends on changes in water temperature, which varies with location and year. This variability does not change the presented models, which compare populations in the same settings.

Epizootological Models

The models used here involve several parameters derived from field observations. The parameter β represents the rate of successful contact between hosts and parasites. It does not include mortality from host death or mortality after metamorphosis. This parameter is estimated by the observed proportion of released glochidia that successfully attach and metamorphose on a host. This number varies between species. Jansen and Hanson (1991) recorded a β of 0.007 for *Anodonta grandis simpsoniana* Lea, 1861, on yellow perch (*Perca flavescens* [Mitchill, 1814]), and Young and Williams (1984) gave a value of 0.00002 for *Margaritifera margaritifera* (Linné, 1758) on salmonids. Both species broadcast glochidia without durable conglutinates or lures. Presumably, β would be higher for species with more sophisticated transmission devices, such as mantle lures and conglutinates. Species using superconglutinates, masses of individual conglutinates formed into a single unit, could theoretically achieve β values approaching unity

(Hartfield, 1994). Values in these simulations were assigned β=0.01 for generalists, and β=0.5 for specialists. The generalist value is probably somewhat high, but it is used for comparative purposes only.

The parameter I represents the number of glochidia released by a mussel in a season. This greatly varies between species: *Anodonta grandis simpsoniana* annually produced 13,000,000 per individual (Jansen & Hanson, 1991); a single *Margaritifera margaritifera* may release 2,000,000-4,000,000 glochidia per season (Young & Williams, 1984; Bauer, 1987); *Glebula rotundata* (Lamarck, 1819) released 531,000 (Parker, Hackney & Vidrine, 1984); and *Quadrula cylindrica strigillata* (Wright, 1898) had 469 in a single conglutinate (114,246 total all conglutinates) (Yeager & Neves, 1986a,b). In this study, I was varied from 0 to 5,000,000.

The parameter N is the number of potential hosts that a mussel may encounter in a reproductive season. This includes hosts that are immune. There is little information on fish densities/mussel, and N was varied from 5 to 1000 in these models and simulations.

Epizootological models for organisms having parasitic larval stages and free-living adult stages may be applied to unionaceans. The value M_t is the mean number of glochidia per host (Anderson, 1982)

$$M_t = [\beta I_0/(\beta N+\mu)][1-e^{[-(\beta N+\mu)t]}] \tag{1}$$

where $1/\mu$ is the life expectancy of a glochidium that does not find a host. Life expectancy has been reported from 1 to 3 days for glochidia under normal temperatures (Sylvester, Holland & Kammer, 1984), and a value of μ=1 (1 day) was used in this study. The parameter t represents the gravid period of a mussel. For this study, a t of 30 days was used as an average of most species, although several species apparently breed continuously (Pekkarinen, 1993) or have multiple broods (Gordon & Smith, 1990; Nagel, 1991). Species with superconglutinates may only release glochidia for a few days. Nevertheless, the value of t was not important to the overall comparisons in this study.

The parameter p is the prevalence of infestation, the proportion of hosts infested. Data from single mussel species varies from 0.022 to 1 (Wootten, 1973; Neves & Widlak, 1988; Jansen, 1991; Jokela, Valtonen & Lappalainen, 1991). Areas with high mussel concentrations often have high degrees of infestation (Cunjak & McGladdery, 1991). In this study p was varied from 0 to 1. This parameter is estimated by the relationship

$$p = 1 - [1 + M_t/k]^{-k} \tag{2}$$

where k inversely measures the degree of aggregation of the parasites in the host population based upon a negative binomial model (Anderson, 1982). Although glochidia are highly aggregated in most fish populations, no estimates of k have been published. Neves and Widlak (1988) gave N=4,800 and p=0.14 for a mussel community in Virginia. Using a value of k=0.025 yields an estimated p=0.135, which is close to the observed value. This estimate represents a very aggregated parasite population, and has been used in this study, although it undoubtedly varies between communities. The value of k influences the magnitude of the infestations, but not the underlying results and models.

Response curves were constructed for p as a function of β and I. β was varied from 0 to 1, and I was varied from 0 to 5,000,000 in one set, and from 0 to 500,000 in a second set. Values of p were calculated for every 0.01 interval of β. For runs in which I increased to 5,000,000, intervals of 100,000 were used; for $I = 500,000$, intervals of 10,000 were used. k was a constant 0.025. Sets of curves were produced for N=10 and N=500 to simulate specialists and generalists, respectively. Response curves also were constructed for M_t as a function of β and I, which was varied as above. Curves were produced as before to simulate specialists and generalists, respectively.

Individual-based Models

Individual-based models were devised to simulate interactions between mussels and their hosts. These models tracked the population levels of mussels across reproductive seasons as a function of glochidial efficiency (β), initial (natural) host immunity (IM), host numbers (N), and mussel numbers (U). In the model, U number of adult mussels are introduced in a system having N potential hosts. A percentage of these hosts have a natural immunity (IM) and may not be successfully parasitized. At the outset of each reproductive season, the remaining hosts have no acquired immunity.

The model tracks the numbers of females within a population. Males are assumed to be in equal numbers, in accordance with field observations (Haggerty *et al.*, 1995). But because there are no estimates of male gamete efficiency in encountering and fertilizing an egg, this aspect of unionacean biology could not be modeled. It likewise is not known what proportion of the male population successfully reproduces. The predicted population estimates represent only approximately half of their actual size. The predicted number of hosts needed to maintain a population is therefore lower than that actually needed, and represents a best-case scenario. The overall conclusions and patterns generated by the model are not changed except in magnitude.

Glochidia from each adult female mussel have a probability, the glochidial efficiency (β), of encountering any potential host selected at random from the host population. If the host has neither natural nor acquired immunity, the glochidium successfully parasitizes the host. Thus the probability of successfully parasitizing a host is dependent on three probabilities: encountering a host; host lacking natural immunity; and host lacking acquired immunity. A successful glochidium is added to the following year's mussel population as a metamorphosed juvenile, and is then subjected to the probabilities of adult mortality. These juveniles could not reproduce until their fourth year. This is consistent with estimates determined by field work, although some species reach sexual maturity later than this (Woody & Holland-Bartels, 1993; Downing, Rochon & Pérusse, 1993). Adults had a 10% probability of death each reproductive season. No host mortality, immigration, or emigration is assumed. No mussel immigration or emigration is assumed. Unless otherwise noted, all simulations are the means of ten replicates, and yearly host numbers were randomly selected as $<= N$. Long-term simulations ran for 100 reproductive seasons.

A total of 10 successful glochidial attachments was necessary to invoke acquired immunity in these simulations. This is strictly a cumulative effect. The onset of acquired immunity is related to the degree and duration of infestation (Arey, 1924, 1932; Seshaiya, 1969; Bauer, 1987; Bauer & Vogel, 1987), and the level of infection chosen here falls within observed values. The acquired immunity apparently is lost by the following spring, or later the same year (Young, Purser & al-Mousawi, 1987). All acquired immunity was lost overwinter in the simulations, i.e., between reproductive seasons. Hosts populations began each mussel reproductive season with only the predetermined levels of natural immunity (*IM*). Subsequent acquired immunity affected only those lacking natural immunity.

Simulations of competition for the same hosts were devised for various scenarios. The distribution of reproductive strategies does not strictly follow a taxonomic scheme (Bauer, 1994), and specialists and generalists may occur as both bradytictic and tachytictic breeders. Thus, although tachytictic and bradytictic breeders may be separated temporally, specialists and generalists are not. Therefore, simulations were conducted in three scenarios. First, specialists reproduced before generalists for N=100 and N=500. Second, generalists reproduced before specialists for N=100 and N=500. Finally, both generalists and specialists reproduced simultaneously, with individuals being drawn randomly from either group. Initial population levels of 50 mussels/group were used. Specialists used β=0.5, and generalists=0.01.

The invasion of exotic, completely immune hosts was simulated by introducing 100 such hosts at season 10 into stable populations parasitizing 200 and 500 native hosts with *IM*=0.4. Both stable populations of specialists (β=0.5) and generalists (β=0.01) were used. The introduction of exotic generalist mussels capable of parasitizing any host was simulated by introducing 50 exotic mussels at season 10 into stable populations parasitizing 200 and 500 native hosts with *IM*=0.4 for both native specialists and generalists.

Results

Host Specificity

The distribution of hosts by fish family for the mussel categories is shown in Fig. 1. There is considerable overlap by mussels using cyprinids and centrarchids, and little overlap for the remaining fish families. The distribution of fish families by tachytictic mussels (Fig. 2) shows that while both the pleurobemines and amblemines use cyprinids and centrarchids, there is a partitioning of these fish families that minimizes competition for them. Margaritiferids also may use cyprinids, but these mussels are sympatric primarily with anodontines, which are bradytictic. The distribution of hosts by bradytictic mussels (Fig. 3) shows that while both anodontines and lampsilines use centrarchids, anodontines also parasitize cyprinids, and lampsilines use percids.

Epizootological Models

Response curves of p as a function of β and I for N=500 (generalist) show that changes in p are caused by different conditions depending on the initial values of β and I (Figs. 4a,b). If β is larger than 0.001, and glochidial numbers are low (I=100,000), then p increases with increasing I, and β has little effect on p. If β is very small, and I>100,000, then only increasing β will increase p. If both β and I are very small, then both must be increased to increase p. If N=10 (specialist), the curves are similar to those of N=500 although changes in I bring about more pronounced increases in p at larger $ß$ (Figs. 4c,d).

Response curves of M_t as a function of $ß$ and I for N=500 show results similar to those for p (Fig. 4e). Changes in M_t primarily are caused by changes in glochidial numbers, except at very low values of $ß$, where increases in $ß$ are necessary first. For N=10, changes in both $ß$ and I bring about increases in p (Fig. 4f).

Individual-based Models

Simulations show that the stability of mussel populations is dependent on host numbers, all things being equal (5a,b). For each combination of model parameters, there may be a threshold level of host numbers if the level of natural immunity is sufficiently high. If host numbers drop below this level, the mussel population will tend toward extirpation. At or above this level, a stable but fluctuating mussel population is achieved. For a generalist, a host population of 110 leads to extirpation (Fig. 5a). Values of N=200 led to stability. For N=150, four of the ten replicates became extirpated (not figured). For specialists, stable levels are attained at lower host numbers than for a comparable generalist, but specialist levels tend to remain low regardless of host numbers (Fig. 5b). In general, specialists tend to have lower stable population levels than do generalists. The sizes of the stable mussel populations are dependent on the values of $ß$.

This is seen more clearly in simulations conducted over the entire range of initial or natural immunity (IM=0 to 1). For small host populations (N=110), generalists do not achieve a stable population size regardless of initial immunity (Fig. 6a). For specialists at the same level of *N*, stable populations are attained if initial immunity is below about 0.7 (Fig. 6b). However, these stable populations are small regardless of immunity loads. For large host populations (N=500), generalists will reach stable levels if $IM < 0.5$, and these populations may be large (Fig. 6c). For specialists, large host numbers do not appreciably change the stable levels or their dependence on immunity (Fig. 6d).

Simulations of mussel competition for the same hosts show that at large β, most mussels may not locate suitable hosts. For β=0.5 (Fig. 7a), 40 of the 50 mussels consistently reproduced that season regardless of host immunity levels, but after the twentieth mussel, subsequent individuals had less than half the reproductive success of the first mussel. At a lower level, β=0.01 (Fig. 7b), all fifty mussels reproduced almost equally, but at low values. In all cases, increasing the amount of initial immunity lowered the probability of individual reproductive success.

Competiton between specialists and generalists resulted in extirpation of the generalists in two of the three scenarios. For high host numbers (N=500), generalists were extirpated if specialists were allowed to reproduce earlier in the year (Fig. 8a). If both groups simultaneously competed for hosts, generalists were extirpated at otherwise stable levels (N=200 and N=500) (Figs. 8b,c). As expected, generalists became extirpated at low host numbers (N=110) whether they reproduced first or not (Fig. 8d,e). Only if generalists reproduced first with high host numbers did both groups achieve stable population levels (Fig. 8f).

The addition of immune, exotic potential hosts clearly is detrimental to native mussel populations. The stable levels of both generalists and specialists are depressed, and lower levels may become extirpated (Fig. 9). Stable levels may be decreased by several orders of magnitude.

Effects of the introduction of exotic generalist mussels, capable of parasitizing any available host, could drive the native generalists to extirpation (Fig. 10a). Specialists however could coexist with these invaders (Fig. 10b). Exotic populations attained such a high level that it exceeded the capabilities of the simulation language, and the exotic population was limited to a 2000 individual ceiling.

Discussion

While many host relationships are unknown, the available data suggest that mussels have partitioned their host resource. Where two host families are used by two or more mussel groups within the same breeding pattern (bradytictic or tachytictic), there is a tendency for one group to "specialize" in one family, and the second group to use the other family. Partitioning primarily takes place within a breeding pattern. There is considerable overlap between them. These occur in time such that they are largely exclusive of each other, i.e., glochidia generally are not released by the two groups simultaneously (although exceptions are not uncommon) (Fig. 11). This seems to suggest that the host resource has been further partitioned by breeding time. However, another explanation may explain this temporal pattern. The origin of bradyticty and tachyticty may have arose as a response to interspecific competition.

If hosts may acquire a season-long immunity from a previous glochidial infestation, then those mussels breeding later in the year (tachytictic) are limited by the number of available hosts that have not been parasitized by earlier breeders (bradytictic). It is hypothesized that bradytictic reproduction evolved as a means of releasing glochidia earlier than that attained by tachytictic (ancestral?) reproduction. Because there is not sufficient time in the temperate spring to spawn and develop glochidia before tachytictic mussels, spawning in bradytictic species takes place in late summer and fall, and glochidia are held over winter to be released the following spring. In this way, mature glochidia are released when water temperatures permit, several months before release by tachytictic species. The parasitized hosts are thus removed from the pool of potential ones available to tachytictic mussels. Tachytictic mussels may recoup some of their losses by parasitizing young-of-the-year juveniles produced by already infested adults, but this has not been modeled in the simulations.

The evolution of bradyticty could have been driven by competition between mussel species for the same hosts. As suggested by the simulations presented here, generalists may coexist with competitors by breeding first, *i.e.*, becoming bradytictic. The anodontines are such a group. They disperse glochidia through broadcasting of individual glochidia or dissolving conglutinates. Anodontines are reported to parasitize more species of hosts than any other unionacean group (Trdan and Hoeh 1982). The evolution of bradytictic specialists, the lampsilines, may have occurred after their generalist ancestors acquired this delayed glochidial release. Lampsiline-like species are not known before the Eocene, but anodontine-like and elliptioid taxa extend back at least as far as the Jurassic (Watters, 1994b). Additionally, the marsupial features and sexual dimorphism of the shells found in lampsilines are considered to be derived traits (Davis & Fuller, 1981). The fact that some lampsilines are generalists (*Lampsilis radiata siliquoidea,* for example) may be a holdover from a prior reproductive strategy. In any event, the combination of bradyticty and specialization represents the most highly derived reproductive strategy among the Nearctic mussels.

Competition seems to favor the specialists in most scenarios. Species having very low β values and great numbers of glochidia (millions) cannot improve their prevalence of infection without increasing β. Margaritiferids are such species. Often, they only partially bury into the substrate. In the Lake Tanganyikan mutelid *Iridina spekii* (Woodward, 1859) this behavior allows glochidia and gametes to be dispersed over a wider area (Kondo, 1986) and this may be true for margaritiferids as well. Notwithstanding, they have few adult morphological or behavioral modifications for increasing their glochidial efficiency (Young & Williams, 1984). Margaritiferids may have circumvented this problem by adapting to conditions where there is little interspecific host competition. They have been shown to occur in habitats with low food resources where few other unionacean species are found (Bauer, Hochwald & Silkenat, 1991). Here, they may achieve a high prevalence of infection under the proper circumstances (Bruno, McVicar & Waddell, 1988).

At higher β levels, smaller numbers of glochidia result in the same prevalence of infection as species with very low β and great numbers of glochidia. This is particularly true when there are relatively few available hosts. Presumably there is an metabolic effort in creating conglutinates or operating lures, but this may be much less energy-consuming than making and maintaining millions of glochidia. Thus, if a species can improve its glochidial efficiency for a small number of hosts, its reproductive effort and overall metabolic requirements may be decreased greatly.

The mean number of glochidia per host, M_p is dependent on glochidial numbers released and efficiency in a similar fashion to prevalence of infection. Glochidial infestation increases more rapidly at higher β values and fewer hosts. At high host numbers, increases in β effect only small changes in M_t (Fig. 4e). At low host numbers, small changes in β greatly increase M_t (Fig. 4f). At these levels, specialists may attain the same glochidial infestation densities as generalists, but with much fewer glochidia. Under certain conditions, such as occurs in hatcheries, generalists also may achieve high levels of infestation to the point of being lethal to the host (Murphy, 1942). But in general, because specialists are more likely to have larger β values and fewer hosts, specialists would be expected to more heavily infest their hosts than generalists. To date, published field observations on glochidial burdens rarely identify the hosts. However, this prediction can be substantiated by future observations.

Within a reproductive season, mussels compete for hosts. If acquired immunity grants immunity from all mussels, then this competition is on a community-wide scale. If acquired immunity is more specific, then competition is between pairs or groups of species that use the same set of hosts. Either way, mussels that can release glochidia and parasitize a host early in the season exclude that host from the remaining mussels through acquired immunity. Subsequent mussels may not be able to find suitable hosts, even though the host pool has not been "used up," simply because of stochastic effects. The amount of competition is related to the efficiency of glochidia acquiring a host and the prevalence of immunity in the host population. Higher β results in pronounced competition, with only a small number of the mussel community successfully reproducing to any extent. Lower values of β may allow all mussels to reproduce to some degree. Very low values result in all mussels either contributing very little, or not at all. At this level, competition is minimal.

Simulations over many reproductive seasons demonstrate the importance of host numbers, and to a lesser extent, the degree of initial immunity. For a given set of population and reproductive parameters, a threshold host population level exists in most cases. Mussel communities having hosts numbers below this threshold will tend to extirpation or extinction. Host numbers above this level will result in a stable but oscillating mussel population size. The stability of the mussel population is dependent on hosts numbers; the size of the stable population is determined by *ß* and *IM*. This has important ramifications for our management of rare and endangered mussels. It is obvious that if a mussel's hosts are extirpated, the mussel also will become extirpated. However, these simulations suggest that simply lowering host numbers below a threshold also may result in extirpation. It is possible to eliminate a mussel species through purely stochastic events although its hosts are still present. Ziuganov *et al.*, (1994) also reached this conclusion in their pioneering study on margaritiferids and salmonids. They relied on an estimate of the probability of glochidia successfully locating a host, and the fecundity of margaritiferids, to define a relationship between numbers of hosts and mussels. Their conclusions differ mainly in the prediction that mussel populations may continue to multiply past any stable level if additional hosts are introduced. Their numbers are based on host density rather than on the absolute number of hosts a glochidium may encounter. The model proposed here predicts that competition between mussels will limit populations at a level dependent on host numbers.

Individual simulations show considerable oscillation due strictly to stochastic features of the model: the probability of mortality, and the probability of successfully infesting a host (Fig. 12). This implies that at any given time, population levels of a mussel may be quite different from the stable population size. In-field estimates of population size may seriously over- or underestimate this average level. Long-term monitoring of a population on the order of decades is required to produce a realistic estimate. During periods of naturally occurring low population sizes, perturbations from natural or anthropogenic causes may be sufficient to drive a population to extirpation. Specialists are more susceptible to extirpation or extinction because of their small population sizes than are generalists.

Populations often are monitored to determine if mussel numbers are increasing or decreasing. This is usually attributed to some extrinsic cause. Decreasing numbers are explained by habitat degradation and loss of hosts. Increasing numbers are touted as indicators of habitat improvement. However, mussel populations are shown to oscillate greatly due strictly to stochastic components of their reproduction. Without obvious and compelling evidence of habitat degradation or improvement, conclusions concerning population size changes must be drawn with great care.

Population size fluctuations are driven by recruitment and the prevalence of host immunity. Even at a stable size, the population may not recruit every year (Fig. 12). In the simulation illustrated, 53 of the 100 breeding seasons had no recruitment, but the population remained stable. Thus, a lack of recruitment in one or more years is to be expected and does not necessarily indicate a declining population. This conclusion is supported by the field observations of Negus (1966), Tevesz , Cornelius and Fisher (1985), James (1985), and Payne and Miller (1989). Again, this underscores the importance of long-term monitoring before attributing causes of population "declines" or "improvements."

Stable population levels must be considered when management and recovery strategies are designed and implemented to protect an endangered or rare mussel. Proposed population sizes may be unnecessarily large, and therefore unattainable, when dealing with specialists. Translocating specialists using these target densities may result in deleterious concentrations of the animals, resulting in loss of "surplus" animals until a stable population size is attained. In such situations, "more" is not necessarily "better." Figure 13 illustrates two such initial or "target" mussel population sizes. Both converge toward a stable population size, with substantial loss of individuals in the unnecessarily large initial population. Although large sample sizes may account for more of the genetic variability than small ones, within a single reproductive season most of the genetic variability is produced by relatively few individuals. The potential for greater genetic sampling by introducing large numbers of individuals must be weighed against the probability that most of those individuals will be lost.

The introduction of exotic hosts or mussels may have serious consequences on native mussel populations. Immune hosts may overwhelm the potential host pool, reducing glochidial efficiency (Howells, 1994). In such a scenario, both generalists and specialists may be driven to extirpation. Exotic fishes have become abundant in many areas, and may constitute a threat to native mussels. However, the degree to which exotic fishes are immune to native mussels is not known. This should be an area of future study.

The introduction of exotic mussels capable of parasitizing any host may lead to extirpation of generalists, but specialists may be able to coexist. There is anecdotal evidence that exotic mussels are using native fishes, but more research is necessary to document this. Certainly, exotic mussels may achieve large population sizes in translocated areas suggesting wide-scale recruitment.

By refining their ability to acquire a host through lures, conglutinates, etc., specialists have lessened their reproductive effort, and with it the metabolic energy that would have been needed to form millions of larvae. These refinements often entail specializations for particular hosts. This is balanced by the increased chances of extirpation and growing competition with increased efficiency. Because population sizes oscillate from stochastic causes, specialists, with their lower population levels, are more susceptible to extirpation from environmental perturbations than are generalists. It is likely that many rare and endangered freshwater mussels occurring today are specialists, brought to the brink of extinction by random anthropogenic perturbations on their oscillating population sizes. Many extinct unionids are lampsilines and pleurobemines that presumably, based on extant cognates, either had conglutinates or luring devices. But it also is likely that some "rare" species may have always been rare, in comparison with generalists, and are stable at normally low population sizes. The simulations show that not all mussel species will exist in stable populations of the same size, and that caution must be taken before ascribing causes of "rarity" to species.

Specialists are able to maintain stable populations at lower host numbers than are generalists, but these population levels increase little with increasing host numbers. Given sufficient hosts, generalists are capable of forming stable populations of many individuals (Fig. 14). There is thus a compromise between specialists and generalists. Specialists can exist at low host numbers, but never establish large populations. Generalists may be extirpated at low host numbers, but can achieve large population sizes under the right circumstances. From an evolutionary perspective, specialists excel over generalists in their glochidial efficiency, which is related to the customization of mantles and conglutinates for targeted hosts. This allows them to maintain stable populations with relatively few hosts present. The evolution of specialists therefore may be a hedge against declining or fluctuating host numbers. Generalists on the other hand are opportunists. By their ability to parasitize a wide range of hosts, they may be able to colonize areas not available to specialists, and build up large numbers of individuals under the proper conditions. But because they are using a wide variety of host types, they cannot develop the customized glochidial dispersal mechanisms found in specialists. Broadcasting is a method of releasing glochidia to this wider host assemblage, but is necessarily inefficient. Thus, vast numbers of glochidia must be formed to compensate. The benefit is that large numbers of mussels may be built up as a hedge against stochastic environmental events that do not entail host numbers. In summary, specialists hedge against fluctuations in host availability, whereas generalists hedge against fluctuations in their own population levels.

Simulations of competition between specialists and generalists demonstrate that in most scenarios, specialists can drive generalists to extirpation. Obviously, this is not the case in nature, where both groups coexist. Most mussel communities are made up of combinations of specialists, generalists, bradytictic, and tachytictic. It seems most likely that these groups coexist by using different hosts, and thereby avoiding competition. The models and simulations presented here pit against each other mussel species that compete for the same hosts. It has been suggested, at least informally, that mussels are not host specific. But the growing body of host studies, and these simulations, suggest that is not so. Host specificity is the most efficient way to alleviate interspecies competition, and represents an important driving force in the evolution of reproductive strategies in the freshwater mussels.

But clearly many mussels do use the same hosts, and these also coexist. Temporal reproductive separation of species may alleviate some of this competition (Rashleigh, 1995). Partitioning through brady- and tachytictic reproductive strategies is such a separation, though giving bradytictic taxa the advantage. Durations of glochidial release undoubtedly differ from species to species. Facets of natural and acquired immunity, yet unknown, could change the scenarios as well. Although more sophisticated models need to be developed to explain coexistence, it is hoped that the basic models given here help to explain some fundamental observations concerning the interactions between and among mussels and their hosts. These models will serve as a foundation upon which to build more detailed paradigms.

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CAPTIONS

Figure 1. Radar plot of use of nine host fish families by five unionacean groups. Radii indicate proportion of host use by each family.

Figure 2. Radar plot of use of nine host fish families by tachytictic unionacean groups. Radii indicate proportion of host use by each family.

Figure 3. Radar plot of use of nine host fish families by bradytictic unionacean groups. Radii indicate proportion of host use by each family.

Figure 4. Prevalence if infection (p) and mean parasite burden (M_t) as a function of glochidial efficiency (β) and numbers of glochidia released for hosts number (I). Figures 4a,b. p as a function .β=0 to 1.0 and N=500. Figure 4a . I=0 to 5,000,000. Figure 4b. I = 0 to 500,000. Figures 4c,d. p as a function of β = 0 to 1.0 and N=10. Figure 4c. I = 0 to 5,000,000. Figure 4d. I = 0 to 500,000. Figures 4e,f. M_t as a function of β = 0 to 1.0 and I = 0 to 5,000,000. Figure 4e. N=500. Figure 4f. N=10.

Figure 5. Plots of populations with two different host abundances (N=110, .200), IM=0.4, mortality=0.1). Solid line - N=200. Dotted line - N=110. Figure 5a. β=0.01. Figure 5b. β=0.5.

Figure 6. Plots of mussel population size as a function of initial host immunity (natural immunity) over 100 reproductive seasons. Figure 6a. Generalist (β=0.01) with N=110. Figure 6b. Specialist (β=0.5) with N=110. Figure 6c. Generalist (β=0.01) with N=500. Figure 6d. Specialist (β=0.5) with N=500.

Figure 7. Plots of number of glochidia/mussel that successfully infest a host by 50 sequentially reproducing mussels at three levels of host immunity. Solid line - IM=0.0. Broken line - IM=0.4. Dotted line - IM=0.8. N=200. Figure 7a. β=0.5. Figure 7b. β=0.01.

Figure 8. Competition between a generalist (β=0.5) and a specialist (β=0.01) mussel species parasitizing the same hosts. IM = 0.4, mortality = 0.1. Solid line - specialist. Dotted line - generalist. Figure 8a. In this scenario, the specialist releases glochidia first. N=500. Figure 8b. In this scenario, both species release glochidia simultaneously. N=200. Figure 8c. In this scenario, both species release glochidia simultaneously. N=500. Figure 8d. In this scenario, the specialist releases glochidia first. N=110. Figure 8e. In this scenario, the generalist releases glochidia first. N= 110. Figure 8f. In this scenario, the generalist releases glochidia first. N=500.

Figure 9. Plots of generalist and specialist populations with three different host abundances (N=110, 200, 500). IM=0.4, mortality=0.1. Fifty exotic immune hosts are added at year 10. Solid line - N=500. Dashed line - N=200. Dotted line - N=110. Figure 9a. β=0.01, no exotics. Figure 9b. β=0.01, exotics added. Figure 9c. β=0.5, no exotics. Figure 9d. β=0.5, exotics added.

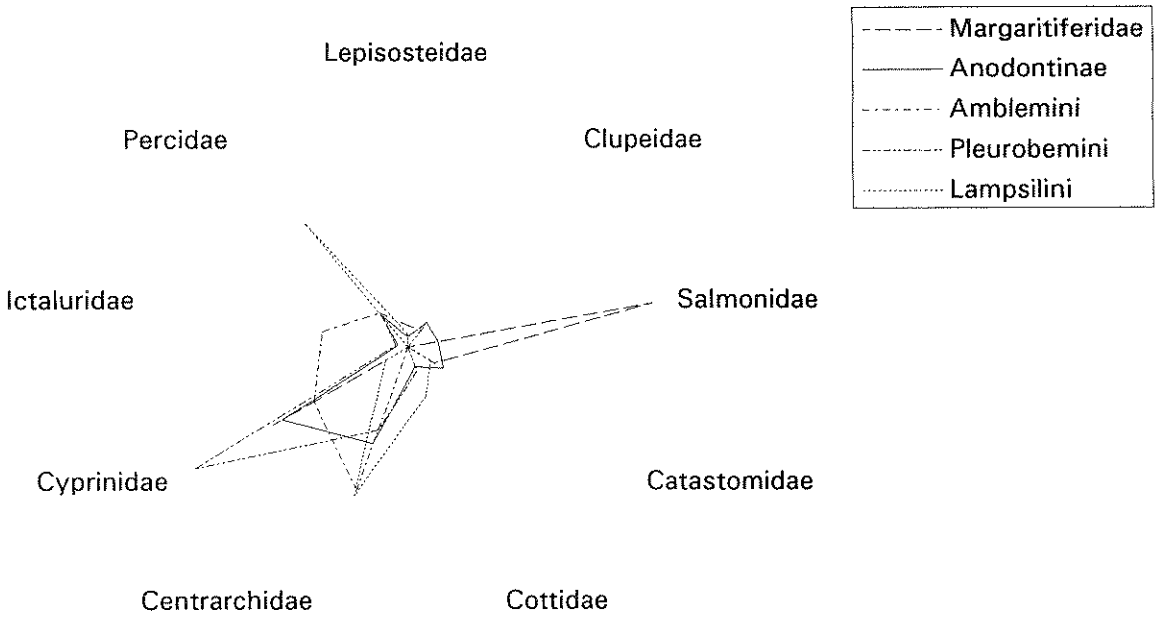
Figure 10. Plots of generalist and specialists populations with 50 exotic generalist mussels added at year 10 (N=200, IM=0.4, mortality=0.1). Solid line - exotics. Dotted line - natives. Figure 10a. β=0.01. Figure 10b. β=0.5. Compare with 9a and 9c for no exotics added.

Figure 11. Spawning and gravid periods of Pennsylvania unionids illustrating tachytictic and bradytictic spawning and gravid periods (data from Ortmann, 1919).

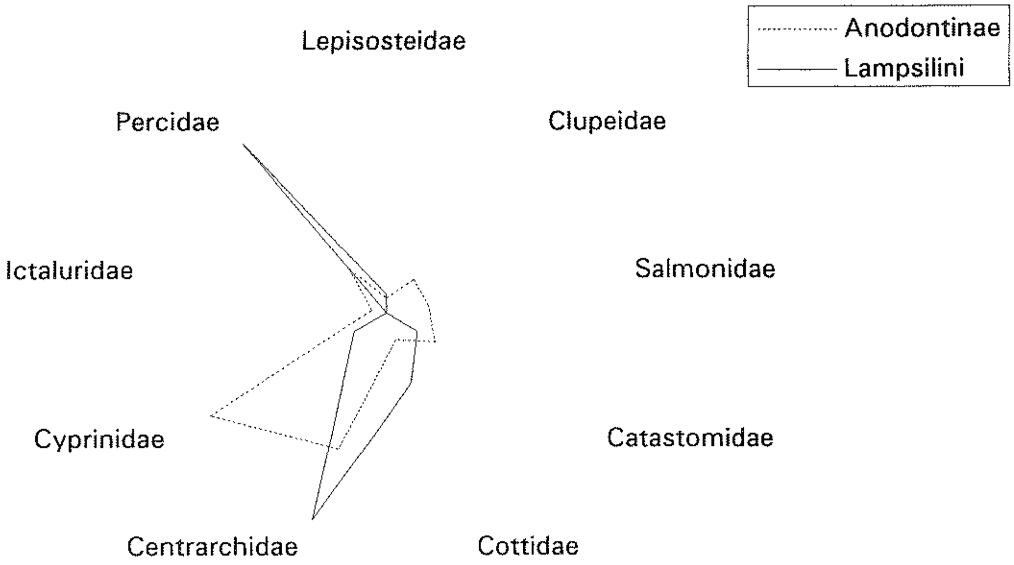
Figure 12. Plot of stable population (N = 200, β = 0.01, IM = 0.4, mortality = 0.1) over 100 reproductive seasons. Dotted line - total population. Solid line - recruits for that season. Fifty-three of the seasons have no recruitment.

Figure 13. Plot of converging stable populations with two starting mussel abundances (N=100, β=0.5, IM=0.4, mortality=0.1) over 100 reproductive seasons. Solid line - 100 mussels. Dotted line - 5 mussels.

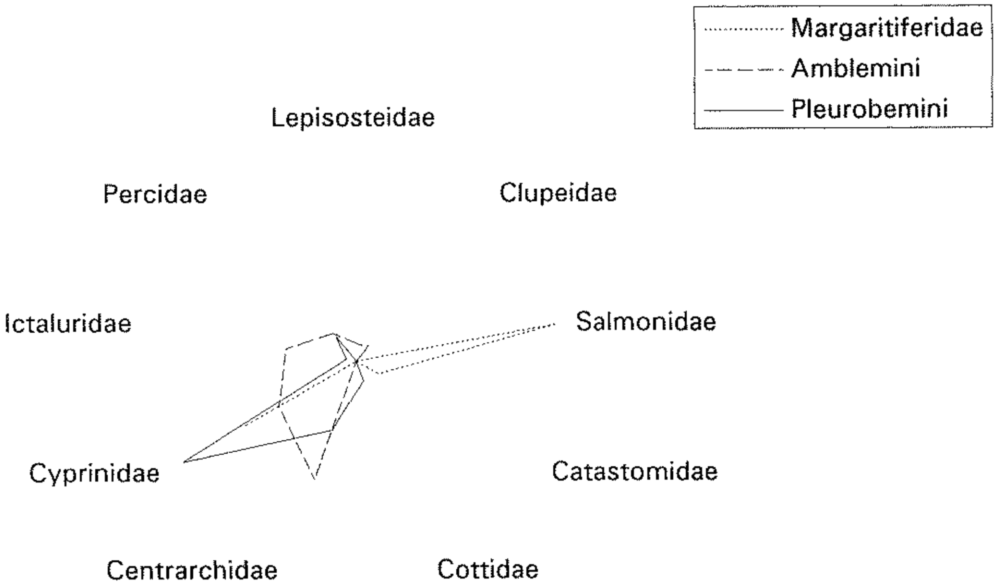
Figure 14. Plot of stable population levels for generalists (β=0.01) and specialists (β=0.5) versus host numbers.



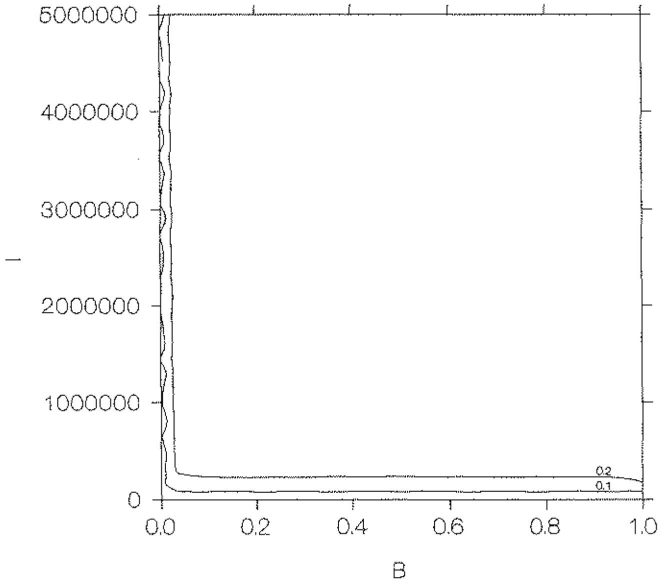
Watters - Fig. 1



Watters - Fig. 2



Watters - Fig. 3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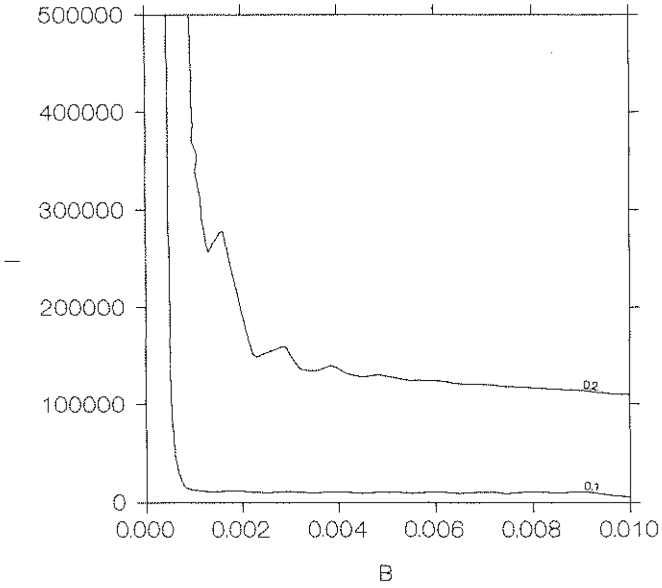
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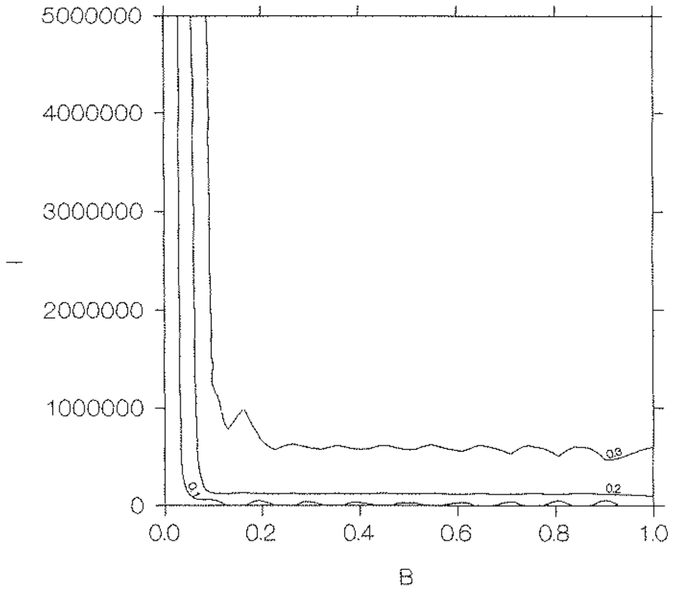
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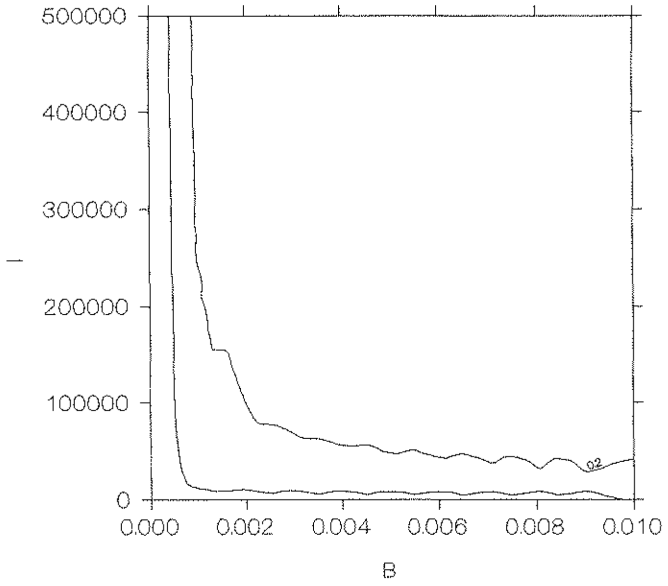
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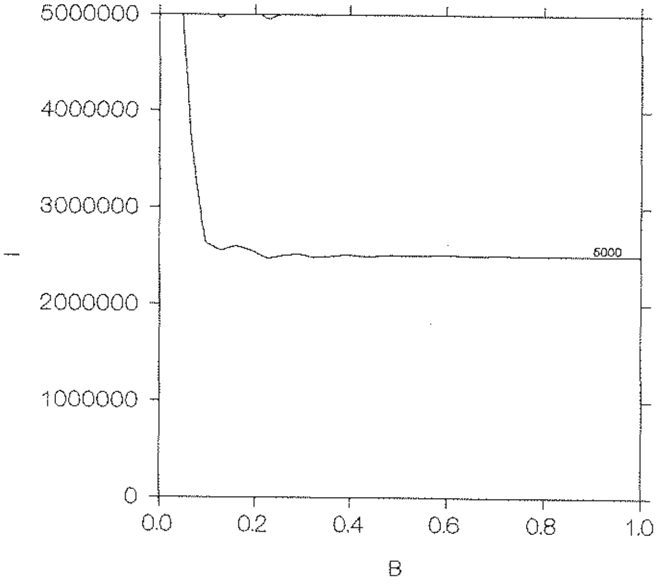
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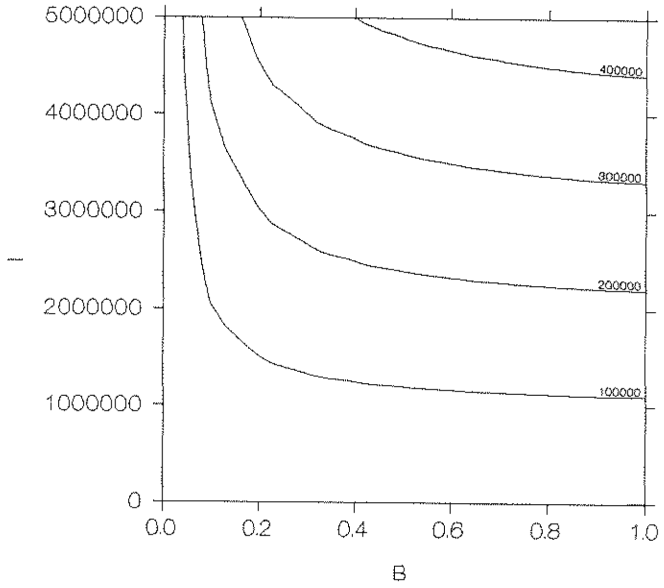

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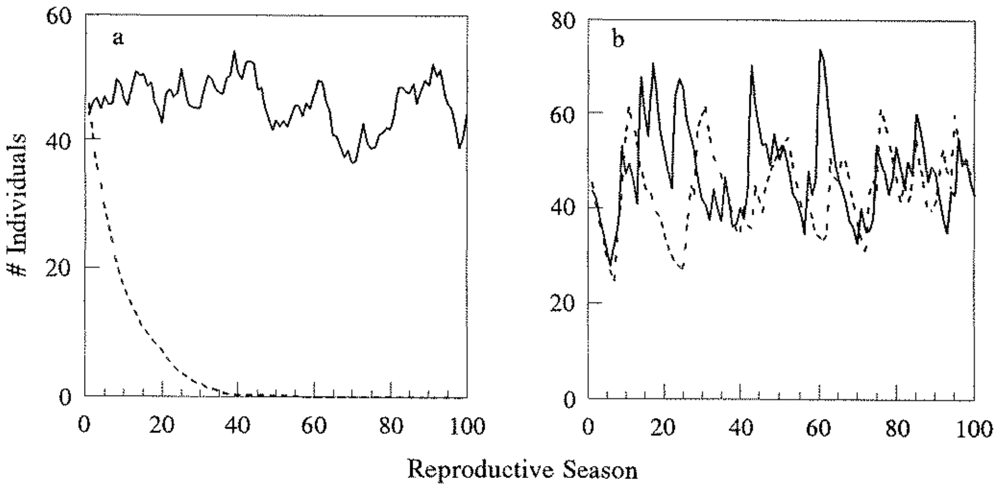
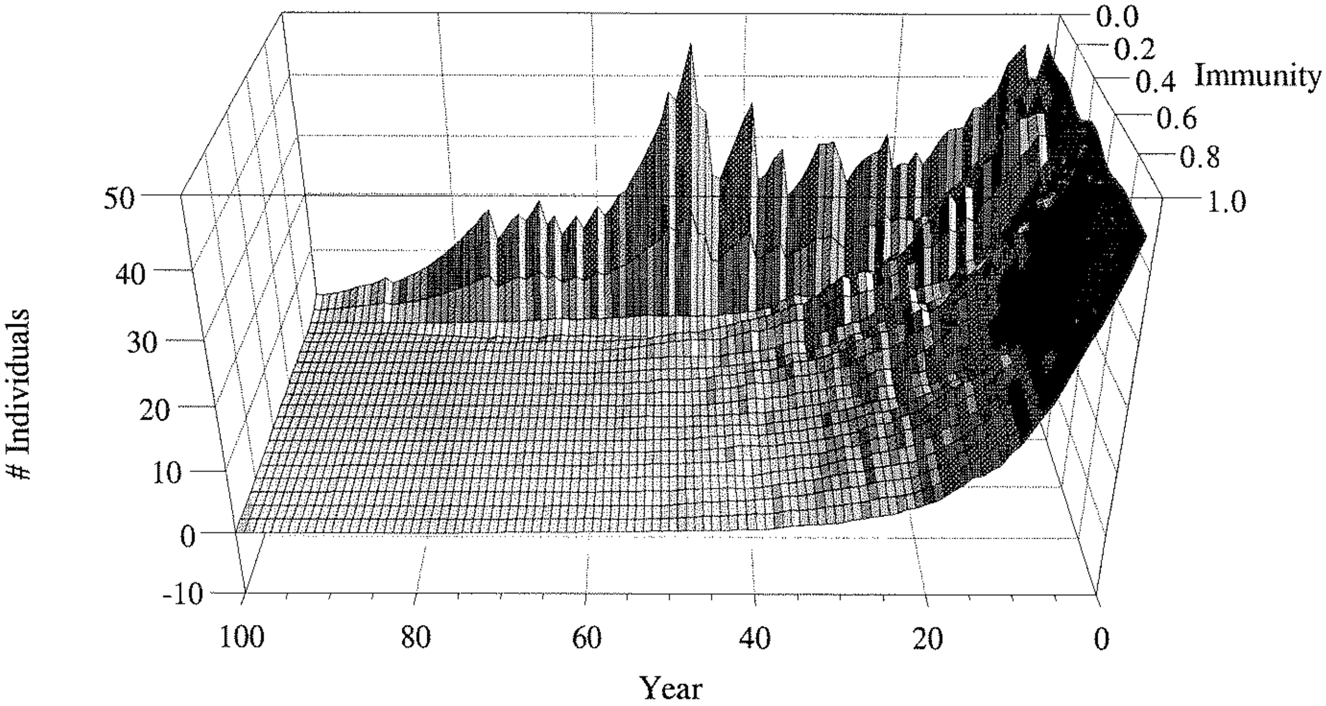
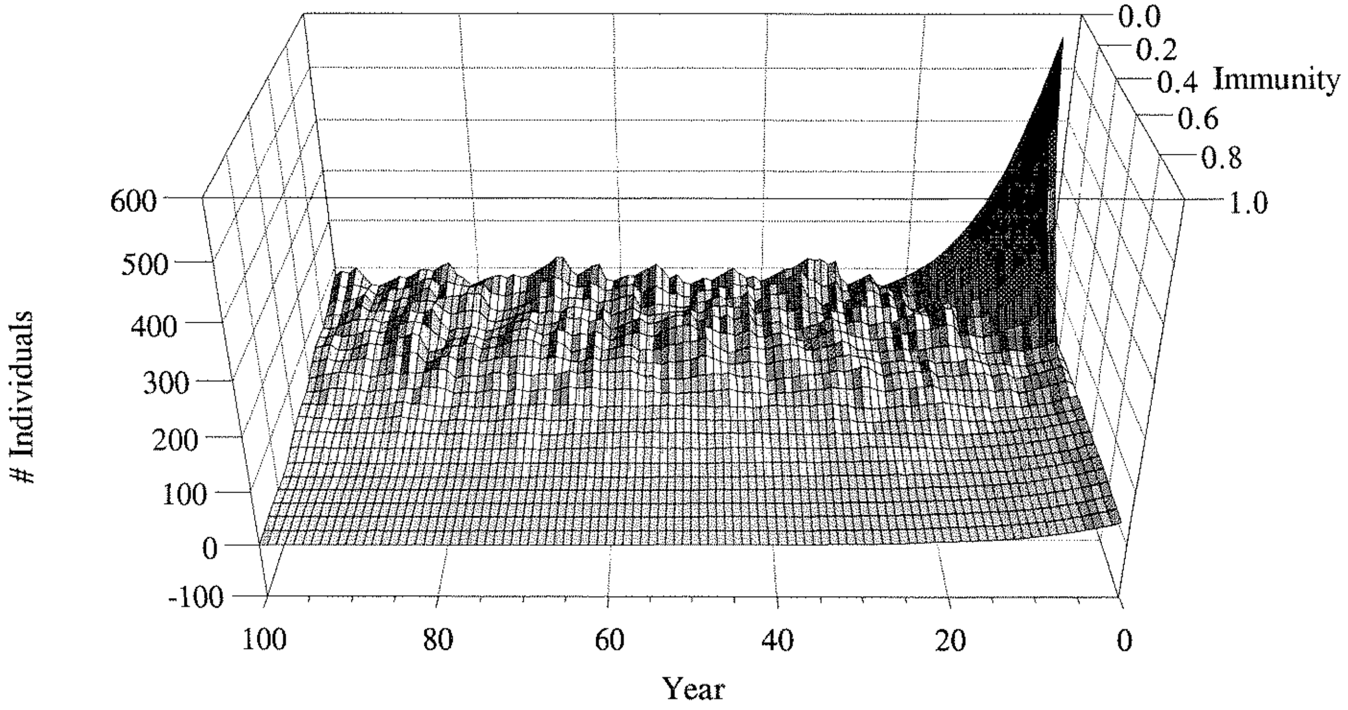


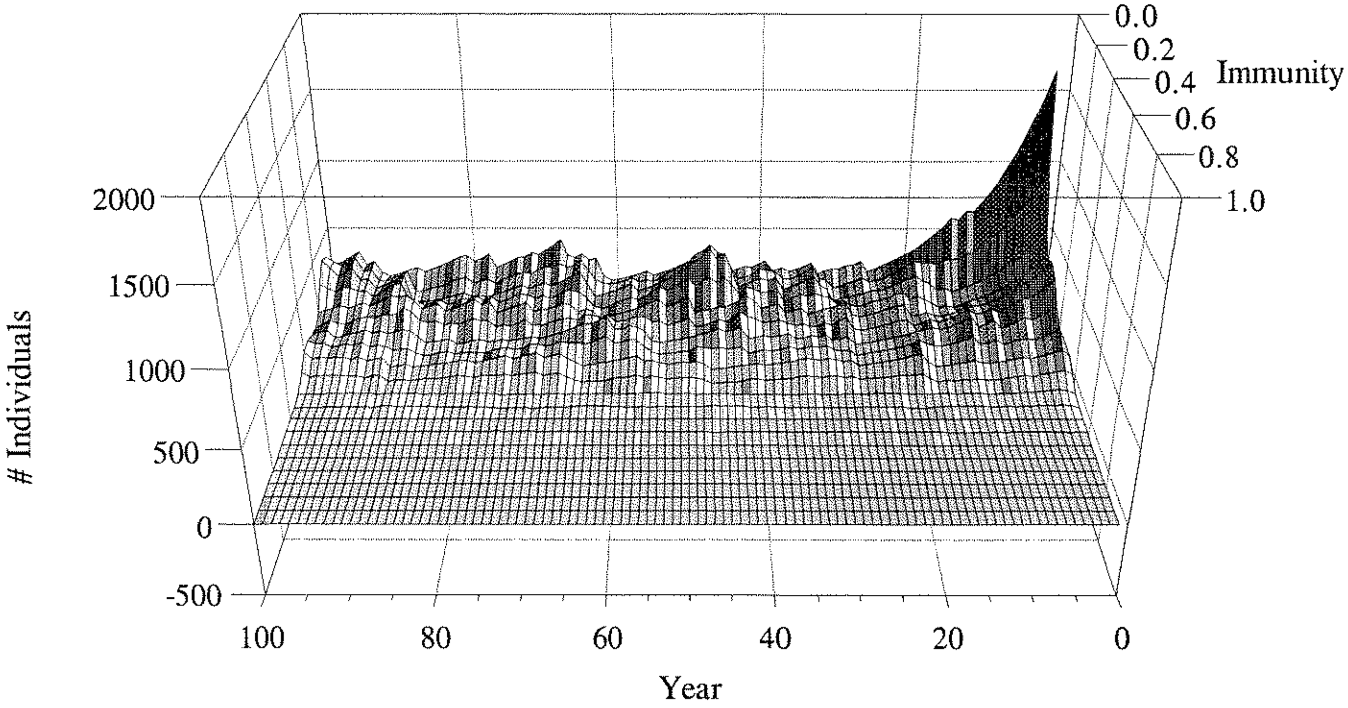
Fig. 5



50
40
30
20
10
0
-10
Individuals
100
80
60
40
20
0
Year
0.0
0.2
0.4
0.6
0.8
1.0
Immunity

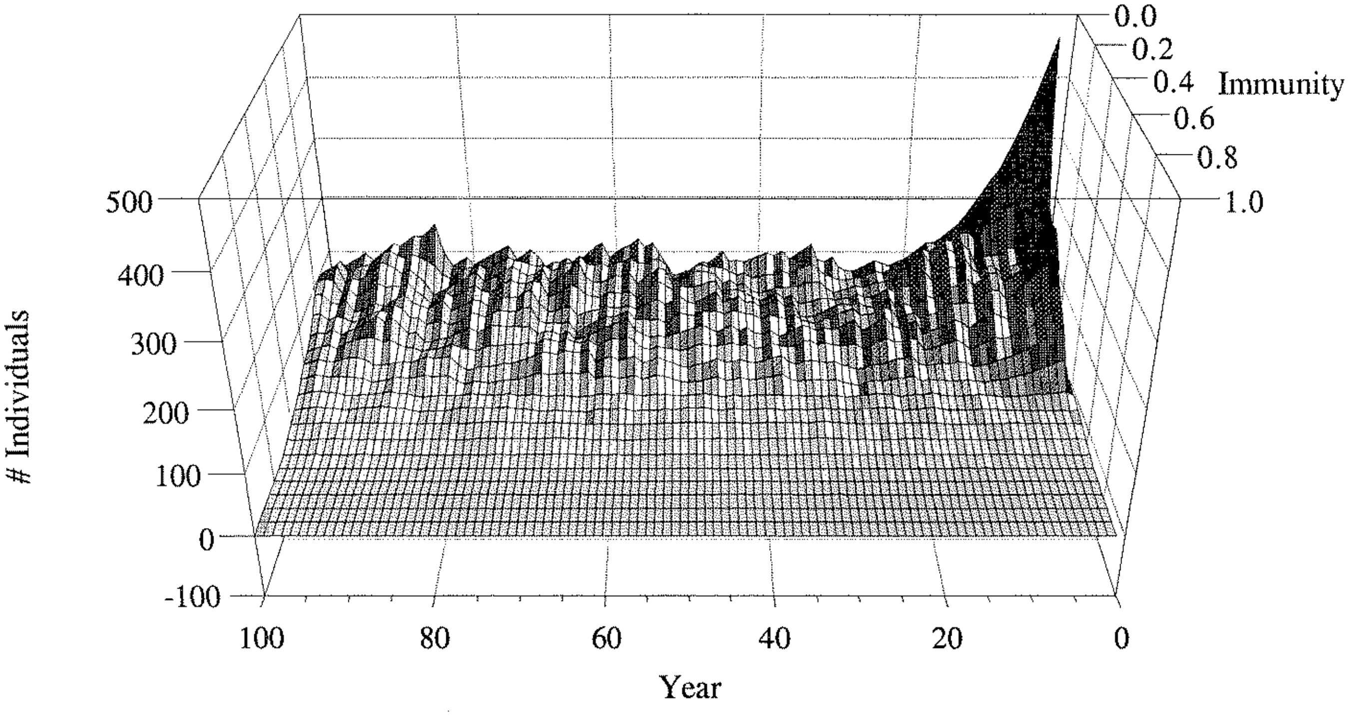
Fig. 6a


0.0
0.2
0.4
Immunity
0.6
0.8
1.0
600
500
400
300
200
100
0
-100
Individuals
100
80
60
40
20
0
Year



0.0
0.2
0.4
0.6
0.8
1.0
Immunity
2000
1500
1000
500
0
-500
Individuals
100
80
60
40
20
0
Year

6c


0.0
0.2
0.4
Immunity
0.6
0.8
1.0
500
400
300
200
100
0
-100
Individuals
100
80
60
40
20
0
Year

6d

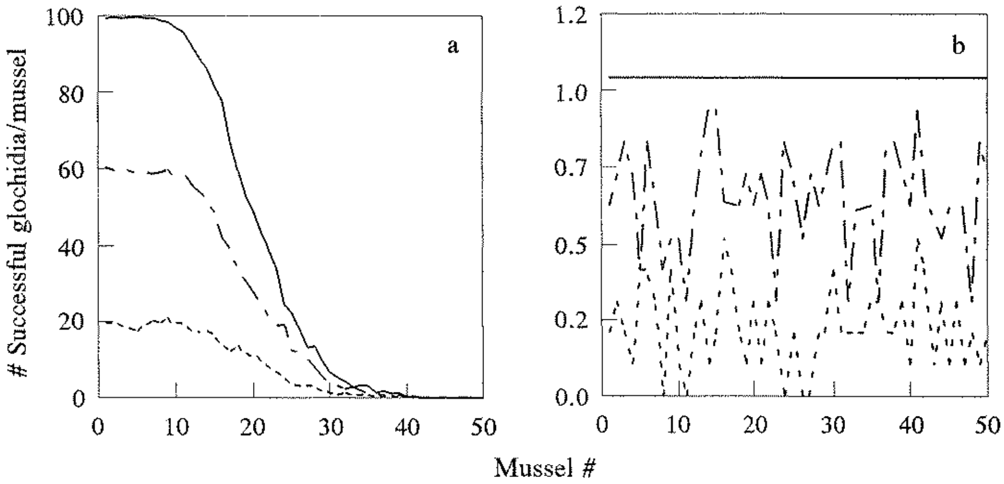

a
b
Successful glochidia/mussel
100
80
60
40
20
0
1.2
1.0
0.7
0.5
0.2
0.0
0
10
20
30
40
50
Mussel #

Fig. 7

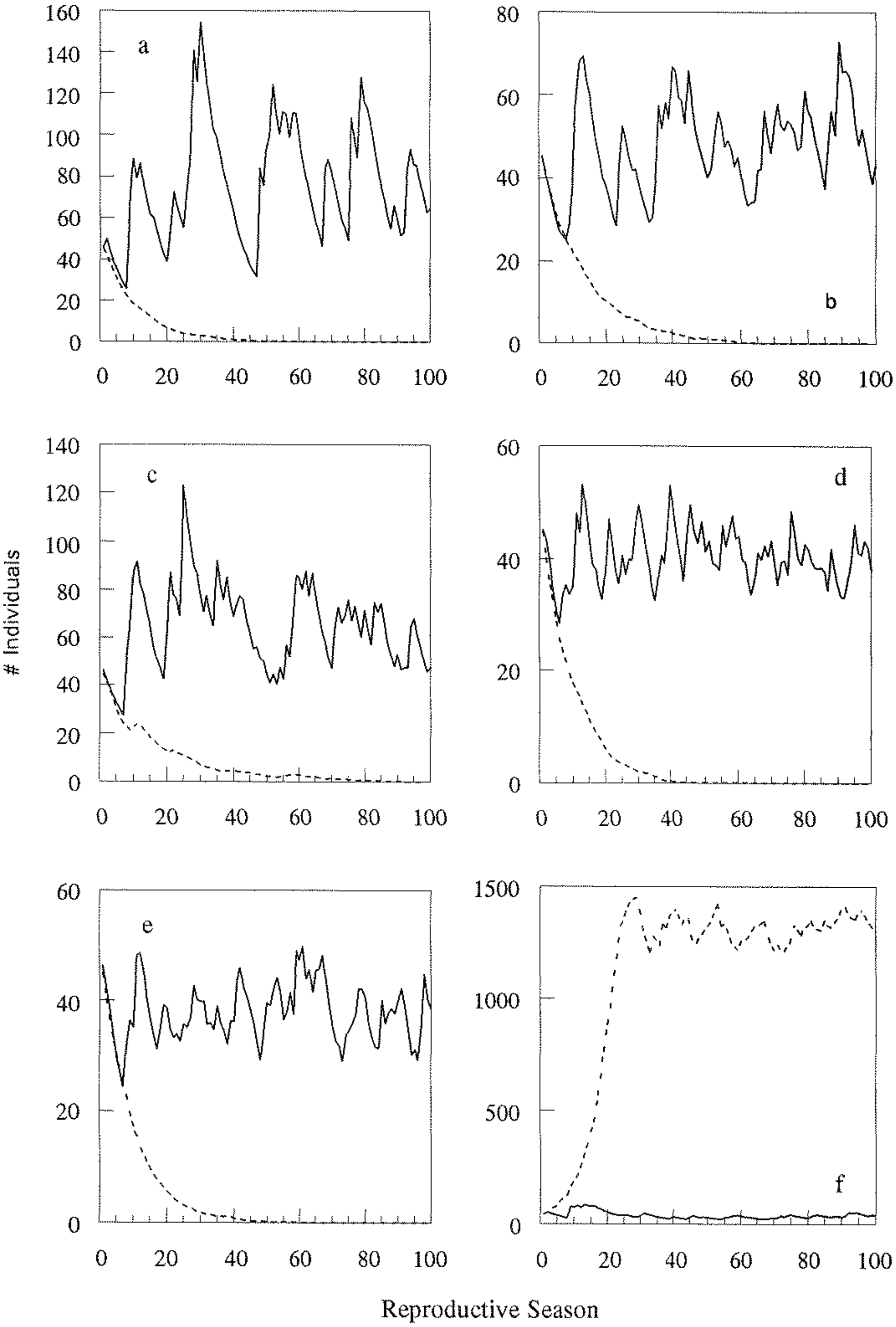

a
b
c
d
e
f
Individuals
Reproductive Season
160
140
120
100
80
60
40
20
0
0
20
40
60
80
100
1500
1000
500

Fig 8

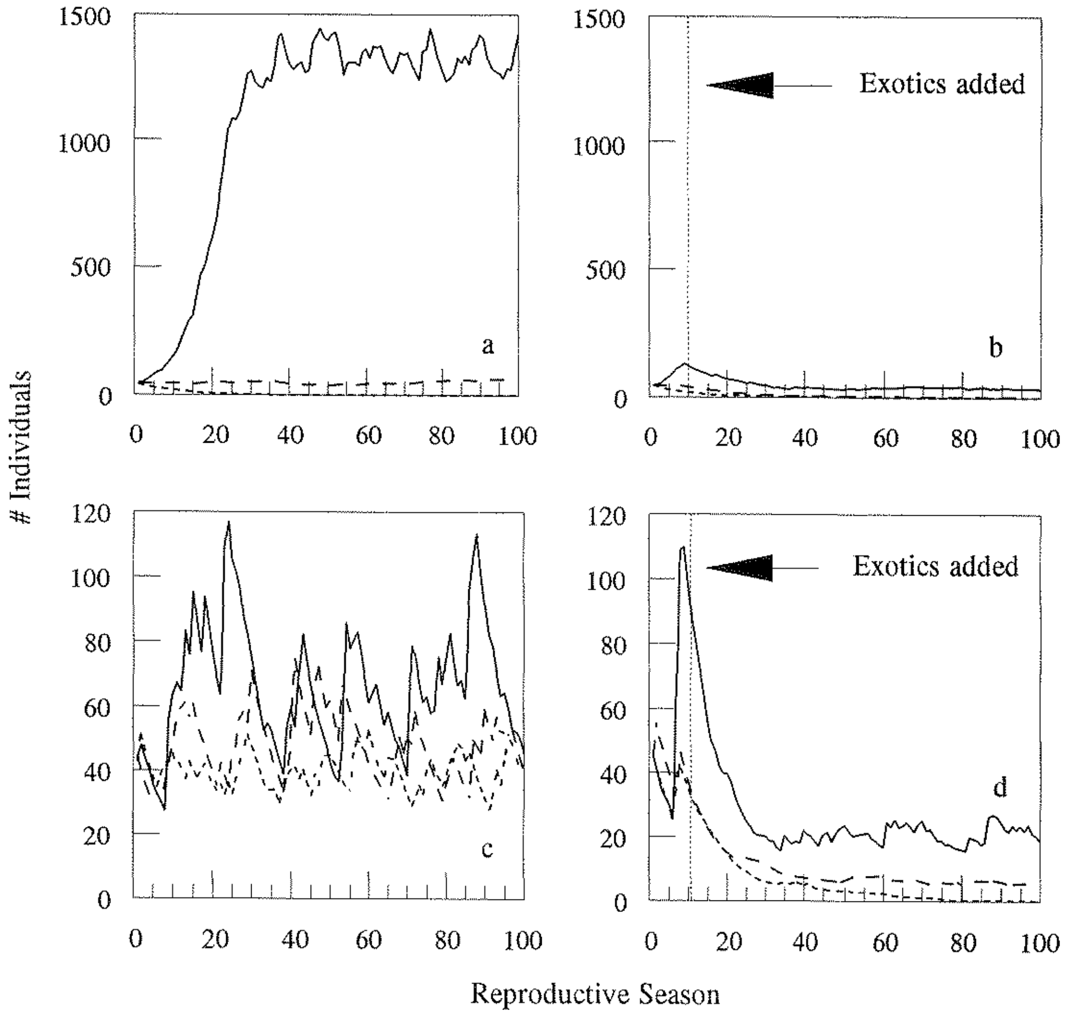

1500
1000
500
0
0
20
40
60
80
100
a
1500
1000
500
0
0
20
40
60
80
100
Exotics added
b
120
100
80
60
40
20
0
0
20
40
60
80
100
c
120
100
80
60
40
20
0
0
20
40
60
80
100
Exotics added
d
Individuals
Reproductive Season

Fig. 9

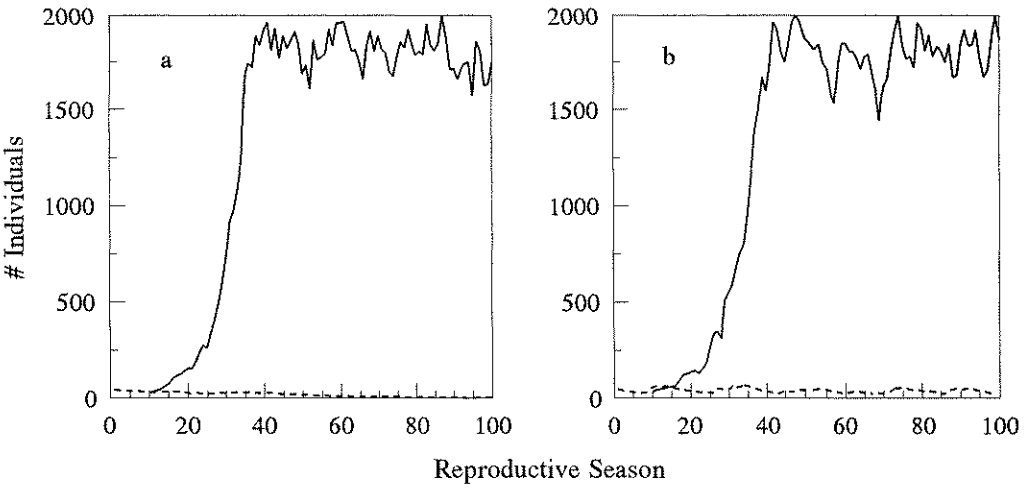

a
b
2000
1500
1000
500
0
Individuals
0
20
40
60
80
100
Reproductive Season

Fig. 10

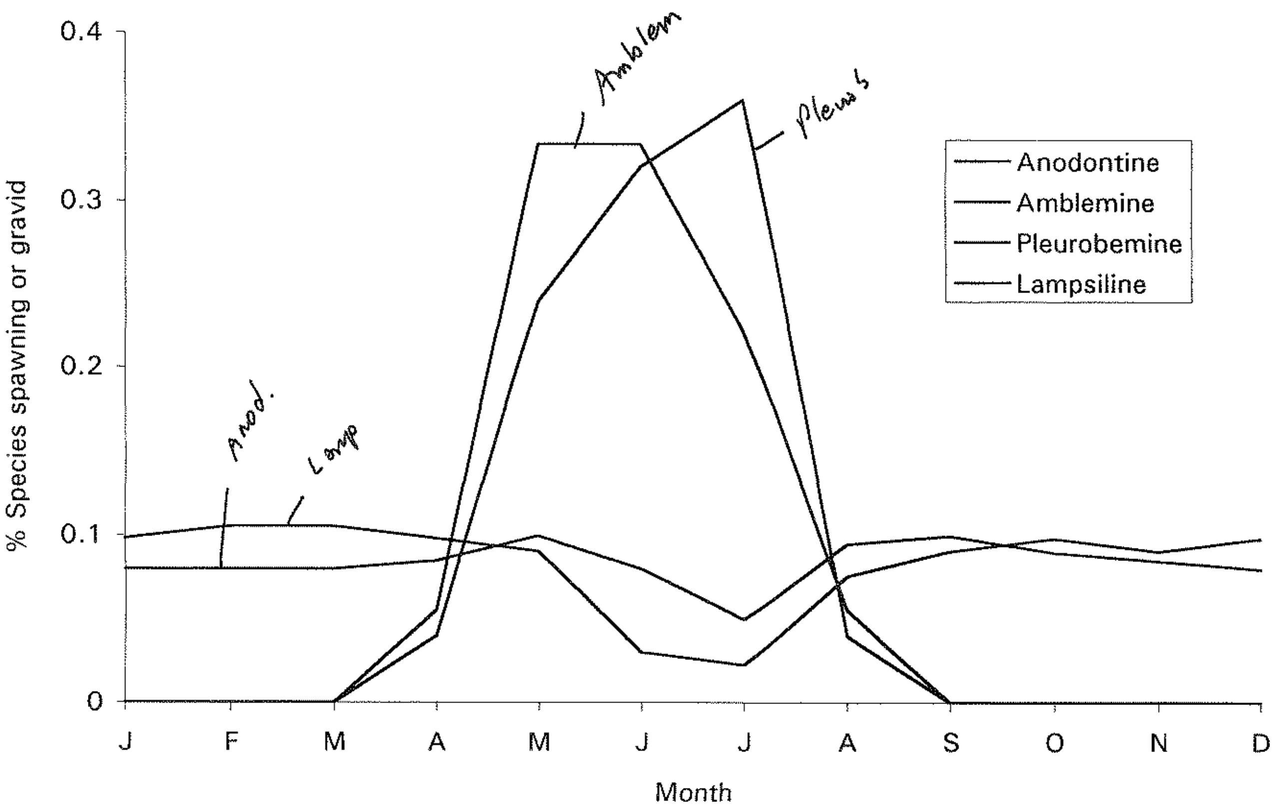

0.4
0.3
0.2
0.1
0
% Species spawning or gravid
J
F
M
A
M
J
J
A
S
O
N
D
Month
Anodontine
Amblemine
Pleurobemine
Lampsiline
Amblem
Pleurob
Anod.
Lamp

Fig. 11

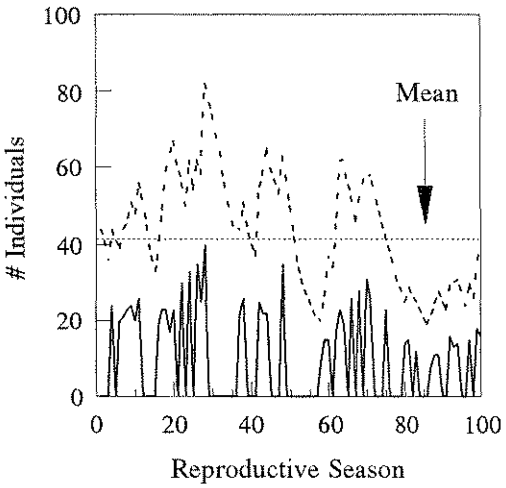

100
80
60
40
20
0
Individuals
Mean
0
20
40
60
80
100
Reproductive Season

Fig. 12

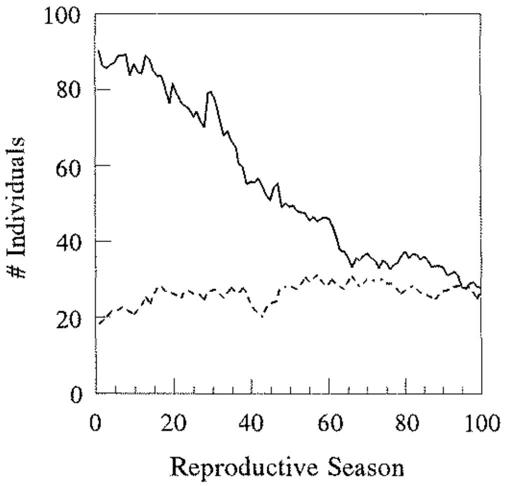
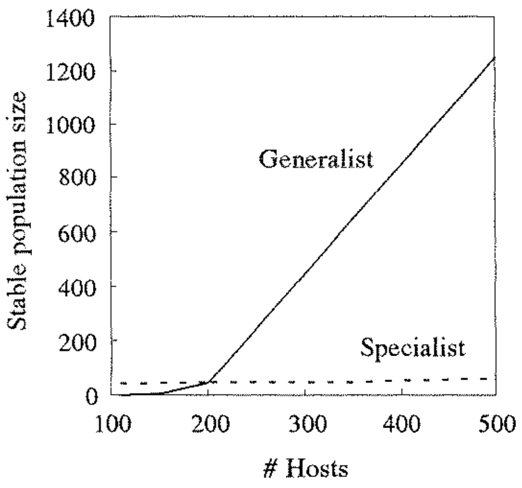

100
80
60
40
20
0
Individuals
0
20
40
60
80
100
Reproductive Season

Fig 13



1400
1200
1000
800
600
400
200
0
Stable population size
Generalist
Specialist
100
200
300
400
500
Hosts

fig. 14