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THE FUTURE OF THE MEDITERRANEAN FRUIT FLY *Ceratitis capitata* INVASION OF CALIFORNIA: A PREDICTIVE FRAMEWORK

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Abstract

The objective of this paper is to predict the state-wide invasion patterns and eventual distribution and abundance of the Mediterranean fruit fly Ceratitis capitata *in California if current eradication efforts fail. The predictions are based on four assumptions: (1) the medfly is established in the state; (2) existing eradication technologies are inadequate; (3) no new and effective eradication technology will be developed in the near future; and (4) the population will not become extinct due to natural causes. Based on climatic, agricultural and demographic information and historical capture patterns, the invasion is predicted to progress in five stages, the first two of which are already completed: Phase I–Introduction and establishment (in Los Angeles Basin and Bay Area); Phase II–Range expansion within LA Basin and Bay Area; Phase III–Escape from LA Basin/Bay Area and spread along Pacific coast; Phase IV–Colonization of the interior; and Phase V–Invasion completion. The highest medfly populations will probably occur along the south coast region of Los Angeles and San Diego as well as in the southern San Joaquin Valley; high population densities will also likely exist along the central coast region (Santa Barbara to Santa Cruz), in the Bay Area and in the Sacramento Valley. Low populations will exist along the north coast and populations will be rare or absent in Sierra Nevadas and in the northeastern and southeastern interior regions. Generalizations and implications for invasion biology are discussed. Copyright © 1996 Elsevier Science Limited*

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INTRODUCTION

On 5 June 1980 three male Mediterranean fruit flies *Ceratitis capitata* were detected in California (Scribner, 1983). These captures turned out to be of considerable historical interest because they were harbingers of the future medfly problem involving the entire state. The three flies were recovered from two separate traps 640 km apart—one fly was captured in the southern California city of Northridge, Los Angeles County and the other two flies were captured in the northern California, Bay Area city of San Jose, Santa Clara County. These medfly captures caused great alarm in the US Department of Agriculture (USDA) and the California Department of Food and Agriculture (CDFA) because this was only the second time in the history of California that this serious pest had been discovered in the state and because its presence threatened the state's multibillion dollar agricultural industry due to the species' potential for attacking and destroying fresh fruit commodities (Hagen *et al.*, 1981). Importing states and countries impose quarantines on fresh fruit commodities shipped from regions of California where the pest is detected and will quarantine the entire state if the species is acknowledged to be permanently established (Walsh, 1981; Carey, 1991, 1992*a*,*b*, 1994; Siebert & Cooper, 1995). The simultaneous detection of medflies at the two remote locations was remarkable because not only were the nearest established medfly populations 3200–4800 km away in the Hawaiian Islands or in the southern tip of Mexico, but the pest had also never been detected in any neighboring regions including anywhere in California's interior such as the Central or Imperial Valleys, in border states such as Oregon, Arizona and Nevada, or the nearby Mexican states of Sonora and Baja.

In the ensuing 15-year period after these medfly captures, new information has become available on the nature and scope of the medfly problem in the state including the history of repeat outbreaks in both northern and southern California, captures of medflies in adjacent outlier areas, genetic analyses of medflies captured in multiple years and different regions of the state, data on entry pathways, medfly outbreaks and patterns of spread in different areas of the world, and model analysis of local and regional movement patterns of medfly invasion in southern California. This collective information suggests not only that the medfly is established in southern California as was argued in previous

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papers (Carey 1991, 1992*a*,*b*, 1996; also see Saul, 1992; Voss, 1992) but that it may also be established in northern California in scattered pockets of residual colonies remaining from the 1980–81 Santa Clara County medfly outbreak. Furthermore, the captures in recent years suggest that the invasion is spreading to other regions, particularly in the south-state.

The specific purpose of this paper is to synthesize information on the current situation in California and, in turn, attempt to predict the future dynamics of the state-wide invasion if current eradication efforts fail (White, 1995). My broad intent is to provide a framework for future research on the medfly invasion as well as an invasion prospectus to guide policy related to control, containment and eradication. Although the specific focus is the medfly, I believe that the overall approach for framing the questions, identifying the main characteristics and forecasting the future trends is general and thus provides conceptual guidelines for predicting invasion patterns for other non-indigenous species.

I organized the paper as follows: (1) I present historical background information on the medfly in both northern and southern California and introduce arguments on why the medfly may be established in both areas; (2) I introduce information on the climatic and biogeographic regions of the state, divide the state into regions based on biogeographic, agricultural and demographic traits and rank each of the region's suitability for medfly population establishment and growth; (3) I predict the pattern of spread throughout the state by dividing the invasion into five phases—introduction and establishment, range expansion, escape from Basin/Bay Area, colonization of the interior and invasion completion; and (4) I discuss the broad ramifications of state-wide invasion and list what I consider are the general properties of the medfly invasion.

This paper is a continuation of a set of papers addressing the medfly problem in California. In the first set (Carey, 1991, 1992*a*, 1994) I examined the nature of the medfly problem by asking whether the captures were due to a reintroduction or to an established population. In the second set of related papers (Carey, 1995, 1996) I developed a general framework for understanding the nature of the medfly invasion process using the concept of an 'invasion stream'. In the current paper I attempt to build on findings from the first two sets of papers and construct a general framework for predicting the invasion spread and ultimate medfly distribution within the state. Background information on medfly ecology, systematics and distribution is contained in Christenson and Foote (1961), Bateman (1972), Foote (1980), Vargas and Nishida (1989), Harris *et al.* (1993) and Robinson and Hooper (1989) and on the medfly in California and eradication protocols in Carnes (1911), Quayle (1929), California Department of Food and Agriculture (1989), Dowell (1985, 1988), Dowell and Gill (1989), Dowell and Penrose (1995), Morse *et al.* (1995) and Huston (1995).

THE MEDFLY IN THE NORTH AND SOUTH STATE

Southern California

The first record of the medfly in California was in the fall of 1975 when 77 were captured in or near Culver City (Carey, 1991, 1996). No further medflies were captured in southern California until 1980 when five adults were detected in the city of Northridge (Figs 1 & 2). The following year (1981) a total of 53 medflies were captured about 64 km southeast of Northridge in the cities of Baldwin Park, West Covina and La Puente. For the next five years only three more medflies were captured in the Los Angeles Basin—one in Los Angeles (Hancock Park area in 1982), one in Beverly Hills (1984) and one in West Los Angeles (1986).

Beginning in 1987, the medfly started appearing in southern California every year, in larger numbers and over greater areas. A total of 279 were captured in a large outbreak lasting from July 1989 to late November 1990, including the discovery of medflies for the first time in San Bernardino and Riverside Counties. In 1991 a total of 26 more medflies were captured—25 in Hancock Park (where one was detected in 1982) and one in the city of San Gabriel. In 1992 and 1993 a total of 595 medflies were captured in southern California—more flies than had been captured in the previous 17 years in which medflies had been detected. Although increased trap numbers and improved trapping technologies and strategies partly account for this increased number of detections, the fact that the flies were found in the same areas as previous years as well as in new areas suggests that they were never completely eradicated (Huston, 1995).

In response to the massive outbreaks in 1992 and 1993 an eradication program was developed by the USDA, CDFA and advisors from the International Atomic Energy Agency (IAEA) in Vienna to eradicate the medfly using the sterile insect technique (SIT). The program was initiated in March 1994 and relies on the weekly release of approximately 100,000 sterile flies per km^2 over a 4200 km^2 area in the Los Angeles Basin (Dowell & Penrose, 1995; White, 1995). However, the release area does not cover areas outside of the Los Angeles Basin and in the fall of 1994 a total of 64 medflies were captured in the city of Camerillo located approximately 32 km west of the San Fernado Valley medfly finds. These were the first records for Ventura County. In addition four medflies were captured in the SIT release zone that same year.

That the medfly was not eradicated in the Los Angeles Basin is reinforced by the recent analysis by Huston (1995) of the geographic captured patterns relative to the eradication treatment zones. She showed that, despite the application of multiple aerial treatments of malathion bait sprays, medflies were detected in each of nine different regions of the Los Angeles Basin several years post treatment. This finding is consistent with

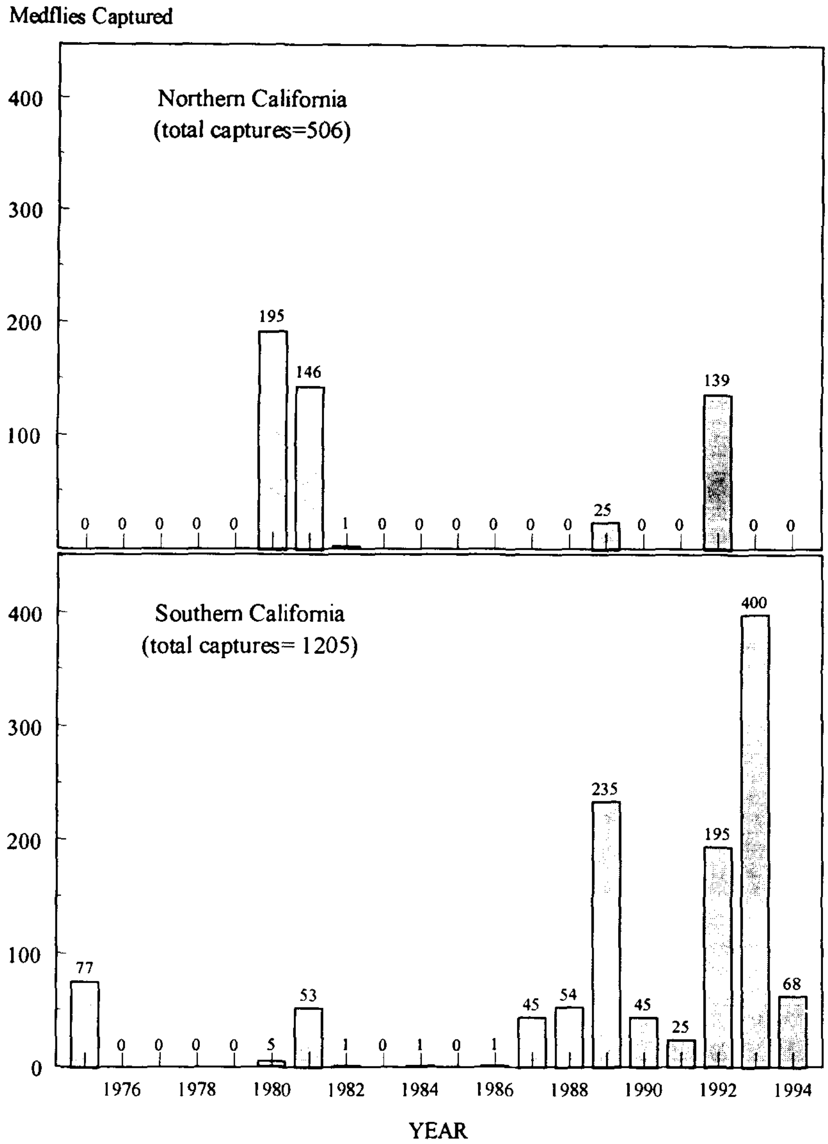

Fig. 1. Medfly captures in northern (Bay Area) and southern California by year.

several of the trends I identified earlier to argue that the medfly is established in southern California including (Carey, 1991): (i) repeat captures in the same vicinity neighborhoods; (ii) lack of captures in or near international ports of entry such as Los Angeles International Airport or Long Beach Harbor; (iii) spread to new areas outside of the Los Angeles Basin; (iv) a distinct seasonality with most captures (95%) in the summer and fall and few (5%) in the winter and spring; and (v) small numbers of interceptions along pathways including mail, vehicles and airplanes.

Northern California

The first two medflies captured in Santa Clara County on 5 June 1980 marked the beginning of what was to be the most expensive medfly eradication campaign in the history of California (Dowell, 1983; Scribner, 1983). A total of 195 medflies were detected that year and 146 the following year with aerial applications of malathion and bait being applied to nearly 3600 km^2 in six counties including Santa Clara, San Mateo, Alameda, Stanislaus, San Benito, Santa Cruz and San Joaquin. The last fly captured in the main outbreak area was in the city of Mountain View on 29 October 1981. However, a single medfly was captured on 24 June 1982, in the city of Stockton. Eradication was declared on 21 September 1982 with Federal and State costs totalling over $100 million (Lindquist & Nadel, 1980; Scribner, 1983; USDA, 1987).

Medflies were not detected again in northern California until 1989 when 25 adults were captured in the city of Mountain View. Many of the flies were captured within five to eight blocks of sites where they were found in the 1980–81 outbreak and corresponded to the same general area referred to as the Mountain View Gap in which high larval densities existed in June 1981 (Lindquist & Nadel, 1980). A sterile fly eradication program was initiated and eradication declared the following year.

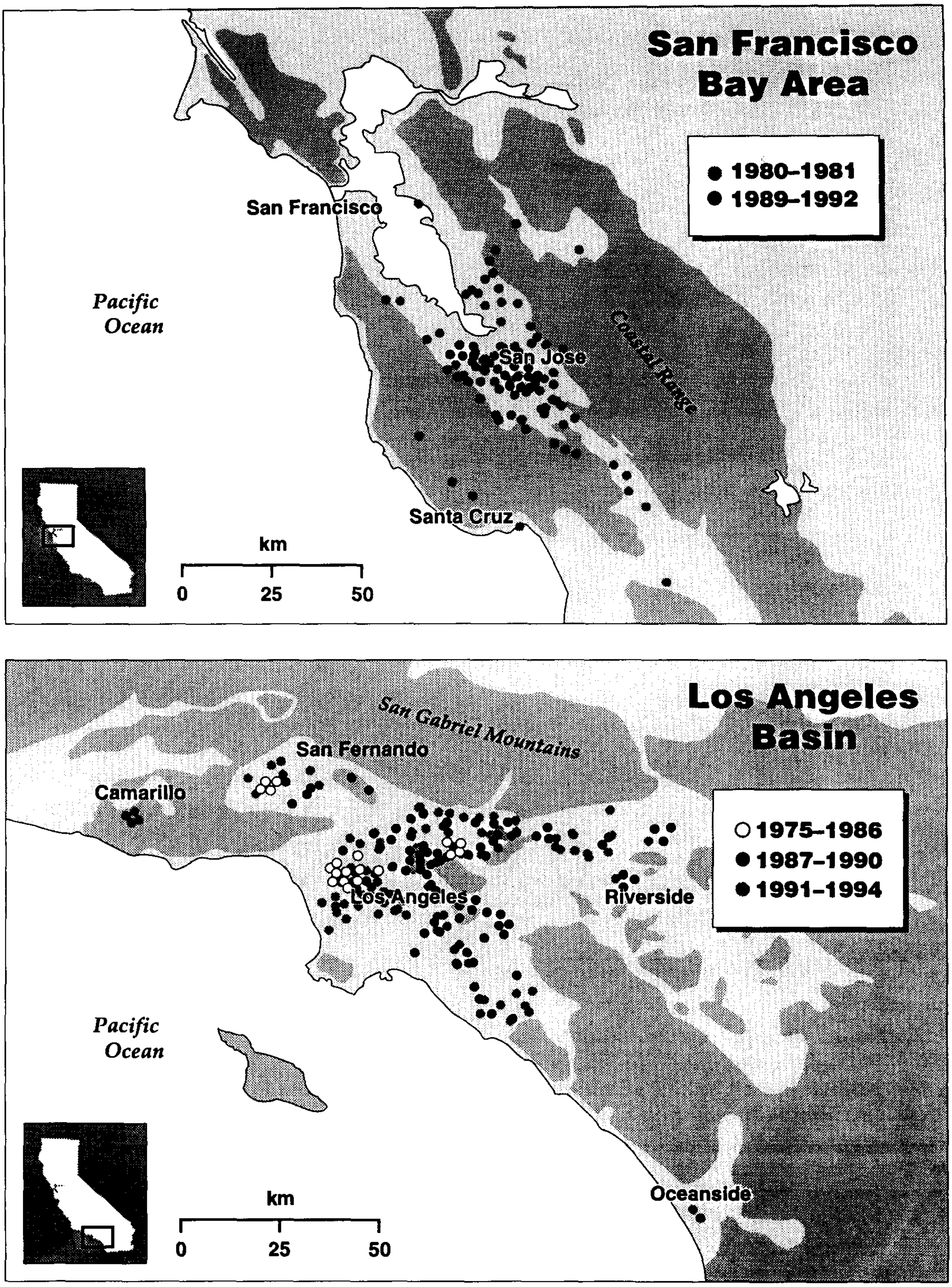

Fig. 2. Medfly captures in northern (Bay Area) and southern California by location and period. For reference, the southernmost captures in northern and southern California were in Hollister (San Mateo County) and Oceanside (San Diego County), respectively.

Three years later in 1992 a total of 139 medflies were captured in the city of San Jose. Like the recent finds in Mountain View, most of these were also found within a few blocks of the 1980–81 finds. Although no medfly outbreaks occurred in 1993 and 1994 in northern California, the proximity of fly finds in 1989 and 1992 to the location of captures in 1980–81 raises concerns that the medfly finds may have arisen from earlier outbreaks, and that small pockets of undetectable populations remained after eradication was declared in 1982.

Lindquist and Nadel (1980) concluded that the 1980 eradication program in the Bay Area failed because the relative inefficiency of the attractant (trimedlure) to detect the medfly may not have been fully appreciated by the eradication project staff. This low trap efficiency may underlie the ability of the medfly to invade California without being detected (Kaneshiro, 1993).

Relationship between northern and southern California medfly outbreaks

Although no direct ecological or genetic evidence exists on the relationship of the medfly populations in both northern and southern California, a number of factors suggest that they may be related.

(1) Medflies were never detected anywhere in California for the first 75 years of this century. However, in a 7-year period there were three outbreaks in southern California and a massive outbreak in the Bay Area. The probability seems remote that four independent outbreaks would occur in the same state when, during the same period, there were no new outbreaks anywhere in the Pacific Rim (Carey, 1995).

(2) Single medflies were captured at two critical locations between the Bay Area and the Los Angeles Basin. In 1981 a medfly was captured in the city of Hollister in San Benito County and in 1984 a medfly was captured 320 km south in the city of Santa Barbara in Santa Barbara County (CDFA, pers. comm.). These flies raise the possibility that an extremely low-level medfly population exists which links the medfly populations in the north and south state. In other words, the medfly may already be present in very low levels along the Central Coast in cities such as San Luis Obispo and Santa Barbara.

(3) Successful colonization of organisms from tropical sources to areas with desert or Mediterranean climates such as California appears to be relatively rare (di Castri *et al.*, 1990). In contrast, spread within or between regions with similar climates appears to be relatively common. For example, if the medfly was frequently introduced to California from Hawaii and was subsequently successful at colonization, then it is likely that genetic analysis would reveal Hawaiian genotypes in captures from either northern or southern California. But there is currently no evidence that any California flies originated from Hawaii (Sheppard *et al.*, 1992). Even laboratory colonization of the medfly is difficult (Leppla *et al.*, 1983)—several hundred live medflies captured in California in 1994 were shipped to Hawaii to found a new colony but the colony went extinct (R. Penrose, pers. comm.). In general, the probability that a small number of individuals introduced to a new area will colonize and eventually become established is quite low even under the most favorable conditions. For example, Beirne (1975) noted from an analysis of the attempts to colonize around 208 different insect species for biological control that the greater the number released the greater the likelihood of successful colonization and that if the numbers were below around 5000 individuals the probability of success was small. It is likely that the number of medflies reaching the outdoors in a single location never exceeds a few dozen.

Genetic analyses (Sheppard *et al.*, 1992; Haymer & McInnis, 1994; Roderick & Villablanca, 1995; McPheron *et al.*, 1995; Roderick, 1996; also see Berlocher 1984 for analysis of walnut husk fly *Rhagoletis completa* in California) and capture patterns in the future will reveal whether medflies captured from northern and southern California stem from one or multiple introductions. The historical linkage of the two populations is not critical to my projections on the future of the medfly invasion although it makes a difference to understanding the nature of the invasion process.

PREDICTING THE STATE-WIDE MEDFLY INVASION

Climatic considerations

The medfly is a tropical, multivoltine, non-diapausing insect species that has invaded a wide range of non-tropical climatic regions (Christenson & Foote, 1960; Bateman, 1972). Although several decades ago there was considerable interest in predicting the potential distribution and abundance of fruit flies in the US using the results of bioclimatic laboratory studies (Back & Pemberton, 1916*a,b*; Baker, 1944; Messenger & Flitters, 1958, 1959; Flitters, 1962), the best predictor of potential establishment and spread of the medfly in California is basically whether it is established in regions of the world with climates analogous to those of California's (Dowell, 1983). This approach was used for crop plants (Nuttonson, 1947) as well as for other pest fruit flies (e.g. Baker *et al.*, 1990) and is thus believed also to be valid for the medfly. Indeed one of the more serious errors early in the 1980–82 medfly program in northern California was the belief by some scientists that the medfly could not survive the winters in northern California (Andrew *et al.*, 1977; Scribner, 1983) despite the knowledge that many countries in Europe such as Spain, France, Italy, Greece and Israel where the medfly was permanently established (e.g. Rivnay, 1941, 1950; Bodenheimer, 1951) have similar climates to the Bay Area and other regions of northern California (Thornthwaite, 1931; Mariolopoulos, 1961; Anon., 1983).

The Koppen classification (James, 1966) divides California into zones based on the relationship of rainfall to potential evaporation, on temperature, and on the seasonal variation of drought. The state has four major climatic zones which are subdivided into eleven categories (Donley *et al.*, 1979). The main climatic regions are shown in Fig. 3. Two subcategories of Mediterranean climates are similar to areas where the medfly is established including the Mediterranean Basin of

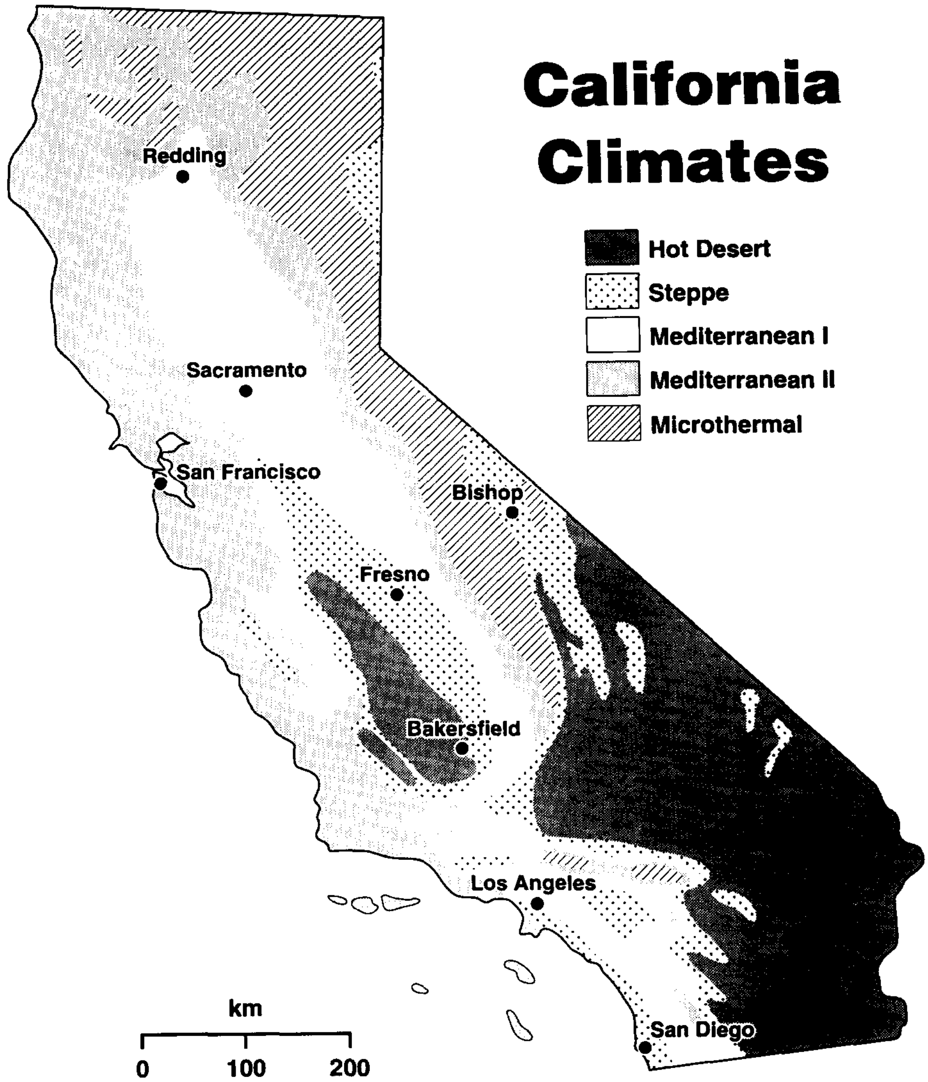

Fig. 3. Climatic regions of California (from Donley *et al.*, 1979). *Hot desert*—precipitation less than half potential evaportation, the average of the coldest month above 0°C. *Steppe*—precipitation more than half but less than potential evaporation. The average of the coldest month is above 0°C. *Mediterranean*—precipitation more than potential evaporation with the summer dry and the average of the coldest month between 0 and 18°C. *Microthermal and Alpine*—average of the coldest month below 0°C (microthermal) and the average of the warmest month below 10°C (highlands).

Europe (e.g. Spain, France, Greece, Italy) as well as Turkey, Southern Chile, South Africa and Western Australia. The climate of approximately half of California is classified as Mediterranean, and slightly over 10% as steppe, including parts of the Central Valley and southern California. Areas of the world where the medfly is established and which has this climatic analog include South Africa, Argentina and Venezuela. The climate in about a quarter of the state is classified as hot desert and includes the southern end of the Central Valley near Bakersfield and also in the Mohave Desert. Similar regions of the world with this climatic analog and where the medfly is found include Northern Chile, Peru, Egypt, Israel and Jordan. Although the medfly has been detected in regions of Europe with microthermal climates such as Austria, Germany, The Netherlands, and Switzerland (Baas, 1959), the distribution within these countries is generally restricted to the lower elevations (valleys) in orchards and farms where medfly hosts can survive. Thus it is unlikely that the medfly would become established in the high mountainous regions (Sierra Nevadas) of the state.

Regional considerations: biogeographic, agricultural and demographic

California is one of the most biogeographically, agriculturally, and demographically diverse regions in North America with indigenous ecosystems including alpine, montane, marine, freshwater, forest, woodland, scrub, and grassland (Mooney *et al.*, 1986), and with agricultural productivity exceeding $18 billion, including fruits, nuts, vegetables, grains and citrus (Scheuring, 1983; Siebert & Cooper, 1995). Because of this enormous diversity, it was necessary to divide the state into several regions based on common geographic, agricultural, climatic and demographic traits (Fig. 4). I then assigned each of the 10 regions a number between 1 and 5 indicating its overall suitability for medfly survival and growth (1 = poor; 5 = optimal). I based this suitability rating on four factors: (i) climate, which influences host plant availability, potential generation time, seasonality and overwintering potential determined by the intensity and duration of low temperatures (Gjullin, 1931; O'Loughlin *et al.*, 1984; Papadopoulos *et al.*, in press); (ii) geography, which affects the extent of isolation (e.g. barriers to movement such as deserts or mountains) relative to an infested region; (iii) agriculture, which affects the host fruit availability as well as the extent of pesticide use directed towards other crop pests; and (iv) human population, which influences the spatial and temporal availability of hosts and refugia (e.g. homeowner backyards).

The information and medfly suitability ratings presented in Table 1 merit several comments.

(1) It is likely that the South Coast region provides the most ideal conditions for the medfly in the state. This region contains three of the most densely populated counties (Los Angeles, Orange and San Diego) with 16 million people constituting over half of the state's population, several million residences with many backyard medfly hosts, over 11% of the total area of the state and an ideal Mediterranean climate for medfly populations. This region is climatically similar to parts of Israel and Greece and there is little question that medfly populations would be among the highest of the state in this region; all backyard hosts would eventually be infested with the medfly throughout much of the year and commercial fruit-growing areas would be under constant attack.

(2) The San Joaquin Valley would also provide highly favorable conditions for medfly population establishment and growth. However, populations in this region may not attain the high levels as in the South Coast Region because: (i) medfly populations would likely be suppressed due to agricultural pesticide use; (ii) unpicked fruit would be less abundant in commercial orchards; (iii) fewer backyards exist due to the smaller urban population; and (iv) the low winter temperatures would prevent large numbers of larvae from overwintering.

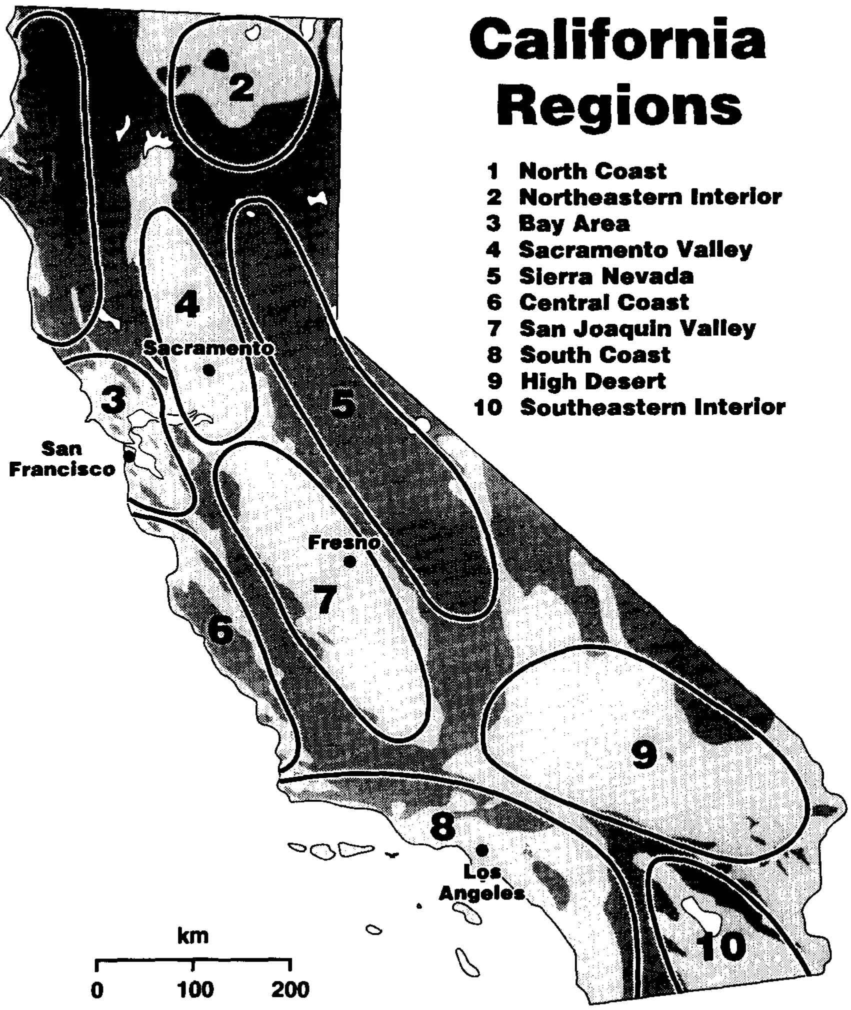

Fig. 4. Classification of California by region based on geographic, climatic, agricultural and demographic criteria. See Table 1 for inclusive counties and general characteristics.

(3) Medfly population levels would likely be moderate in four regions including the Central Coast, Bay Area, Sacramento Valley and Southeastern Interior regions. Cool temperatures would probably prevent medfly populations from attaining extremely high levels in the two coastal areas throughout much of the year. However, low winter temperatures in the Sacramento Valley would reduce overwintering populations which, in turn, would prevent populations from reaching high levels until late summer and fall. Although winter temperatures often fall below freezing in the Sacramento Valley, a thermal belt exists along the edge of the valley which is suitable for many types of medfly hosts such as citrus and stone fruits. The tule fog also acts like a thermal blanket and prevents frosts. Consequently a large variety of medfly hosts are grown in protected backyards in all of the urban areas.

(4) Medfly populations would likely be extremely sparse in four of the regions. In the North Coast region populations would likely remain at low levels due to a combination of the cool coastal temperatures and the lack of primary hosts. The medfly would likely be rare to absent in the Northeastern Interior and Sierra Nevada regions due to the 2–5 months of subfreezing winter temperatures, and populations would be scarce in the High Desert region due to paucity of suitable hosts and to the subfreezing winter temperatures.

In general, changes in the availability of host plants will have an enormous influence on the distribution and abundance of medfly within a region. For example, Vargas *et al.* (1995) noted that surveys on Kauai in Hawaii between 1976 and 1986 indicated that medfly populations were rare. Thus preliminary steps were taken by the US Department of Agriculture to explore the possibility of

Table 1. California counties included in each of 10 biogeographic regions, estimated population in 1994 and common hosts
Medfly suitability indices: 5, high; 1, rare to absent. Population data source: State of California (1994)

Region[a]	Area(km^2) (%)	Population (1000s) (%)	Common hosts	Medfly suitability index
1. North Coast	39,000 (9·5)	851 (2·7)	Apples, cherries, pears, plums	2
2. Northeastern Interior	37,575 (9·1)	219 (0·7)	Apples, cherries, pears, plums	1
3. Bay Area	13,004 (3·2)	5859 (18·3)	Peaches, nectarines, apricots, citrus, apples, pears	3+
4. Sacramento Valley	26,964 (6·6)	1718 (5·4)	Peaches, nectarines, figs, citrus, tomatoes, plums	3
5. Sierra Nevada	56,436 (13·7)	637 (2·0)	Cherry, pears, apples plums	1
6. Central Coast	29,090 (7·1)	1274 (4·0)	Peaches, nectarines, figs, apricots, oranges, lemons, grapefruit	3
7. San Joaquin Valley	71,382 (17·4)	3076 (9·6)	Peaches, nectarines, plums, pear, oranges, grapefruit, apricots, apple	4
8. South Coast	47,272 (11·5)	16,581 (51·9)	Peaches, nectarines, apricots, oranges, lemons, figs, avocados	5
9. High Desert[b]	78,378 (19·1)	1592 (5·0)	Peaches, nectarines, apricots, oranges, figs	1+
10. Southeastern Interior	11,906 (2·9)	136 (0·4)	Vegetables, grapefruit, oranges, peaches, nectarines, apricots	3+
TOTALS	411,012 (100)	31,961 (100)		

[a]Inclusive counties: Region 1, Del Norte, Humbolt, Lake, Mendocino, Napa, Sonoma, Trinity; Region 2, Modoc, Shasta, Siskiyou; Region 3, Alameda, Contra Costa, Marin, San Francisco, San Mateo, Santa Clara, Solano; Region 4, Butte, Colusa, Glenn, Sacramento, Sutter, Tehama, Yolo, Yuba; Region 5, Alpine, Amador, Calaveras, El Dorado, Lassen, Mariposa, Mono, Placer, Nevada, Plumas, Sierra, Tuolumne; Region 6, Monterey, San Benito, San Luis Obispo, Santa Barbara, Santa Cruz; Region 7, Fresno, Kern, Kings, Madera, Merced, San Joaquin, Stanislaus, Tulare; Region 8, Los Angeles, Orange, Riverside, San Diego, Ventura; Region 9, San Bernardino, Inyo; Region 10, Imperial.

[b]Most of San Bernardino County's population resides in the 'South Coast' region. However, the majority of the area is in 'High Desert' region.

eradicating the fly from this island. However, beginning in 1986 large commercial coffee orchards were established on Kauai, providing highly suitable habitat for the medfly (Harris & Carey, 1989) and Kauai now supports one of the highest medfly populations in Hawaii. The same concept of alterations in the host plant composition of regions would apply to California and therefore changes in the intraregional cropping structure of the State would likely have a substantial impact on medfly populations.

Phases of invasion

The purpose of this section is to use principles of invasion biology to predict the patterns and distribution of the medfly in California if current eradication efforts fail (White, 1995). Although I draw heavily on concepts presented in Carey (1996) regarding 'stream-like' movement, I also incorporate concepts taken from a number of previous works on invasion biology including Elton (1958), Simberloff (1989), Groves and Burdon (1986), Hengeveld (1989), Macdonald *et al.* (1986), Drake *et al.* (1989), and di Castri *et al.* (1990).

I consider the medfly invasion of California in five phases (Figs 5(a)–(c):

Phase I

By far the most important phase in any biological invasion including the medfly invasion of California is the first (Ruesink *et al.*, 1995). This phase in the medfly invasion of the State required essentially two steps: (i) introduction of live medflies to the wild (outdoors); and (ii) successful colonization and establishment. If the original infestations resulted from domestic activities such as the carry-in of infested hosts by tourists or workers, then one of two things had to have happened for the medfly larvae inside the hosts to reach the wild: (i) the infested host must have reached the out-of-doors and then larvae survived to adulthood; or (ii) the larvae must have pupated inside the dwelling, emerged as adults and then several of each sex escaped. Once outside, the adult medflies must survive both physical and biological hazards, find suitable food for survival and egg production, locate mates and find hosts for egg laying. This cycle likely repeated itself for several years before the incipient population was large and widespread enough to avoid chance extinction.

This general concept described here involving the complicated steps needed for successful introduction and establishment is consistent with the historical pattern of medfly captures in the state. That is, the medfly has never been recovered at random locations within California as would be expected if colonization was a common occurrence. This perspective underscores the chronic and incipient nature of the medfly invasion at the even the earliest stages (Carey, 1991, 1996).

Phase II—Range expansion

This probably occurred at subdetection levels in northern California during the 1970s prior to detection over 3600 km^2 in 1980. The distribution of the medfly over the six-county area during the 1980–81 outbreak in the Bay Area was undoubtedly due primarily to medfly spread that had occurred prior to the first detection and not to rapid dispersal within a single season. It is likely that the extensive aerial spraying of malathion in the Bay Area in 1981 reduced the medfly populations to scattered, isolated pockets that will require decades to attain detection levels similar to the early 1980s.

Medfly range expansion in the Los Angeles Basin became apparent throughout the 1980s and early 1990s with the occurrence of the series of outbreaks following the first record of the medfly near Culver City in 1975. That the medfly was captured throughout the 4200 km^2 area bounded by the San Fernando Valley in the northwest to San Bernardino and Riverside in the east and Orange County in the south all within a 10-year period attests to the steady, inexorable expansion of its range. The likely reason that this range expansion was misdiagnosed as due to multiple reintroductions was lack of understanding of the underlying invasion dynamics. The model that I believe best describes the southern California invasion and probably also applies to the invasion of northern California is one given in Carey (1996) which characterizes the medfly spread as more tentacle-like than wave-like. That is, the medfly appears to be channeled by the California terrain and thus spreads long linear distances through an area without being widespread within an area. This concept is similar to the findings of Nishida *et al.* (1985) that the medfly is not widespread throughout the Hawaiian Islands but is present in localized areas. These researchers also found that the presence of host fruits did not seem to be a critical factor since many coastal areas of Hawaii had an abundance of fruits but few medflies.

Phase III

I consider the recent medfly captures outside of both the Los Angeles Basin and the Bay Area as the beginning of the third phase of the medfly invasion of California. The medfly captures in San Diego County in the early 1990s and in Ventura County in 1994 indicate that the medfly has moved beyond the Los Angeles Basin and is spreading northward and southward along the Pacific coast. This phase in the statewide invasion is important because it indicates that the spread has not been halted, because many of the regions outside the Los Angeles Basin are agricultural and thus vulnerable to attack and because it indicates that the medfly is spreading to two large metropolitan areas—Santa Barbara in the Central Coast region and San Diego in the far south state. There has been no indication historically that the medfly has spread to the North Coast Region although there is little doubt that the pest could survive in this area of the state inasmuch as it can survive in central Europe (Bass, 1959).

Fig. 5. Predicted patterns of medfly spread in California through five invasion phases. (a) includes Phase I—colonization and establishment, Phase II—range expansion, and Phase III—escape from LA Basin and Bay Area; (b) depicts Phase IV—colonization of California's interior; (c) shows the predicted pattern of invasion completion.

Phase IV

There are several invasion 'gateways' through the mountain ranges separating the coastal areas from California's interior. These include: (i) the San Gorgonio Pass and the Cajon Canyon through which medflies in San Bernardino and Riverside Counties can move to the Coachella and Imperial Valleys (Southwestern Interior Region) and the Mohave Desert, respectively; (ii) the Tehachipi Valley and the Grapevine Pass through which medflies can pass from either the San Fernando Valley or the Mohave Desert; and (iii) the San Francisco Bay delta region of northern California to the Sacramento Valley. The concept of gateways to new regions is similar to what Vargas *et al.* (1983) reported for medfly movement in Hawaii—that features of the terrain such as rivers, canyons and valley mouths funnel medflies to new locations.

Phase V

The completion phase of the state-wide invasion involves a series of local invasions—the slow, inexorable spread of the medfly district-by-district, orchard-by-orchard, and backyard-by-backyard. Many areas of California are sparsely populated and have climatic conditions marginally favorable to the medfly. It is likely that its abundance would be similar to that described by O'Loughlin *et al.* (1984) for the Queensland fruit fly *Dacus tryoni* in marginally-favorable climate in Victoria, Australia. This species undergoes only about three generations per year although it is always present in the region at low population levels.

A related concept concerning the completion phase of the medfly invasion is equilibrium abundance—its characteristic seasonal abundance within a region. Clearly the medfly seasonal abundance will be much different when the medfly first colonizes a region even when that region is favorable for population growth from when it has been present in the region for a long period. At the lower limits of temperatures in California's interior regions it is likely that the interplay between time of infestation, daily temperature fluctuation, and certain fruit factors that vary with the host will determine whether medfly larvae can overwinter and, if so, at what rate (Papadopoulos *et al.*, in press).

Fig. 5. (*continued*)

DISCUSSION

Factors influencing the outcome of the medfly invasion

The approach that I used to predict the future of the medfly invasion of California is based on a number of assumptions: (i) that the medfly is established in California; (ii) that current protocols to eradicate the medfly using the release of sterile insects (White, 1995) or using localized spraying of malathion bait will fail; (iii) that a new and effective medfly eradication technology (i.e. 'silver bullet') will not be developed in the near future (see Chrisman *et al.*, 1995; Service, 1995); and (iv) that the medfly will not go extinct naturally due to chance. The likelihood of chance extinction, though remote, is not without precedent—the medfly became established around Sydney, Australia in the mid-1850s but disappeared in the 1940s (Maelzer, 1990*a*,*b*). There is not universal agreement about the first assumption in particular (Voss, 1992) and there are many who believe that the current eradication approach will be successful (Dowell & Penrose, 1995).

If future genetic analyses reveal that the medfly is not established in California, then the single most fundamental assumption of my forecast is unfounded and therefore my prediction will invalidated. It will also not be accurate if the current eradication efforts are successful or if a new technology is developed that is effective.

Generalizations of medfly invasion

Simberloff (1989) notes that it is depressing to be unable to draw striking generalizations about introduced insects but it would serve no worthwhile purpose to generalize prematurely. Although I agree that there may be no generalizations about introduced insects, I believe that it is possible to generalize about insect invasions. I list below five characteristics of the medfly invasion that I believe are general. Many of these concepts are drawn from the classical literature on invasion biology but also have precedents in the fruit fly and entomological literature.

1. Chance, timing and opportunity in medfly establishment

As a recent report on non-indigenous species in the US notes, (US Congress, 1993), the movement of plants and animals is much like biological roulette—once in a

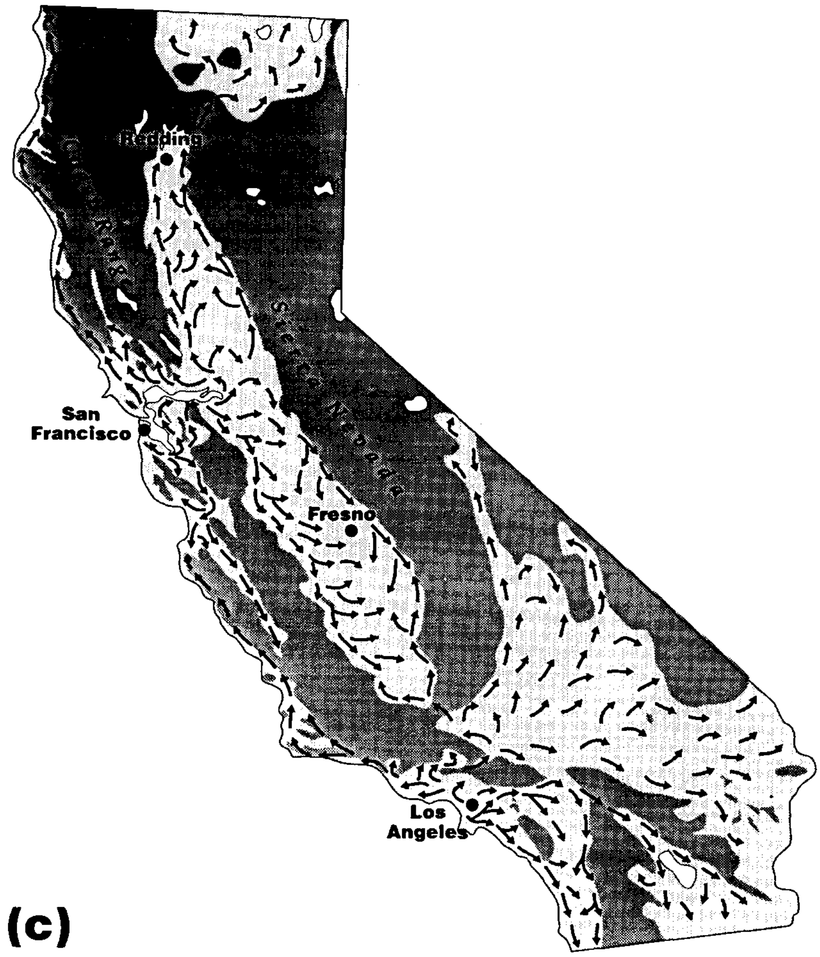

Fig. 5. *(continued)*

new environment an organism may die, may take hold and reproduce with little noticeable effect, or it may sometimes spread with devastating results. But success or failure is often extremely difficult to predict (Simberloff, 1989). Crawley (1987) argued that neither chance nor timing alone was all-important to successful invasions but rather that the interaction between chance and timing was the vital ingredient. Rare chance events such as medfly introduction that occur at just the right time and in just the right place such as during the early spring or summer in an area rich in host fruit were critical to success. There is no doubt that medflies are intercepted along pathways into the state. But it does not follow that these medflies ever escaped to breeding sites.

2. Minimum viable medfly population

As Mooney and Drake (1989) note, the concept of the minimum viable population is central to any consideration of establishment after introduction. They characterize a minimum viable population as some population abundance that is immune to local extinctions due to genetic, demographic and environmental stochasticity. Given the magnitude of population fluctuations caused by these factors, it is presumed that a population has a minimum size below which extinction is likely and above which extinction is unlikely (Landolt *et al.*, 1984; Baker *et al.*, 1990). But even large numbers of colonists introduced into multiple sites under the most favorable conditions have a better than even chance of going extinct (Beirne, 1975; Crawley, 1987). For example, Crawley (1987) noted that over a quarter of the 627 cases of deliberately introduced insects in weed biological control programs went extinct without completing a single generation and 8% more went extinct after one or more generations. These findings are consistent with the notion that the probability of new insect colonies including medflies becoming established is probably quite low. Indeed, the medfly situation in the state may eventually be shown by geneticists (e.g. Sheppard *et al.*, 1992; Haymer & McInnis, 1994; Roderick, 1996) to be similar to the findings of Berlocher (1984) on the walnut husk fly, where it appears that the entire state-wide population of this pest can be traced to a single colonization event around the 1920s in southern California (Boyce, 1934).

3. Medfly refugia

The existence of various kinds of refuges protect the invader (medfly) from the full weight of competitor, natural enemy, or eradication efforts such as sterile insects or insecticidal sprays (Crawley, 1986). A refuge provides a source of invaders for uninfested areas or areas where the population has been eradicated or gone extinct. Thus immigration from the refuges over a protracted period will increase the likelihood of successful reinvasion or spread simply because the experiment of invasion is repeated many times, under what are likely to be different conditions of weather, competitor density and natural enemy abundance. Urban backyards containing a wide variety of medfly hosts are undoubtedly the single most important medfly refuge in California; this host mosaic is probably the major factor determining the success or failure of eradication and serves as a continual source of medfly 'inoculum' for agricultural areas (Carey, 1992*b*).

4. Medfly dispersal and spread

Rate of spread is not only a function of species characteristics but the ecosystems through which the species spreads (Andow *et al.*, 1990; Mooney & Drake, 1989*b*). It is a complex function of a species' ecology and the amount of habitat heterogeneity. The rate of medfly spread through California will depend upon the size and distribution of host 'patches', the distance between suitable patches and the overall characteristics of the patches themselves such as host species and phenology (see Bateman, 1979 for analagous situation in Australia).

5. Climatic constraints and limits

Climatic conditions constitute the single most important set of factors in the success of medfly invasions (Simberloff, 1989), the rate of spread (Andow *et al.*, 1990), the population phenology (Bodenheimer, 1951) and the ultimate distribution (Gjullin, 1931; Flitters, 1962). It also has a major bearing on the interpretation of capture data in the context of eradication efforts. For example, Readshaw (1986) demonstrated the coincidence between screwworm *Cochliomyia hominivorax* outbreaks in Florida and favorable seasonal conditions and suggested that this species, which like the medfly is tropical, could exist at very low population levels in small isolated pockets without being detected by man. When climatic conditions shift over a period of years such as a series of unseasonably warm winters, the pest will increase in numbers. What appears to be new introductions or rapid range expansions may actually be simply the population response to better climatic conditions.

Implications of state-wide medfly invasion

I believe that the analysis and the predictions of the future invasion are useful regardless of the assumption concerning the status of the past or current infestations. For example, the bioclimatic perspectives will enable economists to adjust their predictions of the economic impact of medfly establishment (Siebert & Cooper, 1995), the framework will provide a baseline around which ecologists and entomologists can debate the nature of biological invasions and eradication (e.g. Knipling, 1978; Newsom, 1978; Saul, 1992; Voss, 1992), and the specific predictions may encourage policy makers to develop contingency plans in the event that eradication efforts fail. More generally, the overall process of assembling the data and making forecasts provides a hypothesis that can be tested and thus will be useful for validating or refuting the underlying assumptions and theory (Gill, 1986).

Although of enormous economic consequences, the invasion of California by the medfly is also of considerable scientific importance. This is because, relatively speaking, detailed information exists on its presence, movement and genetics in the early stages of its invasion. In contrast, many biological invasions of other pests are defined using geopolitical criteria such as the 'invasion' of Texas by the Africanized honeybee *Apis mellifera scutellata* or of Michigan by the gypsy moth *Lymantria dispar*. These 'invasions' are more about spread and range expansion than about invasion, *per se*, since the early stages (introduction, colonization, establishment) have long been completed. Thus the best that can be hoped for in these cases is to reconstruct the early invasion history using genetical techniques.

But the medfly offers one of the best opportunities in invasion biology to study an ongoing invasion at a relatively early stage. Questions regarding the number of colonization events, the source of colonists and the struc- ture of the medfly populations including gene flow and effective population size are of fundamental importance to both invasion biologists and to agencies concerned with its eradication (Roderick, 1996). This is because answers to these questions will shed light on diagnostic and tactical issues involving the medfly in California as well as provide important insights into how best to study non-indigenous pest problems in the future.

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