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## Population Dynamics

**Steven A. Juliano**

*Professor of Biological Sciences, Dept. of Biological Sciences, Behavior, Ecology, Evolution, & Systematics Group, Illinois State University, Normal, IL 61790-4120*

### Abstract

This chapter reviews aspects of population dynamics that may be conceptually important for biological control of mosquitoes. Density dependent population regulation among immature stages has important implications for biological control of mosquito populations, primarily because it can lead to compensatory or overcompensatory mortality due to additions of a biological control agent. This can result in control efforts leading to no change in the target population, or actual increases in the target population, respectively. Density dependent effects, and compensatory or overcompensatory mortality, appear to be most common in mosquitoes from container or highly ephemeral habitats. In permanent ground water habitats generalist predators appear to limit mosquito populations and so render mortality additive. Thus, biological control in permanent ground water habitats seems to have the highest likelihood of producing a satisfactory result. A central premise of classical biological control is that pest populations are reduced by enemies to stable equilibrium levels that are both below the pre-control equilibrium level, and well below the level producing detrimental effects. This premise results in predictions that successful biological control is likely to involve specialist enemies (usually parasitoids), with short generation times relative to the victim, high rates of successful search, rapid rates of increase, and needing only a few victims to complete their life cycle. These predictions largely fail for mosquito systems, in which successful biological control seems to be associated with generalist enemies that can kill a large portion of the target population, often causing local extinction, and can persist in the absence of the target organism. Biological control of mosquitoes appears to be inherently unstable, thus contrasting sharply with classical biological control. This review suggests a need for better data on density dependent regulation of mosquito populations.

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“Classical biological control ... is applied population dynamics...”

Murdoch & Briggs 1996

### Population dynamics

Population dynamics is the portion of ecology that deals with the variation in time and space of population size and density for one or more species (Begon et al. 1990). In practice investigations and theory on population dynamics can be viewed as having two broad components: first, quantitative descriptions of the changes in population number and form of population growth or decline for a particular organism, and second, investigations of the forces and biological and physical processes causing those changes. The first of these components involves descriptive data that are useful for quantifying trends, and with appropriate statistical treatment, for forecasting future trends. In the context of biological control of mosquitoes, or more generally, any effort to control mosquitoes, this aspect of population dynamics is important because it provides the data that can answer important questions about control efforts (e.g., Are control efforts justified at this time? What is the expected population of a mosquito species some time in the future and is some intervention desirable to alter that expectation?). The second component, dealing with causal processes, is important because it can provide a general framework for strategies to control mosquitoes. Knowledge of causal processes affecting population dynamics also may improve the forecasts of population trends (e.g., Does

early spring precipitation affect expected populations later in the year?). Consideration of principles of population dynamics may help to answer questions about the choice of biological control agents (e.g., What population characteristics of a predator, pathogen, or parasite are associated with biological control success?) or the life cycle stages of the target species that should be the focus of biological control efforts (e.g., Would introduced predators or pathogens attacking larval stages affect population dynamics sufficiently to reduce the population of a mosquito?). Other sources of guidance in decision making about biological control include natural history of target species and enemies (Murdoch & Briggs 1996), potential for unintended impacts on non-target species (Simberloff & Stiling 1996), and costs and logistics of application (Murdoch & Briggs 1996). Clearly, then, population dynamics is potentially very important for mosquito biological control as both a conceptual area and as a quantitative approach.

Population dynamics as a branch of ecology has a long history and an enormous literature, including numerous studies of insects (reviewed by Speight et al. 1999, Price 1984, Murdoch 1994, Gotelli 1995, Murdoch & Briggs 1996). Population dynamics is an inherently quantitative subdiscipline of ecology, in which modeling of biological populations and their interactions plays an important role. Investigation of mosquito population dynamics has a relatively long history as well, particularly of attempts to discern how causal factors influence population size and what stages in the mosquito life cycle would make the best targets for control efforts (Southwood et al. 1972, Gilpin and McClelland 1979, Frogner 1980, Hawley 1985 a, b, Service 1985, Bradshaw & Holzapfel 1990).

There are several areas within the field of population dynamics that overlap considerably with other chapters in this volume. Modeling (Lord, Chapter #) is of course a prominent topic within population dynamics. Effects of pathogens (Wu, Wesson, Lacey, Kerwin, Federicci,, Becnel, Andreadis, Chapters #, #, #, #, #, #, #, #), predators (Walton, Schreiber, Quiroz, Platzer, Mogi, Marten, Chapters #, #, #, #, #, #), and competitors (Lounibos, Chapter #) also feature prominently as causal processes affecting population dynamics of mosquitoes. In order to minimize redundancy with these other chapters, this one will not provide a comprehensive review of mathematical models of vector populations, nor detailed case studies of effects of particular pathogens or predators of vectors. Instead, this chapter focuses on aspects of population dynamics that may be useful or conceptually important for biological control of mosquitoes. First, it presents density dependent population regulation, and its implications for biological control of mosquito populations. Second, a central premise of classical biological control -- that pest populations are reduced by enemies to stable equilibrium levels that are both below the pre-control equilibrium level, and well below the level producing detrimental effects -- leads to a number of predictions about the characteristics of enemies that are associated with successful biological control. Population level processes that are associated with successful classical biological control, and how those may relate to attempts at biological control of mosquitoes will be evaluated. The goal of this chapter is to use principles of population dynamics to evaluate which ecological settings, which target species, and which natural enemies are likely to foster successful biological control of mosquitoes. The main focus of this chapter will be on metazoan enemies of mosquitoes, with only limited mention of some protozoan and bacterial enemies that have been used in biological control.

## Population regulation

A key feature of any population is whether its size and growth rate are regulated by density dependent processes and if so, what those processes are and at what stage of the life they act (Hawley 1985a, b; Service 1985, Murdoch 1994). "Regulated" in the simplest case means that increases or decreases in population are counteracted by changes in the factors acting on the population, with the result that the population returns to its previous level. Such regulation

implies an equilibrium density at which population growth is 0. Such regulation is an integral part of basic models of populations, such as the classic logistic growth model, and is also built into extensions of that model such as Lotka-Volterra competition models (Gotelli 1995). Processes that may regulate a population must act in a **density dependent** manner, so that as density rises above equilibrium level, changes in the processes produce decreases in birth rate or increases in death rate, and when density falls below equilibrium, increases in birth or decreases in death result (Gotelli 1995). Examples of processes that may act in a density dependent way include predation, parasitism, intraspecific resource competition, intraspecific interference, and other social interactions. Though ecologists typically think of density dependent death as the archetypical regulatory process, density dependent growth or development rates (e.g., Frogner 1980, Kleckner et al. 1995, Lord 1998), or density dependent oviposition deterrents (Zahiri & Rau 1998), can also be powerful population regulation mechanisms because they may affect birth rate via delays in reproduction or reductions in life time fecundity (Lord 1998). Density dependent slowing of development of immatures has the consequence of increasing cumulative pre-reproductive mortality, and thus regulating the number of adults in the population (Frogner 1980). This effect occurs even if daily mortality rate remains constant (Frogner 1980). We tend to think of predation as a cause of mortality, but because predators induce prey behavioral responses that often have costs in reduced foraging success (e.g., Sih 1986, Lima & Dill 1990, Juliano & Gravel 2002, Kesavaraju & Juliano 2004) non-lethal effects of predators can, in principle, be density dependent and regulatory as well.

Regulation can also be defined as boundedness of the population over time (Murdoch 1994). That is, as the population changes over time, a regulated population will have non-zero and non-infinite limits on its lower and upper densities, respectively, whereas an unregulated population will have no such limits (Murdoch 1994). This definition clarifies the distinction between regulated populations that have stable equilibria, and unregulated populations that may have unbounded dynamics despite the presence of an equilibrium (Murdoch 1994). In such cases, where there is an equilibrium but no regulation, the equilibrium is unstable (Murdoch 1994). Boundedness of a population can also be described statistically: in a regulated population, cumulative variance in population size is an asymptotic function of time, whereas in an unregulated population, cumulative variance in population size is a monotonic, increasing function of time (Murdoch 1994).

Many biotic and abiotic processes may affect death and birth rates, and produce effects through alteration of growth and development, but do not do so in ways that are related to density of the population in question. Such **density independent** processes can be extremely important and can have large, even catastrophic, impacts on populations, but cannot produce regulation of a population at equilibrium. Though we tend to think of abiotic factors such as extremes of temperature and desiccation as archetypical density independent sources of mortality, biotic factors including predation and competitively induced food shortage can act in density independent ways. Such density independence arises when there is no feed back of density of the target population on the processes affecting it. It is easy to see that deaths of individuals due to heat stress have no means of influencing the processes (e.g., climate variation) imposing that heat stress. It is also possible for a predator to impose death but also to have a population that is unaffected by the resulting changes in prey density (e.g., when predator populations are themselves not limited by food, or when generalist predators are not limited by the abundance of a particular prey type).

## The importance of density dependence for control of mosquitoes

When a population is regulated by a density dependent process (e.g., density dependent mortality due to intraspecific competition for food) acting at a particular stage, effects of

additional sources of mortality (e.g., control efforts such as added predators or pathogens, or toxic chemicals) acting at other stages can produce counterintuitive effects on total mortality and on population size. **Compensatory mortality** occurs when an additional source of mortality produces a reduction in density that, in turn, reduces the impact of a density dependent source of mortality, so that the net result of imposing the added source of mortality is no net change in total mortality or population size (Washburn et al. 1991, Washburn 1995). This implies that the individuals killed by the additional mortality caused by control efforts would, in a sense, have been victims of mortality in any case, and were not important from the perspective of population growth. It is indeed possible that **overcompensation** may result from addition of mortality sources, when reductions in density and associated reduction in density dependent mortality actually exceed the increase in mortality caused by the added source of death (i.e., the control agent). This circumstance can yield lower total mortality and greater population size after control efforts (Washburn et al. 1991, Washburn 1995, Service 1985). Finally it is also possible that an additional source of mortality may be **additive**, when the added source of mortality has the intuitive effect of increasing observed total mortality (Washburn et al. 1991). Additive effects are desirable from a biological control perspective and are typically assumed in biological control efforts (Washburn 1995). Because mortality sources that produce compensation or overcompensation are consequences of density dependent effects and because the result can be ineffective biological control (i.e., target populations are not reduced), the role of density dependent effects in mosquito populations can be critical for biological control efforts.

For mosquitoes, it is highly likely that density dependent effects, if they occur, act on or originate with, larvae (Gilpin & McClelland 1979, Service 1985). Although intraspecific competition and density dependent mortality have received the most attention (Southwood et al. 1972, Service 1985, Léonard & Juliano 1995) it is also clear that for some mosquitoes, density dependent food shortage resulting from interspecific competition affects survivorship (Juliano et al. 2004). Density also affects growth and development rates, resulting in smaller adults with lower fecundity that would be the case for uncrowded individuals (Cochrane 1972, Hawley 1985a, b, Léonard & Juliano 1995, Frankino & Juliano 1999, Lounibos et al. 2002) or with delayed reproduction (Frogner 1980), and either of these nonlethal effects may regulate population size. Effects of small adult size, induced by food shortage, may also include reduced adult longevity (Haramis 1985). Thus, density dependence among mosquito larvae is common, and this implies that any attempts to use biological control agents to impose mortality on mosquito larvae must consider whether the resulting mortality is likely to be compensating, overcompensating, or additive. Such effects have been observed with conventional chemical larviciding (e.g., Agudelo-Silva & Spielman 1984). Important questions that arise from considering this issue are: 1) Which habitats and mosquito species are least likely to suffer density dependent effects, and so potentially show additive effects of introduction of biological control agents? 2) When during the immature stages does density dependence act on a particular target mosquito? 3) When during the life cycle does a particular biological control agent impose mortality?

## Habitats and density dependence

Service (1985) reviewed the literature on mortality affecting immature mosquitoes and concluded that overcrowding and density dependent mortality were often major factors affecting populations of container breeding mosquitoes, including those in both natural and human-made containers. In contrast, for ground water habitats such as ponds and marshes, Service (1985) concluded that density dependent mortality was less important. Fish (1985) posed similar questions, and assessed patterns of adult size variation and skewness as indices of competition and density dependent effects acting on growth and development of larvae. He concluded that species in more ephemeral habitats (tree holes, temporary pools) had more

variable, and more right skewed adult body size distributions, indicating a high level of intraspecific competition. In contrast, species inhabiting permanent habitats were less variable and not right skewed, suggesting little or no effect of intraspecific competition. He suggested that these differences arise because of the relative rarity of predation in more ephemeral habitats. Presumably predation in permanent ground water habitats keeps larval populations low resulting in most individuals attaining their maximum adult size. This conclusion was also reached by Washburn (1995).

Studies of individual mosquito species in ephemeral or container habitats indicate strong density dependent effects on mosquito populations (e.g., Renshaw et al. 1993, Lord 1998, Gleiser et al. 2000, Gimnig et al. 2002, Arrivillaga & Barrera 2003, Reiskind et al. 2004, Juliano et al. 2004). Chase & Knight (2003) surveyed wetlands categorized as permanent (never dry), semipermanent (drying only in severe drought years), and temporary (drying each year) for mosquito and predator populations. They concluded that in temporary wetlands, mosquito populations were always low and populations of non-mosquito competitors were uniformly high, suggesting strong interspecific competition in these largely predator-free habitats. Mosquito populations were likewise low in permanent wetlands, but in contrast to temporary wetlands, predator populations were always high. In semipermanent habitats, Chase & Knight (2003) observed mosquito populations were typically low, except in years following a drought and habitat drying. In drought years, predator populations crashed, and remained low into the following year. During this year after a drought, mosquito populations increased by about an order of magnitude. These results are consistent with the observations by Fish (1985), and Washburn (1995), implying that density dependent effects of competition are strongest in the most ephemeral habitats, and implicating predation as the process limiting mosquito density (and possibly density dependence) in more permanent habitats. They also provide an example of how following the dynamics of mosquito populations and their enemies could enhance the effectiveness of biological control. Control efforts might target populations that have been released from predation pressure due to climatic effects on predators.

### Biological control in container and ephemeral habitats

The prominence of density dependent mortality and growth affecting mosquito population dynamics in ephemeral or container habitats suggests that compensating or overcompensating mortality may result from introduction of novel predators or pathogens, limiting success of biological control. In contrast, in more stable or larger habitats, introduction of pathogens and predators may be more likely to produce additive mortality and thus reduce production of adult mosquitoes. Empirical data that directly address the question of additive/compensating/overcompensating mortality are limited, complicated, and inconsistent. Washburn et al. (1991) showed that introduction of the parasitic protozoan *Lambornella clarki* to containers harboring *Aedes sierrensis* resulted in additive, compensating, or overcompensating mortality depending on whether resource levels were high, moderate, or low, respectively. In contrast, Nannini & Juliano (1998) found no effect of addition of predatory larvae of *Anopheles barberi* on survivorship to adulthood of *Ochlerotatus triseriatus* in either tree holes or tires, and that additions of food resources did not alter predator-induced mortality of *Oc. triseriatus*, despite obvious evidence for food limitation in these field containers. *Anopheles barberi* is a predator on small larvae and is incapable of capturing large larvae (Nannini & Juliano 1998). The absence of effects of this predator on production of *O. triseriatus* adults suggests that this predator has strictly compensatory mortality effects across a wide range of conditions. Lounibos (1985) showed that pupation success of *O. triseriatus* in Florida tree holes increased with abundance of *Corethrella appendiculata*, a small predator that preys on small, but not large, larvae of *Oc. triseriatus*. This study suggests overcompensation is the likely result of predation by *C. appendiculata* in natural tree holes, which is consistent with density

dependent effects on *Oc. triseriatus* acting primarily on later stage larvae, after predation has exerted its effect on survival.

In addition to these studies directly addressing patterns of predator-induced mortality, a number of studies of container-dwelling predators indicate that presence of predators, either native or introduced, reduce the numbers of prey mosquitoes in the system (e.g., Gerberg & Visser 1978, Bradshaw & Holzapfel 1983, Focks & Sacket 1985, Mogi et al. 1985, Rivière 1985, Marten et al. 1994, 2000, Schreiber et al. 1996, Brown et al. 1996, Lounibos et al. 1997). These studies seem at odds with the inference described above that in container habitats, density dependent food limitation acting on larvae is prominent and that compensating or overcompensating effects of predation are likely. However, in a number of these studies predators have only been shown to affect abundances of **larvae**. In order to evaluate whether compensation or overcompensation occur, data on production of **adults** (or at least of **pupae**) are necessary because density dependent mortality may occur among larvae late in development.

Predatory larvae of the culicid genus *Toxorhynchites* have been shown repeatedly to reduce production of adult or pupal container-dwelling mosquitoes (e.g., Gerberg & Visser 1978, Bradshaw & Holzapfel 1983, Focks & Sacket 1985, Mogi et al. 1985, Rivière 1985, Lounibos et al. 1997). Thus, this predator is capable of imposing sufficient mortality on populations of larvae and pupae to render the effect of that mortality additive, despite density dependence in container dwelling prey. The success of biological control efforts employing various species of *Toxorhynchites* has been variable (reviewed by Collins & Blackwell 2000), but failures have generally not been related to compensating or overcompensating mortality. Most failures have been ascribed to failure of *Toxorhynchites* to oviposit in the target habitat (i.e., a failure of natural history knowledge) or because *Toxorhynchites* has a longer development period, longer generation time, and slower population growth than most of the target mosquitoes (Lounibos 1979, Collins & Blackwell 2000). This latter effect is an example of how population dynamics of an enemy are related to probability of successful control, which is discussed below.

Investigations of predation by cyclopoid copepods have more commonly examined effects of predators on abundances of larvae (e.g., Marten et al. 1994, 2000, Schreiber et al. 1996, Brown et al. 1996, Manriquesade et al. 1998, Rey et al. 2004), hence the potential for compensation and overcompensation to limit the effectiveness of copepods as biological control agents remains unknown. Like *Corethrella* and *Anopheles barberi* (see above), copepods prey primarily on small larvae, and because density dependent effects may impact larger, older larvae, it seems likely that compensation or overcompensation could result from copepod predation in at least some circumstances, and this would be an interesting avenue for further research.

Thus, it seems likely that biological control of container mosquitoes will be difficult because control attempts may be foiled by compensating or overcompensating mortality. There is both direct (Lounibos 1985, Washburn et al. 1991, Nannini & Juliano 1998) and circumstantial evidence for compensation or overcompensation in tree hole and human-made container systems. Merely knowing that the target of a control program is from a habitat (e.g., containers) where density dependent food limitation is common is insufficient for evaluation of the potential for biological control. Quantitative data on density dependent mortality (when?, where?, how much?), and how different sources of mortality combine to affect production of adults would be necessary to evaluate the potential of biological control in those habitats.

Relatively few attempts have been made at biological control of mosquitoes in ephemeral ground water habitats, and no one has explicitly considered whether mortality is additive, compensating, or overcompensating. Introductions of tadpole shrimp (*Triops* sp) to temporary

pools have produced effects on mosquito populations that suggest additive mortality (Fry et al. 1994, Su & Mulla 2002), but population level effects could also be the result of behavioral avoidance by ovipositing females of habitats with *Triops* (Fry et al. 1994). Stav et al. (2005) demonstrated that nymphs of the dragon fly *Anax imperator* produced strong reductions (32 and 78%) of pupation success by *Culex pipiens* and *Culiseta longiareolata* in simulated ephemeral pools. The effects of this predator suggest additive mortality. Further, Stav et al. (2005) showed that addition of competitors (*Daphnia*) to the system also produced reductions in pupation success or pupal size, but that effects of predation and competition on pupation success were additive (i.e., no significant interaction of predator and competitor treatments). These results for experimental ephemeral ground water habitats are consistent with additive mortality imposed by a generalist predator, and thus suggest that biological control by predators would be successful in this habitat. Introduction of *Gambusia* to ephemeral habitats has also produced successful mosquito control (reviewed by Murdoch et al. 1985), suggesting additive mortality. Thus, for ephemeral ground water habitats, limited data suggest that additive mortality may be common, and prospects for biological control may be better than for container habitats.

### Biological control in permanent ground water habitats

In these habitats, consideration of density dependent effects on mosquito population dynamics leads to the expectation that additive mortality should be prevalent, and biological control efforts should be more likely to succeed. The most commonly employed methods of biological control for mosquitoes in permanent ponds are releases of mosquitofish (*Gambusia*) and a few other fish species, and application of *Bacillus thuringiensis* var. *israelensis* (Bti) or *Bacillus sphaericus* (Bs).

Classical biological control of mosquitoes with fish in small permanent ponds, ditches, and rice paddies is generally regarded as successful, in the sense that mosquito populations are reduced (Murdoch et al 1985), although there are many instances in which introduced *Gambusia* have become threats to native fish, amphibians, and invertebrates (e.g., Gamradt & Kats 1996, Rupp 1996, Goodsell & Kats 1999, Leyse et al. 2004). Despite these concerns, a number of state and local agencies in the U.S. routinely recommend or practice the stocking of *Gambusia* in some situations (e.g., Contra Costa Co. CA Mosquito and Vector Control District, <http://www.cmvcd.dst.ca.us/mosquitofish.htm>; Alameda Co. CA Mosquito Abatement District [http://www.mosquitoes.org/control\\_program.htm](http://www.mosquitoes.org/control_program.htm); the City of Albuquerque, NM, <http://www.cabq.gov/bdm/surveillance.html>; Utah Co., UT Health District, <http://www.co.utah.ut.us/Dept/HealthMosq/MosqFish.asp>; Los Angeles Co. West CA Vector & Vector Borne Disease Control District, <http://www.lawestvector.org/MosquitoFish.htm>; Suffolk Co. NY, <http://www.co.suffolk.ny.us/webtemp5.cfm?id=75&dept=9#Biologicalcontrol>; the state of New Jersey, <http://www.nmca.org/Nmca94-16.htm>). However, data documenting the effectiveness of *Gambusia* in reducing pupation or adult production are scarce (Bence 1988). There are instances in which mosquitofish fail to produce reductions of numbers of adults (Blaustein 1992) and in some cases introduction of mosquitofish has resulted in **increased** abundances of mosquitoes (reviewed by Bence 1988). In reviewing these cases, Bence (1988) suggested that when mosquitofish cause increases in mosquito abundance, that effect arises because of indirect effects on mosquito populations mediated via predation by mosquitofish on other predators of mosquitoes. If this hypothesis is correct, these failures have not arisen because of compensation or overcompensation in the mortality of the target mosquitoes, but rather through community wide impacts of the biological control agent. Such effects seem particularly likely (and worrying) for generalist predators (see below). These kinds of potential effects suggest that in addition to reviewing the implications of population

dynamics for biological control of mosquitoes (i.e., this chapter), a volume on biological control of mosquitoes should also include a review of the community ecology of mosquitoes.

Bti and Bs have been used effectively as biopesticides, producing reductions of mosquito populations (e.g., Rodrigues et al. 1999, Blanco Castro et al. 2000), but this success is probably a result of the overwhelming inputs of these bacteria (or their toxins) that result in such high mortality that population declines are inevitable. Reintroduction of the pathogen or toxin is typical. No studies have specifically investigated whether these pathogens cause additive, compensating, or overcompensating mortality in these habitats, hence we cannot evaluate the role of density dependent mortality in these systems. Because larviciding can result in compensatory mortality of mosquitoes, at least under laboratory conditions (Agudelo-Silva and Spielman 1984), it is at least possible that larviciding with Bti or Bs can also produce this effect.

For permanent ground water habitats, the data suggest that additive mortality is common and thus successful biological control may be likely in these habitats. Across habitats, consideration of density dependent effects and additive/compensating/overcompensating mortality suggest a division between, on one hand, container habitats, with prominent density dependent effects and a tendency toward compensating/overcompensating mortality, and on the other hand, ground water habitats with less evident density dependent effects and additive mortality. Biological control seems a better prospect in the latter group.

### When during the life cycle does density dependence occur?

Service (1985) argued that added mortality imposed by a control agent should act after density dependence has taken its toll on a target mosquito population. He suggested that enemies that attack late larval or pupal stages would therefore be most effective as biological control agents and that killing eggs or early stage larvae would be less effective (Service 1985). Service based this suggestion on the expected effects of density dependent death and the potential for compensating mortality from control efforts, however, the conclusion that targeting late larvae and pupae is most effective also derives from consideration of reproductive value for individuals, which is maximal just prior to the transition to adulthood, rendering control of these stages more effective for reducing population size (Lounibos et al. 1997). These considerations would suggest that predators such as *Toxorhynchites*, *Gambusia*, *Notonecta*, and nematode parasitoids (which kill late instar larvae and pupae) are likely more desirable control agents than are copepods and other small predators like *Corethrella* and *A. barberi* (which prey upon early instar larvae). Paradoxically, the most thorough analysis of density dependent mortality in mosquitoes (Southwood et al. 1972, as cited by Service 1985), concluded that mortality from egg to 2<sup>nd</sup> instar was density dependent in *Aedes aegypti*.

### Population dynamics and success of biological control

Most population dynamic theory related to biological control involves a single pest population and an enemy that feeds as a specialist on that pest (reviewed by Hassell 1981, Murdoch et al. 1985, Murdoch & Briggs 1996). These models have focused primarily on the population dynamics of insect parasitoids attacking herbivorous insects (Murdoch & Briggs 1996). Further, a key assumption of most models of population dynamics has been that there will be stable coexistence of the target and the enemy, with the target population in the presence of the enemy attaining an equilibrium density that is far below the equilibrium density without the enemy (Murdoch & Briggs 1996). Empirical work on classical biological control, verbal theory, and formal mathematical theory support the general ideas that biological control agents most likely to produce this stable two-species equilibrium: 1) are specialists; 2) have populations that develop in synchrony with the target (i.e., have generation times that match that of the target); 3) can increase rapidly when the target population increases; 4) need only



one or a few victims to complete their life cycle; and 5) have a high rate of successful search (i.e., can find and attack victims even when they are rare) (Huffaker & Messenger 1976; Murdoch et al. 1985, Murdoch & Briggs 1996). These characteristics are direct outgrowth of the aforementioned assumption: the key to success is that the introduced enemy and the target pest reach a stable two-species equilibrium, with the target population's equilibrium density much lower than that attained in the absence of the enemy (Murdoch et al. 1985). These characteristics also lead to the conclusion that specialist enemies like parasitoids are the ideal biological control agent, and that generalist enemies are poor candidates for biological control (Murdoch et al. 1985). If accurate, these considerations are not cause for optimism about biological control of mosquitoes. Most of the enemies available for biological control efforts against immature mosquitoes are generalists, with generation times longer than those of target species, a requirement of multiple victims during development, and some have relatively slow population growth (e.g., *Toxorhynchites*, *Gambusia*, copepods). All stages of the mosquito life cycle seem to be virtually free from attack by insect parasitoids (which is itself an interesting observation worthy of investigation), but mosquito larvae are attacked by mermithid nematodes that have most of the characteristics of insect parasitoids and are of interest for biological control (Petersen 1985). They also fit very well most of the characteristics described above for ideal biological control agents. This situation leads to questions about the applicability of population dynamic theory for biological control to mermithids attacking mosquitoes: Do these parasitic nematodes attain a stable two-species equilibrium with target mosquitoes, and produce a greatly reduced equilibrium density of target mosquitoes? If so, what biological mechanisms stabilize this host-parasite interaction?

Field trials have established that mermithids in the genus *Romanomermis* can be released into mosquito habitat and reduce larval densities (Santamarina Mijares & Perez Pacheco 1997, Peng et al. 1998, Mijares et al. 1999, Perez-Pacheco et al. 2005), demonstrating the ability of these parasitic nematodes to reduce mosquito populations. However, successful control may require repeated releases of nematodes indicating that the populations of target mosquitoes and parasitoids were not in stable equilibrium (Perez-Pacheco et al. 2005). Most of these releases have not been followed for a long period (e.g., Santamarina Mijares & Perez-Pacheco 1997, Peng et al. 1998), hence we have no data sets sufficient for rigorous evaluation of the question of a stable equilibrium. Models of parasitoid-host systems typically must incorporate one or more stabilizing mechanisms (e.g., aggregation of attack by the parasitoid, or refuges from attack for hosts) to enable host populations to persist in equilibrium with parasitoid populations that are highly efficient at locating and killing hosts (Murdoch 1994, Murdoch & Briggs 1996). The necessity of repeated reintroduction or re-inundation of habitats with mermithids suggests that instability arises because these parasitic nematodes are **not** particularly efficient foragers and maintaining a sufficiently high killing rate over a wide space and time is the central problem for controlling mosquitoes with mermithids. Peterson (1985) alluded to this problem, suggesting that human dissemination of mermithids would likely be necessary for any successful control program targeting mosquitoes. Thus, although mermithids are the mosquito enemy that most resembles the ideal biological control agent described by many authors, successful control using mermithids probably will require tactics that differ from those using insect parasitoids in an agricultural setting. Additional empirical data on long-term dynamics of mermithid and mosquito populations, foraging efficiency of mermithids, and whether they can establish a stable two-species equilibrium in a field setting, would be useful in deciding whether the strategy of classical biological control is likely to work for this group of enemies of mosquitoes.

The central assumption that successful biological control yields a low, stable, equilibrium population of the target species has been challenged. Murdoch et al. (1985) and Murdoch & Bence (1987) have provided convincing evidence that such a stable equilibrium is not always desirable for biological control, and that often the ideal biological control effort results in

**unstable** population dynamics of the target species, including local extinction. The evidence consists of both models of population dynamics of control by generalist predators, showing that extinction of the target species is often the expected result, and empirical data showing that such generalist predators can produce successful control (Murdoch et al. 1985, Murdoch & Bence 1987), and that such successful control often involves local prey extinction (Murdoch & Bence 1987). Two of the empirical examples used by Murdoch et al. (1985) were control of mosquitoes by *Gambusia* and *Notonecta*. Reductions of mosquito abundances by factors of 10 to >100 were observed when *Notonecta* were present, and local extinction of the target populations was common (Chesson 1984, Murdoch et al. 1985).

Murdoch et al. (1985) and Murdoch & Bence (1987) argue that these generalist predators can be highly successful control agents precisely because they lack the characteristics identified in investigations of classical biological control by parasitoids (monophagy, synchrony, rapid population growth). They argue that unstable population dynamics and local extinctions of the target population due to the introduction of a generalist predator may be a more desirable goal for biological control efforts. This then raises the question of what characteristics of a generalist enemy are desirable for this kind of unstable biological control? Murdoch et al. (1985) and Murdoch & Bence (1987) suggest that: 1) ability to survive periods of starvation; 2) ability to persist on a variety of alternative prey; 3) population dynamics of the generalist predator that are not tightly linked to dynamics of the target prey; and 4) destabilizing (i.e., not type 3) functional responses that do not reach saturation until very high prey availability, resulting in high rates of predation at any prey density, are all likely to lead to success in this type of unstable biological control. In short, persistence of the predator and a high killing rate of the target species seem to be essential. Based on these hypotheses, many of the generalist enemies of mosquitoes seem more attractive as biological control agents (e.g., *Gambusia*, *Notonecta*, *Toxorhynchites*). The variable success of *Gambusia* was discussed above. Control efforts using *Toxorhynchites* have also yielded variable results (reviewed by Collins & Blackwell 2000) and the reasons for those failures appear to be heterogeneous. The difficulties of controlling mosquitoes that arise from strong density dependent limitation of mosquitoes in container habitats (see above) may have contributed to some of these failures of control by *Toxorhynchites*. Nevertheless, consideration of population dynamics of generalist predators suggests that there is potential for control of mosquitoes using either specialist or generalist enemies. Considerations beyond population dynamics of the target and enemy, such as potential for unintended effects (Simberloff & Stiling 1996), will potentially be an even greater concern for biological control efforts with generalist predators.

## Conclusions

Considering general principles of population dynamics as they apply to biological control of mosquitoes suggests that success of biological control depends on the choice of habitat, target species, and enemy. General conclusions from considering the role of density dependent mortality are that groundwater habitats, particularly permanent habitats, may be better choices for biological control efforts than are container habitats, and that enemies killing late stage larvae and pupae may be the best control agents. Considering the admittedly limited literature on dynamics associated with stable biological control systems, it appears that among mosquito enemies, only mermithid nematodes fit the mold of the specialist parasitoids widely used in biological control. In most mosquito systems, the paradigm and models of control by generalist enemies resulting in unstable dynamics (Murdoch et al. 1985) seems to be most applicable, and enemies capable of killing a large proportion of the target population and capable of persisting after target species are eliminated may, in some cases, be good choices for biological control of mosquitoes. For all mosquito-enemy biological control systems, empirical data to evaluate the impact of density dependent effects, whether mortality is additive, compensating,

or overcompensating, and stability and persistence of populations would be major contributions to the application of basic principles of population dynamics to mosquito biological control.

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