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BIONOMICS AND SYSTEMATICS OF THE ORIENTAL *ANOPHELES SUNDAICUS* COMPLEX IN RELATION TO MALARIA TRANSMISSION AND VECTOR CONTROL

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Abstract. The taxonomic history, distribution, bionomics, systematics, and vector control strategies for the *Anopheles sundaicus* complex are reviewed in relation to malaria epidemiology. The lack of data on the bionomics, insecticide resistance, and vector capacity, as well as the general lack of surveillance and monitoring of potential vector populations, make the development of targeted control measures problematic. It will be necessary to elucidate, characterize and identify all members of the complex to determine their distributions, disease relationships, ecologic relationships, and resistance to insecticides. This knowledge is essential for epidemiologic studies, the design and implementation of appropriate vector control measures, and the development of strategies for monitoring and assessing the potential risk of malaria outbreaks due to members of the complex.

INTRODUCTION

Malaria control strategies aim to decrease human morbidity and mortality by limiting parasite transmission.[1] The identification of vector species and knowledge of their ecology and behavior is essential for epidemiologic studies and the design and implementation of appropriate vector control strategies. Among morphologically indistinguishable anopheline species, distinct ecoethologic differences have been used to identify putative species associated with malaria transmission.[2–4] These putative species are now recognized as distinct genetic species.

In southeast Asia, vector studies and malaria control are focused mainly on three major species complexes: *Anopheles dirus* Peyton & Harrison, *An. minimus* Theobald, and *An. sundaicus* Rodenwaldt. The *An. dirus* and *An. minimus* complexes are well known because they are widespread throughout southeast Asia, whereas the *An. sundaicus* complex has been investigated to a much lesser degree because the species occur mainly in coastal areas.[5–15] The ecology, behavior, and/or vectorial capacity of *An. sundaicus s.l.* have been described for populations in India, Indonesia, Malaysia, Vietnam, Myanmar, Thailand, and Cambodia.[16–20] However, comparisons of the main characteristics of populations across the distribution of the taxon are wanting.[21]

The probability that *An. sundaicus* represents a complex of species was hypothesized on the basis of ecoethologic differences and isolation of populations on the coastal areas and islands of southeast Asia.[11,22,23] The recent use of genetic and molecular tools confirmed the genetic isolation of species that comprise the *An. sundaicus* complex.[24,25] Considered an efficient malaria vector taxon, *An. sundaicus s.l.* has been a principal target of mosquito control programs even though links between biologic characteristics and vectorial capacity have not been clearly defined.

The aim of this report is to consolidate available information about the *An. sundaicus* complex as a foundation for further investigation and a better understanding of the individual species across their ranges of distribution. Unless otherwise noted, *An. sundaicus* refers to *An. sundaicus s.l.* in the discussion of this report.

DISTRIBUTION

The distribution of *An. sundaicus* includes coastal areas (Figure 1) from northeastern India to southern Vietnam (below the 11th parallel), south to the Nicobar, Andaman, and Indonesian islands.[24,26,27] The taxon occurs in southern Sulawesi,[27,28] but is absent from The Philippines[29,30] and has not been reported from southern Borneo[31,32] (Figure 1). It has been observed in Pakistan[33–35] and two localities in northwestern India,[36] but these observations require verification.

Environmental changes due to human activities seem to be causing the disappearance of the taxon from coastal areas.[5,11,14,37,38] Recent field surveys in northwestern peninsular Malaysia and the eastern coastal region of India (Figure 1) suggest that *An. sundaicus* no longer occurs there.[31,39,40] Earthen embankments were built in peninsular Malaysia to prevent intrusion of sea water[41] and profound ecologic and salinity changes occurred in India,[37] which probably altered or eliminated potential larval habitats. In other countries such as Pakistan, field records are not recent and the occurrence of *An. sundaicus* is uncertain. In addition, local populations of *An. sundaicus* are known to have a fluctuating, patchy distribution in space and time, changing through the year in response to the availability of adequate breeding sites.[27,42,43] In general, the distribution of *An. sundaicus* on the coastal areas and islands of southeast Asia is poorly known due to a paucity of available data.

BIONOMICS: FIRST EVIDENCE OF A SPECIES COMPLEX

Immature stages. The immature stages of *An. sundaicus* inhabit sunlit bodies of stagnant water, including ponds with vegetation and floating algae,[14,42] swamps,[11] mangrove,[18] wells, rockpools,[22,31] and particularly shrimp/fish ponds along the coast or irrigated by inland sea water canals,[14,15,28,30,32,44] which are reported as favorable habitats in Vietnam and Indonesia. Sea water aquaculture was known during the 18th century in Jakarta to be favorable for malarial mosquitoes, which were most likely *An. sundaicus*.[45] Lagoons and creeks[11,15,31,46–48] and blocked river mouths[8,16] are also favorable sites for *An. sundaicus* larvae. Since the majority of suitable larval habitats are provided with saline water from the sea, *An. sundaicus* has been described as mainly a brackish water breeder in coastal areas.[14,15,49] However, the taxon has been found in inland sites with either brackish or freshwater. In southern Vietnam, where no permanent freshwater breeding sites have been encountered, sea water canals contribute saline water to larval habitats.[30] In contrast, *An. sun-*

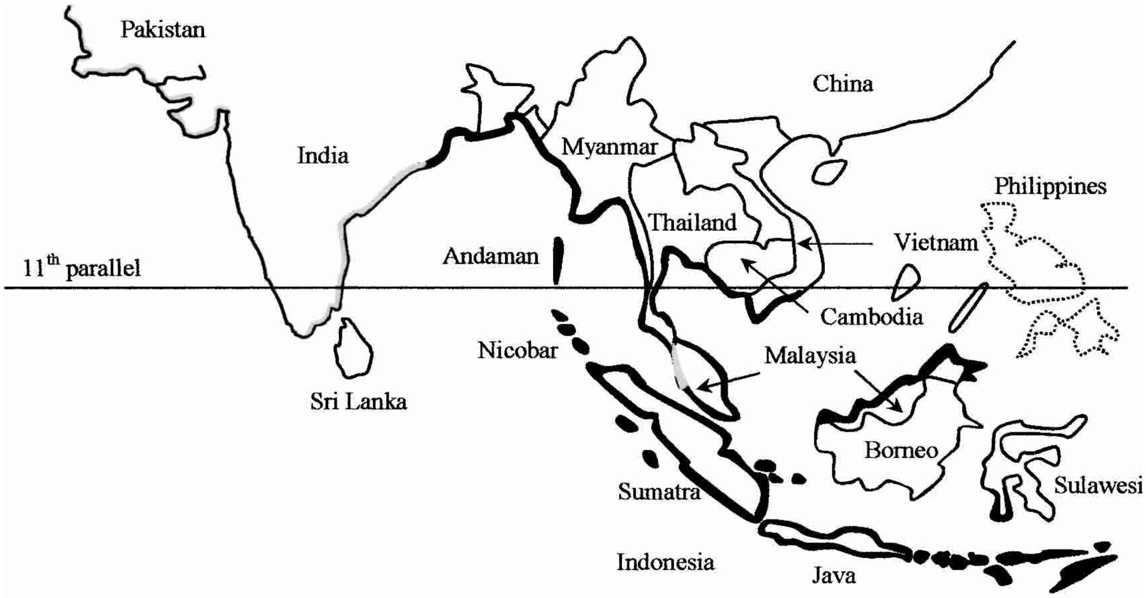

FIGURE 1. Distribution of the *Anopheles sundaicus* complex. Coastal areas in marked in black represent the currently recognized distribution. Gray zones are areas where *An. sundaicus* reportedly disappeared. The taxon is absent or has never been recorded in the uncolored areas.

daicus larvae breed in inland freshwater ponds in India,[31,50] Car Nicobar island,[46] peninsular Malaysia,[51] Sarawak (Malaysian Borneo),[22] and Indonesia.[15,24,28] Published data indicate that larvae tolerate salinity ranging from 0% to 11% (Figure 2), i.e., from freshwater (<0.05%) to much greater concentrations than sea water (3.5%). Over time, salinity in ponds changes as a result of rainfall, inundation by sea water, and evaporation.[27,30] Soeparno and Lair[15] and Kikuchi and others[52] noted that the levels of salinity in coastal habitats are affected by tidal movements. Therefore, any comparison of salinity must be done cautiously, as indicated by the different optimal ranges shown in Figure 2. Phan[30] noted a positive correlation between salinity and vector density, with peak density at the start of the rainy season. This correlation shows the importance of salinity tolerance in larval development. In addition, Collins and others[28] noted that *An. sundaicus* females in southern Sulawesi readily oviposit in freshwater if no brackish water sites are available.

The wide range from freshwater to saline breeding sites was one of the differences that led mosquito workers to hypothesize that *An. sundaicus* was a species complex.[22] Either different species accounted for observed ecologic differences or one euryhaline species was tolerant to a wide range of salinity.

Compared with salinity, the pH of larval habitats is not so variable, ranging from 7 to 8.5 in India, Vietnam, and Java (Indonesia).[9,14,31,47]

Filamentous floating algae and aquatic plants appear to be crucial for the development of *An. sundaicus* larvae.[14,47] Aquatic flora supplies food (micro-algae and bacteria) and protection against predators.[15,53,54] In Bengal, India, Iy-

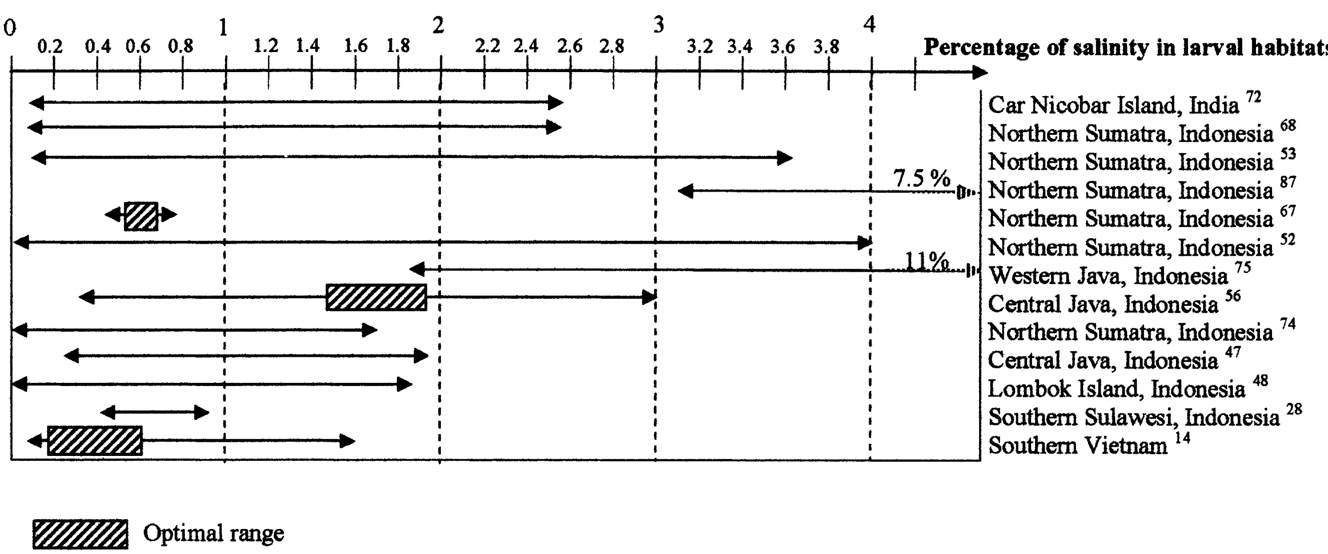

FIGURE 2. Range and optimal range of salinity reported for breeding sites of *Anopheles sundaicus* in various countries.

enger[55] found a direct relationship between surface algae together with submerged vegetation and breeding sites. Exceptions include sites on the Coral Beach of India[32] and rock-pools on Pandan Beach in the Lundu District of Sarawak (Malaysian Borneo),[22] where no vegetation was present. Freshwater plants such as *Salvinia* sp.[53] and *Eichhornia crassipes* (water hyacinth)[52] are associated with the absence of *An. sundaicus* larvae, but since immature stages occur in freshwater habitats these plants seem to be more a barrier to oviposition than indicators of unfavorable breeding places.[52]

Adult behavior. Differences in adult behavior are also indicators of species diversity. *Anopheles sundaicus* exhibits both endophagy and exophagy. It is mainly endophilic and anthrophilic, but also exhibits exophily and zoophily (Table 1). Indoor application of insecticide for vector control showed the presence of exophagic, exophilic, and zoophilic *An. sundaicus* in areas of the Nicobar islands and Vietnam where the vector was previously known to be endophagic, endophilic, and anthropophilic.[11,30] Females exhibit a peak of biting activity from 8:00 PM to 3:00 AM depending on locality. Adventitious biting in dark houses during the day has been observed in Vietnam,[10,14] but humans are generally at higher risk of being bitten indoors while sleeping during the night. *Anopheles sundaicus* is capable of flying long distances, ranging from 1.6 to 9 km,[13,27,40,56] but blood feeding depends on the location and availability of hosts and insecticide pressure.

Due to its ecologic and behavioral plasticity, *An. sundaicus* has adapted to a range of coastal and inland environmental situations. The main requirement is the presence of sunlit breeding sites with fresh or brackish water, floating algae, and non-invasive vegetation in coastal areas and on islands. Adult females are mainly anthropophilic and endophilic. Comparison of the biology of *An. sundaicus* with that of the more intensely studied *An. gambiae* complex in Africa or the *An. minimus* complex in Asia suggested the existence of a species complex in the absence of other evidence. Investigation based on genetic tools confirmed that *An. sundaicus* is a complex of species.

GENETIC CONFIRMATION OF A SPECIES COMPLEX

Genetic tools were used to establish beyond doubt that *An. sundaicus* is a species complex. Cytogenetic and enzymatic studies were first carried out on populations from Thailand and Indonesia (Java and Sumatra) that resulted in the discovery of three forms, informally designated forms A, B, and C.[24,25] A fourth cytotype named D was identified on Car Nicobar Island.[57] Form A was collected from coastal areas of Thailand, Sumatra, and Java. Form B was mainly collected in the freshwater sites at South Tapanuli in northern Sumatra in association with form A, where it comprised 92.9% of the females captured in September 1993 and 87.5% in September 1994. Form B was also found with form A in a brackish water area at Purwojero in southcentral Java, where it comprised 9.9% of the collections. Form C was only found in one coastal locality at Asahan in northeastern Sumatra, where it occurred in sympatry with both species A and B (48.4% A, 14.5% B, and 37.1% C). The presence of forms A and B at both freshwater and brackish water sites seemed to dispel the hypothesis that populations with different ecologic requirements might represent different species. In fact, use of the cytochrome b and cytochrome oxidase I mitochondrial markers later showed that mosquitoes reared from an inland freshwater pond near Miri and a brackish water rock pool on the shore of the South China Sea in the Lundu District of Sarawak were the same species.[58] Based on the formal taxonomic recognition and definition of *An. sundaicus s.s.* as the species encountered in Miri and Lundu,[26] Dusfour and others[58] demonstrated that form A in the coastal areas of Vietnam and Thailand is a different genetic species of *An. sundaicus* complex.

The genetics of *An. sundaicus* are poorly explored, but the limited chromosomal, isozyme, and molecular studies confirmed that the taxon is a species complex. However, the molecular studies were based on some different populations than the chromosomal and isozyme studies, and the results cannot be correlated entirely. Further investigation using the

TABLE 1
Behavior of *Anopheles sundaicus* observed in different localities

Country	Trophic preference	Resting preference	Biting preference	Source
Cambodia	Exophagy		Anthropophily	Chow 1970[16]
Cambodia	Exophagy/endophagy	Endophily	Zoophily/anthropophily	Webster 2000[49]
India (Nicobar/Andaman)	Endophagy	Endophily	Anthropophily	Covell 1927[70]
India (Andaman/Orissa)		Endophily	Anthropophily	Covell and Singh 1942[71]
India (Nicobar/Andaman)	Exophagy	Exophily	Zoophily/anthropophily	Kalra 1978[11]
India (Nicobar)			Zoophily	Kumari and others 1993[61]
India (Nicobar)	Endophagy	Endophily		Kumari and Sharma 1994[72]
India (West Bengal)			Zoophily/anthropophily	Nandi and others 2000[73]
Indonesia (northern Sumatra)	Exophagy/endophagy	Exophily		Ikemoto 1982[74]
Indonesia (western Java)	Endophagy	Endophily		Akiyama 1984[75]
Indonesia (central Java)	Endophagy	Endophily		Kirnowardoyo and Yoga 1987[47]
Indonesia (Sulawesi)	Endophagy	Endophily	Anthropophily	Collins and others 1979[28]
Malaysia	Exophagy	Exophily	Zoophily	Moorhouse and Wharton 1965[76]
Malaysia	Exophagy		Anthropophily	Chow 1970[16]
Malaysia (Sarawak)	Endophagy			Chow 1970[16]
Thailand		Exophagy	Zoophily	Gould and others 1966[59]
Vietnam		Endophily	Anthropophily	Giang and others 1980[77]
Vietnam		Exophily		Phan 1998[30]

same markers and the same populations is required to clarify the number of species that comprise the complex.

ANOPHELES SUNDAICUS: A MALARIA VECTOR

Differences in the adult behavior and larval habitats of *An. sundaicus* are indicative of an increased risk of contact with humans. *Anopheles sundaicus* is considered as either a major vector or secondary vector of malaria depending on region and country.[13,54] It was previously regarded as a secondary vector in Thailand.[18,59] However, because of its occurrence close to tourist sites, it is now considered as a potential major vector.[17] In contrast, it has been regarded as the principal vector in coastal areas of India[23], Vietnam,[14] and Indonesia.[15,48] Kirnowardoya and Yoga[47] observed that malaria transmission at Chilacap on Java fluctuated widely, not only from year to year, but also from locality to locality during the same year. In the meantime, *An. sundaicus* was responsible for local epidemics in Orissa, India from 1930 to 1940,[31] in Calcutta in 1936,[60] in Vietnam from 1965 to 1985,[30] and in Indonesia in 1985.[47] Outbreaks in Indonesia are also linked to the increase of shrimp and fish farming.[32,45] The development of such farms induced first an increase in mosquito densities and second a greater proximity of mosquitoes to human hosts in important social and economic areas.[15] Knowledge of fluctuations in densities of *An. sundaicus* is crucial for understanding malaria transmission in inhabited coastal areas. This taxon has been found in large numbers in certain areas of central Java (Indonesia) and Nicobar Island where the incidence of malaria is very low.[56,61] Huehne[62] found that although *An. sundaicus* occurred in high densities in coastal areas of Malaysia, it was not involved in malaria transmission. Coosemans and others[29] showed a null sporozoite rate in Bac Lieu Province of southern Vietnam where humans receive an average of 12.78 bites from *An. sundaicus* per hour. Coosemans and others[63] explained that a drastic increase of density can induce a reduction in transmission as a result of decreased mosquito longevity whereby sporogonic development of malaria plasmodia cannot be completed. This situation could occur anywhere where *An. sundaicus* occurs in very high densities. Conversely, Poolsuwan[64] reported that a low sporozoite rate is compensated for by high density in areas of transmission. However, no studies have examined mosquito densities in relation to decrease in sporozoite rate. Additionally, few recent data are available for sporozoite rates in *An. sundaicus*, and published observations show considerable disparity in different localities and countries (Table 2).

Apart from the transmission of human malarial parasites, *An. sundaicus* has been found to transmit monkey malaria in the Andaman Islands.[12] Although previously defined as anthropophilic, endophagic, and endophilic, Kalra[12] found that *An. sundaicus* was more zoophilic, exophagic, and exophilic. Sporozoite detection showed that *An. sundaicus* was transmitting *Plasmodium cynomolgi*, which is closely related to *P. vivax*, to both monkeys and humans. This is interesting in view of laboratory studies that have shown that *An. sundaicus* is not able to transmit *P. gonderi*[65] or other parasites on Nicobar Island.[9]

The role of *An. sundaicus* in malaria transmission has been defined as heterogeneous. As such, it poses a threat for malaria epidemics and endemism in areas of economic development, notably shrimp farming and tourism. Consequently, it is important to monitor populations to better define the actual or potential role of *An. sundaicus* in malaria transmission. The ecologic and behavioral plasticity of this taxon poses difficulties for the development of appropriate vector control strategies.

CONTROL STRATEGIES

Eradication of *An. sundaicus* was included in the antimalarial programs undertaken in many southeast Asian countries in the 1950s. The strategy was based on the application of DDT inside houses.[7,13,30] The unforeseen consequence was the rapid resistance of mosquitoes to DDT (Table 3). However, *An. sundaicus* remained susceptible in a few malaria foci of India.[9,31] Other insecticides were used in areas where DDT resistance occurred, but few records report whether *An. sundaicus* has developed resistance. To circumvent or decrease the extent of resistance and avoid wasteful indoor spraying where *An. sundaicus* is exophilic or exophagic, control efforts focused on environmental alteration of breeding sites, particularly in Indonesia.[42] The elimination of brackish water habitats by drainage was effective in decreasing vector den-

TABLE 2
Sporozoite rates observed in different populations of *Anopheles sundaicus*

Country	Year	Sporozoite rate (%)	Source
Bangladesh	1952	4.3	Nasiruddin 1952[33]
Cambodia	1977	0.4	Klein 1977[19]
India (Calcutta)	1936	3.6	Sen 1938[60]
India	1948	2.7	Nagpal and Kalra 1997[31]
Indonesia (Sulawesi)	1953	0.04	Bonne-Webster and Swellengrebel 1953[78]
Indonesia (Sulawesi)	1973	0.07	Collins and others 1979[28]
Indonesia (Java)	1952–56	0.04–0.3	Sundaraman and others 1957[56]
Indonesia (Flores)	1991	4.2	Marwoto and Arbani 1991[79]
Malaysia (Sabah Province)	1957	1.65	Malaria Report 1957 cited in Chow 1970[16]
Thailand	1966	0	Gould and others 1966[59]
Vietnam (Go Cong Province)	1961	2.9	Phan 1998[30]
Vietnam (Go Cong Province)	1971	4.4	Phan 1998[30]
Vietnam (Ho Chi Minh Province)	1968	1.03	Nguyen Tang Am and others 1993[14]
Vietnam (Mekong Delta)	1968	0.18	Hien 1968[80]
Vietnam (Tra Vinh Province)	1975	2.7	Giang and others 1980[77]
Vietnam (Bac Lieu Province)	1998	0	Coosemans and others 1998[29]

TABLE 3
Chronologic listing of insecticide resistance in different populations of *Anopheles sundaicus*

Date	Country	Resistance status	Source
1954	Indonesia	DDT resistant	Crandell 1954[81]
1956	Indonesia (Java)	DDT resistant	Chow 1970[16]
1962	Malaysia (Sabah)	Dieldrin resistant, DDT susceptible	Chow 1970[16]
1973	Indonesia (Sulawesi)	DDT susceptible	Giang and others 1980[77]
1976	Indonesia	DDT and dieldrin resistant	WHO* 1976[82]
1978	India	DDT resistant	Kalra 1978[11]
1979	Singapore	Susceptible to 3 organochlorines, 5 organophosphates, and 1 pyrethroid	Ong Keng Ho and others 1981[83]
1989	India (Kamorta Island)	DDT susceptible, temephos susceptible	Das and others 1989[9]
1985	Vietnam	DDT resistant, others susceptible	Nguyen Tang Am and others 1993[14]
1985	Indonesia (Java)	DDT susceptible	Kirnowardoyo 1985[84]
1987	Indonesia (central Java)	DDT resistant	Kirnowardoya and Yoga 1987[47]
1994	Vietnam	DDT resistant, others susceptible	Gornostaeva and others 1994[85]
1997	India	DDT susceptible	Nagpal and Kalra 1997[31]
2000	Indonesia	DDT resistant	Webster 2000[86]

* WHO = World Health Organization.

sities.[15] The main idea of such drainage is to confine the tidal influence to well-kept channels where the movement of water will prevent the breeding of *An. sundaicus*.[40] Bunds and sluice gates built at the outlet of main drains are commonly used methods to prevent the invasion of seawater,[40] but such constructions are expensive. Fortunately, control measures against *An. sundaicus* coincide with the complete exclusion of salt water in agriculture.[40] Efforts to eliminate vegetation and algae from ponds and plant mangrove in lagoons were also undertaken. However, these practices required ongoing attention and follow-up.[55,66] Takagi and others[67] attempted to suppress larval development in western Java by shading fishponds with the leaves of *Nipa* palm, or by adding larvivorous fish to these habitats. This strategy was cheap, easy to develop, and efficient, but it required the monthly renewal of *Nipa* palm leaves and was not suitable for fisheries and large ponds. Larvivorous fish were used successfully in combination with *Bacillus thuringiensis israelensis* and chemical larvicides in northern Sumatra,[42] and Schaefer and Kirnowardoyo[54] introduced *B. thuringiensis* H-14 in western Java for the successful control of *An. sundaicus*. Unfortunately, subsequent application was inefficient.[66] Similar trials were undertaken with *B. sphaericus* 2362 in Thailand.[17] All of these strategies were considered successful in controlling *An. sundaicus*,[13,42,68] but they were impractical for large-scale application at national levels.

CONCLUSIONS

Due to its plasticity and capacity to transmit malaria, members of the *An. sundaicus* complex represent a threat to coastal and island populations of humans in southeast Asia. The capacity of *An. sundaicus* to develop in seawater, various concentrations of brackish water, and freshwater is not linked to a particular species, but to an ability of the species to adapt to available sites. However, its presence is restricted along the coast, supporting the hypothesis of larval tolerance to freshwater rather than a wide degree of adaptability. The capacity to develop in a range of habitats from freshwater to seawater is not unusual in anopheline mosquitoes that is known for other species, such as *An. pseudopunctipennis*.[69] Moreover, the lack of recent data on the bionomics, insecticide resistance, and vector capacity, as well as the general lack of surveillance and monitoring of potential vector populations, make the development of targeted control measures problematic. The results of recent molecular and phylogenetic analyses of the *An. sundaicus* complex[58] will foster further study of these mosquitoes. The next step should be the elucidation, characterization, and identification of all members of the complex that includes four identified species: *An. sundaicus s.s.* and species A confirmed by molecular markers[58] and species B and C.[24,25] Such work is needed to determine the distributions, disease relations, environmental characteristics, and insecticide resistance of the individual species. This knowledge is essential for epidemiologic studies, the design and implementation of appropriate vector control measures, and the development of strategies for monitoring the spatiotemporal fluctuations of *An. sundaicus* needed to assess the potential risk of malaria outbreaks.

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