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ORIGINAL PAPER

A review of the role of fish as biological control agents of disease vector mosquitoes in mangrove forests: reducing human health risks while reducing environmental risk

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Abstract The saltwater mosquito, *Aedes vigilax*, is prolific in coastal wetlands including mangroves and saltmarshes. *Ae. vigilax* is a vector for arboviruses such as Ross River and Barmah Forest viruses, with significant consequences for human health and economic productivity. In Australia the dominant form of mosquito control is chemicals. For mangroves, this is because there is a critical lack of knowledge supporting alternative approaches, such as environmental modification or biological control using larvivorous fish. This review examines the potential of fish as biological agents for the control of mosquito larvae in mangroves. We consider two key aspects: how larvivorous fish use mangroves; and can larvivorous fish reduce larval mosquito populations sufficiently to provide effective mosquito control? The link between fish and mangroves is reasonably well established, where mangroves act as refuge habitat for small and juvenile fish. Also, research has established that fish can be significant predators of mosquitoes, and therefore may be effective control agents. However, studies of fish activity within mangroves are limited to study of the fringe of the mangroves and not the internal structure of mangrove basins and as a result, fish populations within these areas remain unstudied. Also, until recently there was little appreciation of the mangrove-mosquito habitat relationship and, as a consequence, the importance of the mangrove basin as the key mosquito habitat has also been overlooked in the literature. Similarly, the predator/prey relationships between fish and mosquitoes within mangrove basin environments also remain unstudied, and therefore the importance of fish for mosquito management in mangrove basins is not known. There are substantial knowledge gaps regarding the potential of fish in controlling larval mosquitoes in mangroves. The gaps include: understanding of how larvivorous fish use mangrove basins; the nature of the fish-mosquito predator/prey relationship in mangrove basins; and whether larvivorous fish are effective as a mosquito control option in mangroves.

Keywords Mangroves · *Aedes vigilax* · Predator/prey relations · Mosquito control · Minimal environmental impact

Introduction

Coastal wetlands including mangroves and saltmarshes are habitats of the saltwater mosquito, *Aedes vigilax*, where it is prolific. *Ae. vigilax* is a vector for arboviruses such as Ross River Virus (RRV) and

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Barmah Forest Virus (BFV) (Kay and Jorgensen 1986). RRV and BFV are polyarthritic diseases (Flexman et al. 1998) that have significant health and economic impacts, costing AUD 3-6 million in health care and lost productivity annually (Woodruff et al. 2006).

Reducing the threat of mosquito borne disease involves reducing the potential for contact between mosquitoes and humans. This is especially important in areas where the mosquito's mangrove habitats lie near human populations. Most Australians live in coastal areas and in Queensland many low lying coastal regions are adjacent to mangroves that harbour significant mosquito breeding sites. As a result, Queensland has rates of RRV and BFV infection that are some of the highest in the country, accounting for between a third and three quarters of all RRV cases (Russell 2002) and around half of all BFV cases (Naish et al. 2011).

In order to reduce the exposure of humans to mosquito borne disease, the disease vector (mosquito) needs to be controlled. There are three broad categories of mosquito control: using chemical agents (chemical control); altering the structure and/or hydrology of mosquito habitat (physical control or source reduction); and increasing the presence of predators, pathogens and competitors of mosquitoes (biological control) (Dale and Hulsman 1990). In Australia, the dominant form of mosquito control is to use chemicals as part of an integrated mosquito control program that considers a range of approaches. An integrated program has been shown to be more effective than programs that rely on a single approach (Tomerini et al. 2011). For example, successful integrated programs for mosquito control in saltmarshes are well established, and include a range of approaches including chemical and physical methods, such as runnelling in saltmarshes (Hulsman et al. 1989; Dale 2008). However, for mangrove systems there remains a critical lack of knowledge limiting the development of integrated approaches. For example, approaches such as environmental modification and biological control using larvivorous fish need to consider the essential ecological role and ecosystem services provided by mangroves (as identified by Badola and Hussain 2005; Mitsch and Gosselink 2000; Nagelkerken et al. 2008). Research into the mosquito-mangrove habitat has received recent attention (Knight 2011; Knight et al. 2012), that has led to new studies looking at environmentally focused minimal impact mosquito control methods where habitat modification involves restoring tidal processes. A complimentary consequence of restoring tidal processes is enhanced access for fish as predators, but for optimal integrated mosquito control (including chemical, physical and biological approaches) in mangroves, much remains to be done.

This paper reviews the literature on mosquito-fish-mangrove relationships and how these relate to mosquito control. Specific aspects include: fish as a control mechanism for mosquitoes; mangroves as a fish habitat; fish as predators of mosquitoes; and how mosquitoes respond to fish predation. The purpose of the review is to identify gaps in knowledge that currently limits the adoption of larvivorous fish as a mosquito control agent.

Fish as a biological control of larval mosquitoes

Fish that are predators of the aquatic larval stage of mosquitoes are referred to as larvivorous fish. Many other organisms are predators of mosquito larvae including tadpoles, insect larvae (Kumar and Hwang 2006), amphibians (Brodman and Dorton 2006) and even other mosquito larvae (Kerridge 1971); however, fish are the most common and widely studied type of predator used for biological control of mosquitoes. Predation of mosquitoes has been recorded in many habitats, from small plastic containers (Connor 1922) to complex natural ecosystems including coastal wetland environments (Harrington and Harrington 1961, 1982; Hess and Tarzwell 1942; Morton et al. 1988). As a biological control agent larvivorous fish have been demonstrated to be very effective at reducing mosquito larval populations in many parts of the world, in a variety of habitats (Chandra et al. 2008; Kumar and Hwang 2006; Van Dam and Walton 2007).

Environmental hazards: use of exotic fish species to control mosquitoes

Despite its potential, biological control using fish can be environmentally damaging, especially in complex, ecologically important, systems like mangroves. Releasing exotic predatory fish into a wetland to control mosquitoes may disrupt natural ecosystems, with the fish outcompeting native predators and feeding on nontarget organisms (Bence 1988; Hoddle 2004). Notable examples were the introduction of the mosquitofish (*Gambusia affinis* and *Gambusia holbrooki*), two species native to North America, which have been introduced into waterways worldwide (Angelon and Petranka 2002; Chandra et al. 2008; Kumar and Hwang 2006; Morton et al. 1988). Significant declines in populations of native fish species have been observed worldwide following the introduction of these mosquitofish (Arthington and Marshall 1999; Kumar and Hwang 2006; Laha and Mattingly 2007), resulting in their designation as significant exotic pests and their use as a control agent being banned in Australia.

Environmentally sound biological control using fish

The mosquitofish experience illustrates the risk of introducing exotic species; however, biological control does have potential to be an effective, environmentally sound form of mosquito control, by using fish that are compatible with the environment. These fish may also be just as, or even more effective at controlling mosquitoes than hazardous species like *Gambusia affinis* and *hoolbrooki.* Van Dam and Walton (2007), experimenting in ponds in California, found that relatively small, slow breeding populations of *Gila orcutti* reduced mosquito numbers as effectively as large, fast breeding *Gambusia affinis* populations, with far less predation of nontarget invertebrates. In laboratory tests Hurst et al. (2004) compared predation of *Culex* mosquitoes by seven native Australian fish species and *Gambusia holbrooki*, and found that three of these species, *Melanotaenia duboulayi*, *Ambassis marianus* and *Hypseleotris compressa*, were equally or more effective predators of *Culex* mosquito larvae than *Gambusia holbrooki*.

Improving the conditions for native larvivorous fish that already live in the mangrove forest and enhancing their access to mosquito larvae is a far more environmentally sound approach than introducing an exotic predator. This may be accomplished by improving tidal processes within the mangrove basin, allowing fish access to isolated larval pools. In order to do this, several aspects of the fish-mosquito-mangrove interaction need to be understood: Firstly, how fish use the mangrove habitat, and how environmental factors such as structure, water quality and hydrology influence fish populations within mangroves; secondly, the predator/prey relationship between native fish and mosquitoes, in particular whether the endemic fish eat mosquito larvae; and thirdly, whether this predation is substantial enough to be a viable mosquito control option.

Mangroves as fish habitat

Mangroves are no doubt an important habitat for fish (Laegdsgaard and Johnson 1995; Vidy et al. 2004; Wang et al. 2009), for both permanent (Faunce and Serafy 2006; Nagelkerken et al. 2000) and transient species (Sheridan and Hays 2003). The importance of mangroves for fish has been assessed indirectly, by examining the densities and species richness of fish in habitats adjacent to mangroves, such as mangrove-lined estuaries (Aburto-Oropeza et al. 2008; Hajisamae and Chou 2003; Laegdsgaard and Johnson 2001; Nagelkerken et al. 2001) and tidal creeks adjacent to mangrove stands (Bell et al. 1984; Beumer 1978; Robertson and Duke 1987). A common finding has been that the presence of mangroves created stronger, more robust fish populations in adjacent waters than in waters not adjacent to mangroves.

Mangroves as refuge habitat for fish

In order to understand the importance of mangroves for fish, fish populations need to be studied directly, by sampling fish entering or leaving mangroves, and those residing within the mangrove forest itself (Hindell and Jenkins 2004; Laroche et al. 1997; Morton 1990; Nagelkerken et al. 2000; Robertson and Duke 1990). Studies focusing on these fish populations have recognised the key role mangrove forests play as a refuge habitat for small fish and juveniles, providing a predator-free environment. Tree shading, turbid water and structurally complex forest substrates (due to roots and pneumatophores) provide protection from predators (Abrahams and Kattenfeld 1997; Blaber and Blaber 1980; Cyrus and Blaber 1992; Faunce et al. 2004; Johnston et al. 2007; de la Moriniere et al. 2004; Nagelkerken et al. 2008; Nagelkerken and Faunce 2008; Payne and Gillanders 2009; Robertson and Duke 1987; Thollot et al. 1999; Tse et al. 2008). Mangroves also support a base for food webs, providing a surface on which algae can grow (Aikanathan and Sasekumar 1994; Hyde 1990; Nagelkerken and Faunce 2008; Potts 1980; Proches 2004; Proches and Marshall 2002; Proches et al. 2001; Verweij et al. 2006).

Water quality and distribution of fish in mangroves

Water quality is factor critical for the health of the whole ecosystem, in particular fish communities. Factors such as salinity, pH, temperature and dissolved oxygen (DO) can significantly affect fish growth, metabolism and behaviour (Augley et al. 2008; Brandt et al. 2009; Buentello et al. 2000; Frick and Wright 2002; Howells et al. 1983; Leung et al. 1999; Teien et al. 2004), where extremes can lead to fish mortality with potential for rapid changes in the fish community structure and distribution (Dunson and Dunson 1999; Faunce et al. 2004; Lorenz 1999; Sheaves and Johnston 2008; Weatherley 1972). For example, Dunson and Dunson (1999) examined the effects of low DO on *Rivulus marmoratus* in mangrove pools. Fish held in hypoxic conditions (at the bottom of pools or in isolated pools with low DO) experienced stunted growth rates and higher mortality rates.

Hydrologic factors

Other environmental factors, such as evaporation (Molles 2005), terrestrial runoff (Easton 1989) and tides (Sheaves and Johnston 2008) can cause water levels and water quality to fluctuate over a wide range. Terrestrial runoff and tides can create hydrologic connections within mangroves (Knight et al. 2008) that enable fish to travel within mangroves and between mangroves and associated coastal waters (Ritchie and Montague 1995). Studies investigating hydrologic mechanisms within mangroves have been focussed on physical processes such as interaction of vegetation and water flow physics (Mazda et al. 1997) and the nature of tidal hydrodynamics into and within mangrove swamps (Mazda et al. 2005; Wolanski 1992). The Manual for the Preservation and Utilization of Mangrove Ecosystems by Mazda et al. (2007) brings together a significant number of mangrove physical process related studies. However, only a few studies have looked at the mosquito–mangrove–hydrology relationship. Ritchie (1990) for Florida mangroves, and most recently Knight (2011) for eastern Australian mangroves, detailed the interaction between tidal hydrodynamics and topographic structure required to create the mosquito's mangrove habitat. Tidal flow and topography in mangrove systems have been identified as critical factors that create a highly variable environment.

In habitats similar to mangroves, fish populations have been shown to be dramatically affected by variations in tidal flushing. For example, Sheaves and Johnston (2008) examined tidal and freshwater flooding in a sub-tropical Queensland estuary floodplain and found that variations in flooding frequency influenced the distribution of fish in isolated pools. More frequently flushed pools had higher connectivity to the estuary, better water quality, more fish immigration and thus a larger fish population.

Limitations in knowledge of fish mangrove habitats

Despite all the evidence presented above, fish populations within mangroves remain poorly understood. Why there are so few studies of fish related processes within mangroves, including fish ecology studies, is unclear, but it may be largely due to lack of attention paid to internal basin areas as fish habitat. Almost all studies of the fish-mangrove ecosystem have focussed either on environments adjacent to mangroves, or on the mangrove fringe. There is significant heterogeneity in connectivity and water flows within mangroves, and hydrologic processes can vary greatly between the fringe and internal basin areas (Knight et al. 2008). Studies cutting trenches into the mangrove and examining movement of fish across the mangrove fringe strongly indicate that significant fish populations do exist within mangroves, but these remain largely unstudied (Huxham et al. 2008; Vance et al. 1996).

The main reason why fish have not been studied in internal areas of mangroves may be the difficulties of sampling in mangrove basins. Morton (1990) and Hindell and Jenkins (2004) argued that mangrove basins, with their mosaic of open pools and dense pneumatophore stands, were impossible to study using conventional netting techniques (such as cast or drag nets), and therefore kept to the mangrove fringe. Whatever the reason, as a result of this, the effects of physical, water quality and tidal factors on fish populations in mangrove basins are not understood.

Fish as predators of mosquitoes

While it is likely that fish populations do exist within mangrove basins where mosquitoes breed, evidence that these fish predate upon mosquitoes is required if these fish are to be considered as potential biological control agents. Predation by fish on mosquitoes has been observed across a variety of habitats, including freshwater and coastal wetland systems, where a number of factors influence predation efficiency. Many coastal wetland species have been observed feeding on larvae, either in wetlands, other habitats or in laboratory studies, including *Psuedomugil signifier* and *Gobidiiae* sp (Morton et al. 1988; Hurst et al. 2004, 2006) in Australia and *Rivulus marmoratus* (Taylor et al. 1992) and *Gambusia affinis* (Hess and Tarzwell 1942; Harrington and Harrington 1961) in the USA.

Ecological factors

Ecological factors such as habitat structural complexity and prey preference by predators affects predation of mosquitoes. Structural complexity affects the physical access of predators to prey, where larval habitats easily accessible to predatory fish result in higher predation of mosquitoes (Hess and Tarzwell 1942).

The developmental stage of both predator and prey is another important factor influencing the predator–prey relationship. Younger (smaller) individuals of a species eat the earlier instar mosquito larvae, whereas older (larger) individuals feed primarily on older instars and pupae (Harrington and Harrington 1961; Taylor et al. 1992). Harrington and Harrington (1961) examined this occurrence in detail, looking at *Aedes taeniorhynchus* (Wiedemann) predation by a number of larvivorous fish in salt marshes in Florida. There was a strong correlation between the size of the fish and the stage of development of the larval prey; smaller fish mainly ate 1st–3rd instar larvae and larger fish ate 4th instar larvae. This has also been demonstrated in more recent studies, for example Taylor et al. (1992), found that the developmental stage of larvae of *Ae. taeniorhynchus* and *Culex quinquefasciatus* larvae consumed was directly proportional to the size of *Rivulus marmoratus* individuals.

Behavioural factors

Behavioural factors are also important for determining predation efficiency of mosquitoes—in particular, feeding habits of predators is important. Due to the episodic and seasonal nature of mosquito production, populations are often low (or virtually non-existent) in winter months and periodically very high in summer months. Ergo, fish that predate upon mosquitoes need to be able to shift their diet to other prey items when mosquitoes are scarce (Morton et al. 1988). Therefore, the presence of generalist fish species is important for mosquito control, as generalists are more likely to be opportunistic predators of mosquito larvae (Harrington and Harrington 1961; Laufer et al. 2009; Murdoch 1969; Pen and Potter 1991; Schleuter and Eckmann 2008). Morton et al. (1988), examining the feeding habits of salt marsh fish species, found that species that preyed upon *Ae. vigilax* mosquito larvae in peak mosquito seasons (*G. affinis*, *P. signifier* and *Gobiidae* sp) were able to radically shift their diet during non-peak seasons, substituting crustacean larvae for mosquito larvae in winter.

The preference of alternate prey, and their abundance, also affects predation on mosquito larvae, where fish seek out larger or less agile prey to consume (Bence 1988; Knight et al. 2004; Manna et al. 2008). Preference for alternative available prey can reduce the effectiveness of fish as a biological control, and can even benefit mosquitoes because of reduced competition by competitors (Blaustein 1992; Chesson 1989; Manna et al. 2008; Walton 2007). For example, Manna et al. (2008) concluded that *Poecilia reticulata* was an effective predator of *Culex quinquefasciatus* larvae, however its effectiveness was severely reduced in the presence of alternate prey (worms and chironomid larvae).

While predation has been documented in many habitats, and the above factors are known, the predator/prey relationship between larvivorous fish and mosquitoes has not been directly examined in the context of the fish-mosquito-mangrove ecosystem. While it is clear that larvivorous fish do predate on mosquitoes, there has been no research specifically examining this form of predation within mangroves. In addition, further research is required to determine if larvivorous fish predation on mosquitoes is sufficient to reduce mosquito populations in mangrove systems, and therefore be eligible as a control strategy.

Mosquito responses to predation by fish

The effects of predation may be seen by focusing on the prey species, rather than focusing on the activities of the fish as predators. Mosquitoes respond to predation in two main ways: at a population level and at an individual behavioural level. Understanding the mosquito response is critical for modelling the effects of predation on mosquito populations.

Mosquito population responses

Many studies have examined mosquito populations following the introduction of predatory fish, and have documented significant reductions in the size of the mosquito population when fish are introduced into a system (Bence 1988; Chandra et al. 2008; Kumar and Hwang 2006; Van Dam and Walton 2007; Walton 2007). However, most studies were conducted in smaller and far less complex habitats than mangroves, such as containers and freshwater ponds, and therefore may not be comparable to mangrove fish-mosquito interactions.

Two studies identified fish predation as the driver of changes in mosquito populations in mangroves (Ritchie 1984 and Kokkinn et al. 2009). Ritchie (1984) documented unusually low adult populations of *Ae. taeniorhynchus* in Florida mangroves, which were attributed to heavy winter rainfall sustaining large larvivorous fish populations within the mangroves. However, rather than observing predation this study relied on changes in the adult mosquito population as evidence of increased predation by fish, which has to be done with caution, considering the wide dispersal of adult mosquitoes (Chapman et al. 1999). Kokkinn et al. (2009) made qualitative observations of larvivorous fish preying on, and effectively controlling, mosquito populations in coastal pools (including in mangroves). Most predation occurred as the pool connected with the flood-tide with some fish retiring with the ebb and others remaining in the isolated pools, potentially perishing.

Behavioural responses: evolved predator avoidance traits

Evidence of the effects of predation by fish can also be observed by examining evolved responses to the presence of fish. Mosquitoes are able to detect chemical cues in the environment (Davis 1976), which may include detecting the presence of fish in adjacent waterbodies, and therefore avoiding laying eggs in areas where hatching larvae would be at risk of predation. This trait was first identified by Petranka and Fakhoury (1991), who observed a decline in *Anopheles* oviposition in ponds containing caged-off predatory fish and tadpoles. Since then many other studies have found similar results (Chivers and Smith 1998; Kats and Dill 1998; Kumar and Hwang 2006; Pamplona et al. 2009). The evolution of this behaviour suggests that predation is an important ecological process affecting mosquito populations. However, this is not a trait shared by all mosquitoes. The ability to sense predators varies considerably between species (Louca et al. 2009; Van Dam and Walton 2007), ranging from being completely unable to sense predators (Zuharah and Lester 2010) to being so sensitive that they can detect residual chemicals in the water long after predators have left the waterbody (Angelon and Petranka 2002).

Chemo-avoidance has been demonstrated for coastal wetland mosquito species. For example, Ritchie and Laidlaw-Bell (1994) found that there was significantly less oviposition by *Ae. taeniorhynchus* on the margins of salt marsh pools containing fish compared to those without, providing evidence that the mosquito is able to sense predators. The study was very significant as it demonstrated chemo-avoidance in a species that lays its eggs on soil, rather than on the water's surface (most other studies focus on *Anopheles* and *Culex* species). Despite the promise this study shows, it conducted in salt marshes, not mangroves, and therefore chemo-avoidance in ovipositing on substrate adjacent to mangrove pools remains to be demonstrated.

Modelling mosquito populations in mangroves

Another way to assess the role of fish as a predator of mosquitoes in mangroves is by examining existing mosquito population models. If fish are an important predator of mosquitoes, the role of predation should be identified in both mosquito population models and models of mangrove ecology. This was seen in a model of *Ae. taeniorhynchus* populations in Florida mangrove forests (Ritchie and Montague 1995). Using knowledge of feeding habits of fish documented in Australian and American studies, Ritchie and Montague estimated that a predatory fish introduced into a mangrove pool would consume approximately 500 mosquito larvae per week. The capacity for such high rates of predation per fish, combined with oviposition deterrence, has potential for very significant control of the mosquito population, even in very small numbers.

Actual patterns of mosquito distribution within mangrove basins appear to reflect this; areas of higher hydrological connectivity (caused by more frequent tidal flow) have larger fish populations (Hess and Tarzwell 1942; Sheaves and Johnston 2008) and smaller mosquito populations than those less tidally connected (Griffin et al. 2010; Knight et al. 2009) suggesting predation by fish reduces mosquito populations. A limitation of this type of approach is that the model can appear conclusive or complete when neither may be the case. There may be more than one cause of an observed population shift. For example, although predation may be modeled as a cause of population decline (as above), the decline may equally be due to changes in the hydrology that disrupt the mosquito life cycle.

Summary and conclusions

This review has examined the literature surrounding fish in mangroves, and the potential for larvivorous fish to control mosquitoes as an effective biological control approach. Mangrove forests are important habitats for fish, providing an important refuge habitat. However, water quality and tidal hydrology influence fish habitat patterns. There is evidence that fish are significant predators of mosquitoes in mangroves, and thus fish are potential biological control agents for mosquito management.

However, several knowledge gaps were identified that limit our understanding of how fish use mangroves and the predator/prey relationship between fish and mosquitoes. Knowledge of how fish are distributed across the mangrove basin is limited. Mangrove forests can be highly variable environments, both structurally and hydrologically, however as almost all studies of fish relating to mangroves are limited to the mangrove fringe rather than mangrove basin, how this variation affects the size and distribution of fish populations is unknown. As a result, while fish are known predators of mosquitoes, the lack of knowledge of endemic fish populations within mangrove basins means the extent to which fish predation affects mosquito populations is not known.

Enhancing larvivorous fish populations in mangroves has potential as an effective and environmentally acceptable mosquito control approach. Integrating biological control using larvivorous fish into a mosquito control program should improve mosquito control effectiveness. There are three main benefits of integrating biological control into a mosquito control program: reduced mosquito production in mangroves, lowered cost of existing control approaches and a reduction in the risk of mosquito borne disease for people living in coastal regions.

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