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Distribution, Habitat, and Current Status of the San Pedro Mártir Rainbow Trout, Oncorhynchus mykiss nelsoni (Evermann)

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Abstract.—The distribution, habitat, and current status of Oncorhynchus mykiss nelsoni (Evermann) were evaluated in the two main drainages of the western slope of the Sierra San Pedro Mártir (Santo Domingo and San Rafael), Baja California, México. The known localities of distribution (type locality and transplant sites), as well as other previously unsurveyed localities, were monitored during a period of seven years (January 1987 to March 1994) to document occurrence of the trout and to evaluate their habitat characteristics. The conservation status for this subspecies was determined as stable in the two main drainages, which range in altitude from 540 to 2030 m above sea level. Recommendations for future conservation and management of the trout and their habitats are provided.

Resumen.—La distribución, habitat, y estatus actual de Oncorhynchus mykiss nelsoni (Evermann) fueron evaluados en los dos sistemas hidrológicos principales de la pendiente occidental de la Sierra San Pedro Mártir (Santo Domingo y San Rafael), Baja California, México. Las localidades conocidas de distribución (localidad tipo y sitios de introducción), además de otras previamente no investigadas, fueron muestreadas durante un período de siete años (Enero 1987 a Marzo 1994) para documentar la ocurrencia de la trucha y para evaluar sus características de habitat. Su estatus de conservación fue determinado como estable para los dos sistemas hidrológicos principales, a través de un rango altitudinal de 540 a 2030 msnm. Recomendaciones para la futura conservación y manejo de esta trucha y de sus habitat son aquí establecidas.

The San Pedro Mártir rainbow trout, Oncorhynchus mykiss nelsoni (Evermann, 1908), also called Baja trout or Nelson's trout, is endemic to the western slope of the Sierra San Pedro Mártir (SSPM), Baja California, México (Miller 1950; MacCrimmon 1971; Smith 1984; Ruiz-Campos 1993). Its conservation status is categorized as "special concern" (Williams et al. 1989) or "rare" (Secretaría de Desarrollo Social 1994) due to its restricted distribution and low abundance. Both statuses were based mainly on old collecting records in the type locality of Río Santo Domingo [=Río San Ramón or Arroyo San Antonio de Murillos] near Rancho San Antonio (cf., Evermann 1908; Snyder 1926; Needham 1938, 1955; Needham and Gard 1959), and strengthened by more recent observations of potential threats to its habitat by changes in land use practices (increased livestock grazing, logging, etc.).

The first record of this trout was based on four specimens collected by E. Heller in June 1902 in the Río Santo Domingo near Rancho San Antonio (Meek 1904). Subsequently, a second collection of nine specimens from the same locality was made on July 30, 1905 by E. W. Nelson (Nelson 1921). These specimens were given to Dr. B. W. Evermann, who described them as a new species, Salmo nelsoni (Evermann 1908). In the same locality C. C. Lamb and A. E. Borell collected approximately 150 trout on April 24-27, 1925. Snyder (1926) concluded that Nelson's trout closely resembled the coastal rainbow trout Salmo irideus (=Oncorhynchus mykiss irideus). The peculiar traits of Nelson's trout such as the wild and non-migratory nature, plus its temperature tolerance, encouraged P. R. Needham and collaborators to make three collecting trips to Rancho San Antonio between 1936 and 1938 in order to obtain a trout brood stock for hatchery culture and for planting in California and Oregon waters (Needham 1938, 1955; Needham and Gard 1959). During the first trip (May 17, 1936) 30 trout were caught and preserved for study. On the second trip (May 23, 1937) 50 yearlings were captured and transported alive to the Forest Home State Fish Hatchery near Redlands, California. Needham's final collecting trip was made on May 14, 1938 and yielded 325 fingerlings ranging from two to three inches in total length (TL). These fish were sent to the U.S. Fisheries Station at Clackamas, Oregon. However, both introductions failed. The first failure occurred in California in March 1938 when a torrent of water, rocks, and debris wiped out the entire hatchery and its ponds. The second happened in Oregon in 1940 when about forty trout between 254 and 356 mm TL died due to problems in the water supply to the pond where they were held (Needham 1955).

The original natural distribution of *O. m. nelsoni* was a 24 km section of the Río Santo Domingo from above Rancho San Antonio to the base of a high waterfall that blocks upstream migration (Evermann 1908; Nelson 1921; Snyder 1926; Needham 1938; Smith 1991). In addition, Needham (1938) reported the occurrence of this trout in the Arroyo La Zanja (not Arroyo Santa Cruz as was originally reported), a small tributary of the Río Santo Domingo near Rancho San Antonio.

The ancestor of this trout was probably an anadromous coastal rainbow trout (steelhead), coming from Southern California coastal streams, which passed southward through the sea from stream to stream as far as the Río Santo Domingo during a period when climatic conditions were favorable (Evermann 1908; Snyder 1926; Needham 1938; Hubbs 1946; Smith 1991). The trout of the Río Santo Domingo have presumably been isolated from contact with other trout of the rainbow series for a long time, perhaps as much as 10,000 years (Dr. Robert R. Miller's letter dated on September 17, 1977, addressed to Mr. Carlos Yruretagoyena). In an electrophoretic study, Berg (1987) found that Nelson's trout possess a unique allele of creatine kinase, Ck-2 (115), which is not found in other trout of the coastal rainbow series. In addition, Nelson's trout has a strong genetic affinity to the coastal rainbow trout from Southern California.

Several transplants of Nelson's trout into other streams on the western slope of the SSPM have been reported: La Misión (=San Pedro Mártir), La Grulla, La Zanja, El Potrero, and San Rafael (Charles E. Utt's letter dated June 15, 1945, addressed to Dr. Carl L. Hubbs). However, the establishment of trout in all of these localities had not been confirmed before the current study.

This paper evaluates the current distribution and conservation status of O. m.

nelsoni on the western slopes of SSPM. Research was conducted during 1987 to 1994 in order to obtain information for its future conservation and management.

Study Area

Geology.—The SSPM is the most elevated of several batholithic terrains that comprise the Peninsular Ranges of southern California and Baja California. The Picacho del Diablo is the highest peak in the SSPM (ca. 3095 m above sea level). The range is bounded on the east by the great escarpment of the SSPM fault and by the strike-slip Agua Blanca fault to the north (O'Connor and Chase 1989). The summit plateau slopes to the south and west, and the tilted surfaces are broken by one or two faults associated with approximately 1000 m of relief (Woodford and Harris 1938). The geologic formations of the SSPM are similar to the Sierra Nevada of the United States, with outcrop areas composed of Mesozoic batholithic rocks having metasedimentary wall rocks, and igneous rocks primarily constituted by tonalites and granodiorites (Gastil et al. 1975).

Hydrology. — Three main river systems drain the SSPM: Río San Rafael to the northwest and the ríos San Telmo and Santo Domingo to the southwest (Yruretagoyena-Ugalde 1992). The annual discharge of the Río Santo Domingo during dry years between 1950 and 1977 did not exceed 10 million m³/y, but in the period between 1978 and 1985 it increased to 180 million m³/y (Secretaría de Agricultura y Recursos Hidraúlicos 1983). The streams of the SSPM have perennial flows in their headwaters but are intermittent in their middle and lower courses during extremely dry conditions (Tamayo and West 1964). The mouths of all these streams are blocked from the ocean by the formation of sandbars, except during extreme flooding events after storms (Tamayo 1962).

Riparian vegetation.—Three zones of vegetation are found along streams in the SSPM, which are similar to those described for the coastal streams of Southern California (Faber et al. 1989). First is the active zone, which is inundated during winter rains and has a variable and unstable morphology. Arroyo Willow (Salix lasiolepis), Red Willow (S. laevigata) and Fremont Cottonwood (Populus fremontii) are representative. Second is the border zone, that is less subject to disruption but has a reliable water supply. This zone is occupied by larger trees of willow, cottonwood, and Western Sycamore (Platanus racemosa). Finally is the outer zone, which is occasionally affected by flooding events and is occupied by Coast Live Oak (Quercus agrifolia) and Western Sycamore.

Aquatic macrophytes are uncommon in the streams of the SSPM (Delgadillo-Rodríguez 1992) but may be found in some large deep pools. Emergent plants such as Southern Cattail (*Typha domingensis*) and Water Cress (*Rorippa nasturtium-aquaticum*); rooted floating plants (e.g., Floating-leaved Pondweed, *Potamogeton natans*); free floating plants such as duckweeds (*Lemna gibba* and *L. trisulca*); and submerged plants (*Berula erecta, Ceratophyllum demersum, Ranunculus aquatilus*, and *R. hydrocharoides*) are typical.

Methods

Forty-nine collecting trips were carried out to various localities on the western slopes of the Sierra San Pedro Mártir (Fig. 1) from January 1987 to March 1994. Special attention was given to those localities where trout had been previously recorded or transplanted. The number of collecting trips to each locality, indicated

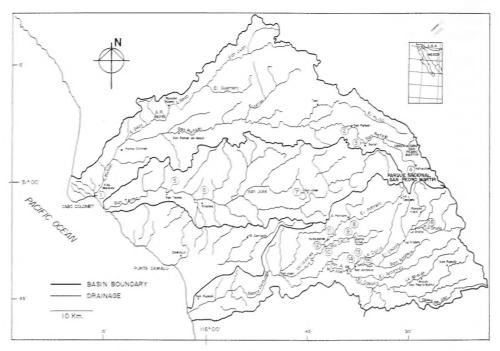


Fig. 1. Location of collecting stations in the Sierra San Pedro Mártir, Baja California, México. Exact locations and elevations of stations are given in Appendix 1.

in parentheses, was dependent on its accessibility: Arroyo San Rafael between Rancho Mike's Sky and Rancho Garet (27); Arroyo San Rafael at its mouth (1); Arroyo San Telmo between San Telmo and Rancho San José (1); Arroyo El Potrero at Rancho El Potrero (2); Arroyo Santa Cruz at Rancho Santa Cruz (3); Arroyo Santa Cruz at its confluence with Arroyo Valladares (2); Arroyo La Grulla at La Grulla meadow (4); Arroyo San Antonio de Murillos at Rancho San Antonio (3); Arroyo La Zanja at its confluence with Arroyo San Antonio (3); Arroyo Vallecitos at Vallecitos meadow (1); and Arroyo Valladares between the Rancho [Viejo] Valladares and the Rancho [Nuevo] Valladares (2).

Place names and geographic features varied among available maps. We used 1:50,000 topographic maps published by the Comisión de Estudios del Territorio Nacional (CETENAL) as the authority. Where a particular physical feature or locality received other names in the literature we provide the equivalent.

Trout were collected using AC electrofishing equipment (120 V) along 200 m stream sections. At remote localities with difficult access (e.g., arroyos La Grulla, La Zanja, and San Antonio de Murillos), trout were captured by hook and line and dip nets. Trout were measured in the field (standard length [SL] in millimeters) and weighed to the nearest gram. Some specimens were preserved in 10% formalin buffered with sodium borate. Five scales per specimen were selected for age determination (Ruiz-Campos 1993). Most of the trout preserved were utilized for life history and population ecology analyses (Ruiz-Campos 1993), and other specimens were deposited in the Colección de Vertebrados (Sección Peces) at the Facultad de Ciencias, Universidad Autónoma de Baja California, Ensenada.

To describe stream morphology and hydrology, we selected three sampling points along each stream surveyed, including all available habitat types such as pools, riffles, etc. These sampling points were marked as reference positions for future measurements. The stream cross-section measurements were made along a line perpendicular to the streambank, considering the following features: (1) stream width, (2) velocity of water, measured with a current meter (Swoffer model 2100), and (3) stream depth (Duff and Cooper 1978; Platts et al. 1983). Both velocity and depth were measured at 50 cm-intervals.

Discharge was calculated in m^3/s for each stream cross-section using the following equation (Hynes 1970): $Q = [W \times D \times V]$ (0.9), where: Q = rate of discharge; W = average stream width; D = average stream depth; V = average water velocity; and 0.9 is the constant for friction on sandy bottoms.

Historical data on trout length reported in total length (TL) were transformed to SL by dividing TL by 1.145 (Carlander 1969).

Results and Discussion

Oncorhynchus mykiss nelsoni is now distributed in two main drainages: Río Santo Domingo (arroyos San Antonio de Murillos, La Zanja, El Potrero, La Grulla, and La Misión) and Río San Rafael (Arroyo San Rafael), within an altitude range of 540 m (Rancho San Antonio) to 2030 m (La Grulla) (Fig. 1).

Río Santo Domingo Drainage

The Río Santo Domingo drainage has seven major tributaries (arroyos La Grulla, El Potrero, Valladares, Santa Cruz, La Zanja, La Misión and San Antonio; Fig. 1). The Río Santo Domingo is called various names through its course towards the Pacific coast. At its headwater it is known as the Arroyo San Antonio, but after its junction with the Arroyo La Zanja it is called Arroyo San Antonio de Murillos. Finally, it is called the Río Santo Domingo after its confluence with Arroyo Valladares.

Arroyo San Antonio de Murillos.—This second order stream of the Río Santo Domingo is the type locality for O. m. nelsoni. The sampled section of this stream was from its confluence with Arroyo La Zanja to in front of the Rancho San Antonio (Fig. 2A).

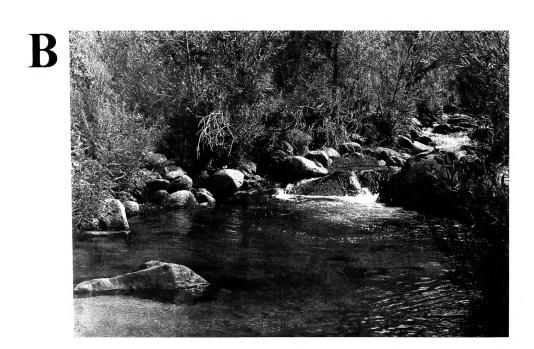
Historical records: Arroyo San Antonio de Murillos was first visited by E. Heller (June 1902) and later by E. W. Nelson (July 30, 1905), who both made collections of trout. During Nelson's visit in 1905, stream characteristics included a mean width of 3.0 m, a maximum depth of 25.4 cm in the middle of the channel, and a current of 2.68 m/s. Subsequent collections in this same locality were made by P. R. Needham and collaborators on May 17, 1936, May 23, 1937 (Needham 1938), and May 14, 1938 (Needham 1955; Needham and Gard 1959). In May of 1936, young-of-the-year (YOY or age-0) from 27.7–66.6 mm, were abundant. However, specimens between 88.7 and 155.3 mm were relatively scarce. Stream

Fig. 2. (A) Arroyo San Antonio de Murillos ca. Rancho San Antonio. (B) Arroyo La Zanja ca. confluence with the Arroyo San Antonio.

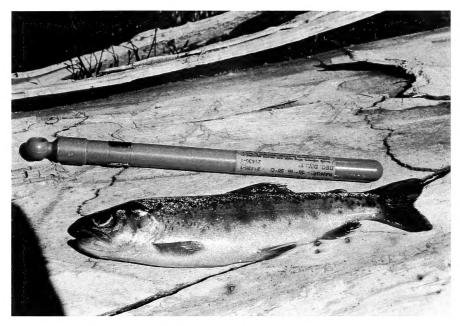
Fig. 3. Specimens of *Oncorhynchus mykiss nelsoni*. (A) From Arroyo San Antonio de Murillos (105 mm SL). (B) From Arroyo La Grulla (181 mm SL).

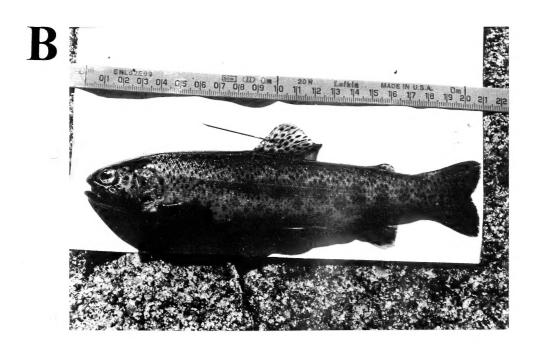


















width was 3.6 to 4.5 m with a discharge of 0.113 m³/s. In May of 1937, only two YOY were observed and individuals 110.9 to 199.6 mm were fairly common. Discharge was 0.170 m³/s. Low densities of trout were noted in this same locality during 1904 (Nelson 1921) and in the winter of 1936–1937 (Needham 1938). Both authors speculated that this was caused by severe floods that strongly alter stream morphology and eliminate most riparian vegetation. Almost a half century later (October 28, 1983), E. P. Pister collected 19 trout 115 to 205 mm by hook and line. At that time, the stream had large, deep pools and heavy riparian vegetation.

Current status: We visited and sampled this locality again on April 26–27, 1991, June 29–30, 1991, and June 17–18, 1992. Predominant riparian vegetation is Arroyo Willow, Coast Live Oak, Western Sycamore, Fremont Cottonwood, and Mule Fat (*Baccharis salicifolia*). Vegetative cover was scarce and discontinuous, probably resulting from high erosion and siltation caused by flooding during the winter of 1991–1992. Morphological and flow characteristics of the stream exhibited little variation among the sampling dates. Ranges registered were as follows: discharge, 0.159 to 0.171 m³/s; width, 4.86 to 5.82 m; stream velocity, 0.337 to 0.380 m/s; and depth, 8.0 to 11.6 cm. In June 1991, eleven trout 85.9 to 152 mm (Fig. 3A) were captured during 3 hours of intensive sampling, mostly YOY (N = 5). During June 1992, 10 YOY (46 to 60 mm) were captured, and only one adult specimen was seen in this locality.

Arroyo La Zanja.—The site surveyed (Fig. 2B) was 200 m upstream from the confluence with the Arroyo San Antonio.

Historical records: Arroyo La Zanja was stocked with trout from Arroyo La Misión in 1935 and 1936 by E. C. Utt. The number of trout stocked in 1935 is unknown. However, approximately 16 were stocked in 1936 in a pool of the Arroyo La Zanja near "Young Ditch" (a mining ditch now abandoned).

Needham (1938) confused this creek with the Arroyo Santa Cruz, a tributary of the Arroyo Valladares near Rancho Valladares. His collections were taken from Arroyo La Zanja because at that time fish were scarce in Arroyo San Antonio de Murillos due to altered morphology after a flooding event. Discharge in the Arroyo La Zanja was ca. 0.037 m³/s (May 17, 1936) and 0.042 m³/s (May 23, 1937).

Current status: Arroyo La Zanja was sampled on June 18, 1992, at which time the collecting site consisted of many small pools and long riffles averaging 2.5 m in width and 25 cm in depth. Moderate riparian vegetative cover was represented primarily by Arroyo Willow and Mule Fat. Four YOY (55 to 75 mm) were collected along a 100 m stream transect. No adult trout were captured or seen.

Arroyo El Potrero.—This stream (Fig. 4A) represents the middle tributary of the Arroyo Valladares with its confluence near Rancho El Potrero.

Historical records: Trout brought from the Arroyo La Misión were stocked into Arroyo El Potrero by C. E. Utt during 1937 and 1941. There is no previous information on habitat characteristics for this locality.

Current status: Arroyo El Potrero was visited three times in 1989, and habitat was evaluated, on March 11, June 17, and November 26; but only twice were

Fig. 4. (A) Arroyo El Potrero ca. Rancho El Potrero. (B) Arroyo La Grulla at La Grulla meadow.

trout collected. In March, we collected only one trout, a 3-year-old adult (166 mm). However, in June, six specimens 53.9 to 145.1 mm (age, 0 to 2) were captured. Riparian vegetation was Arroyo Willow, Mule Fat, and Coast Live Oak. Morphology and stream flow varied as follows during the three different dates: width, 1.88 to 4.11 m; depth, 7 to 23 cm; velocity, 0.16 to 0.32 m/s; and flow, 0.050 to 0.142 m³/s.

Arroyo Valladares.—The segment surveyed was from Rancho [Nuevo] Valladares to Rancho [Viejo] Valladares. This stream is a tributary of the Río Santo Domingo, with its confluence near Rancho San Juan.

Historical records: No historical information was discovered regarding the occurrence or stocking of trout in this locality.

Current status: An electrofishing survey was conducted on June 19, 1992 and again on March 11, 1994 to investigate the presence of trout in the stream. Three 100 m transects were made between the confluence of the Arroyo Santa Cruz and the Rancho [Viejo] Valladares (abandoned mines). No trout were seen or collected during sampling efforts. Morphology and discharge of the stream during June 1992 and March 1994, registered the following average values, respectively: width (4.52 and 10.06 m), depth (31.6 and 10.2 cm), velocity (0.26 and 0.50 m/s), and discharge (0.341 and 0.452 m³/s). The site surveyed exhibited only sparse cover by riparian vegetation (Narrow-leaved Willow [Salix exigua], Mule Fat, Western Sycamore, and Broom Baccharis [Baccharis sarothroides]). Also noted was the absence of large and deep pools due to extensive sand accumulation. The stream's physical features might explain the absence of trout in this locality.

Arroyo Santa Cruz.—The site surveyed was from the Rancho Santa Cruz to the confluence with Arroyo Valladares near Rancho [Nuevo] Valladares.

Historical records: There are no historical records concerning the occurrence or stocking of trout in this stream. It should be noted that this arroyo was confused with Arroyo La Zanja by Needham (1938).

Current status: Three sampling trips were made in 1989 to the stream near Rancho Santa Cruz (March 12, June 18, and November 26). No trout were collected or seen during electrofishing sampling along the stream. During all three visits, the stream was very narrow and shallow (width, 2.56 to 3.15 m; depth, 4.5 to 5.8 cm). A low flow was also observed (velocity, 0.05 to 0.25 m/s; and discharge, 0.007 to 0.038 m³/s). Riparian vegetation was scattered and in low density and was represented by Arroyo Willow and Coast Live Oak. The stream was judged to have a low potential for trout habitat due to the absence of pools and the sparse cover by riparian vegetation. On March 11, 1994, we made a 100 m stream transect near the confluence with Arroyo Valladares. No trout were collected or seen during the sampling. Average stream characteristics in that locality were: width, 3.25 m; depth, 9.73 cm; velocity, 0.217 m/s; and discharge, 0.054 m³/s.

Arroyo La Grulla (the main stream flowing in La Grulla meadow; Fig. 4B).— This stream is the most extreme headwater for the Río Santo Domingo. In La Grulla meadow there are two small ponds whose outlets discharge into a small stream that flows to Arroyo La Grulla.

Historical records: During 1935 and 1936, C. E. Utt stocked trout from Arroyo La Misión into the Arroyo La Grulla. The number of trout stocked in 1935 is unknown. However, approximately 30 specimens were stocked in 1936. On June 18 and 19, 1984, we captured 32 specimens (65 to 210 mm) in the Arroyo La

Grulla near its confluence with the small stream from the meadow. Two additional trout (215 and 232 mm) were taken from the small stream itself.

This meadow has been used since the time of the missionaries for cattle grazing during the spring and summer (Nelson 1921; Meling 1991). In July 1905, E. W. Nelson visited the meadow and noted that the borders of the ponds and all of the valley bottom had been heavily grazed and trampled.

Current status: This locality was surveyed three times in 1990 (March 23, August 11, and September 30) and one time in 1992 (October 24) in areas where trout had been previously recorded. The locality of Arroyo La Grulla near its confluence with the small stream from the meadow was the only site with trout (Fig. 3B). On March 1990, seven specimens were captured (111 to 181 mm; age, 1 to 3). During the August 1990 trip, 30 specimens were collected (48.8 to 163.0 mm), mostly age-1 fish. In September 1990, 11 trout were collected, ranging from 60.4 to 143.5 mm (age, 0 to 2). Four adult trout and several YOY were seen in October 1992. The average morphology and flow characteristics of the stream were variable among sampling dates: width, 2.08 (March) to 8.90 m (October); depth, 17 (September) to 31 cm (March); velocity, 0.055 (October) to 0.170 m/s (March); and flow, 0.071 (September) to 0.203 m³/s (August). Small pools with abundant aquatic macrophytes such as P. natans, C. demersum, and R. nasturtium-aquaticum were common. Bank vegetation was mainly rushes (Eleocharis sp.), which provided little cover to the stream. Most cover was supplied by aquatic macrophytes and in a lesser proportion by Jeffrey Pine (*Pinus jeffreyi*). High livestock grazing activity was noted in the meadow, principally along riparian vegetation, with accompanying ground alteration due to trampling.

Arroyo La Misión (near Misión San Pedro Mártir). — This stream is also known as the Arroyo San Pedro Mártir or El Horno. It is a tributary of the Arroyo San Antonio.

Historical records: C. E. Utt stocked the Arroyo La Misión with trout from Arroyo San Antonio de Murillos in the summer of 1929. This stream is the first site where Nelson's trout were introduced. Subsequent visits by Utt between 1934 and 1938, confirmed the establishment of trout in this locality.

Unfortunately, it was not possible to visit this locality during our investigations. However, in the last five years it has been repeatedly visited by Carlos Lazcano, a geologist/explorer of the SSPM. He collected various specimens of trout, mainly adults, by hook and line (Carlos Lazcano, pers. comm.).

Río San Rafael Drainage

The Río San Rafael basin is the second most important hydrologic system in the Sierra San Pedro Mártir. This river drains into the Pacific Ocean near Bahía Colonet [Colnett]. Major tributaries are San Rafael, La Fresa, Vallecitos and Agua Zarca.

Arroyo San Rafael.—The site studied is located between Rancho Garet also known as Gárate or Las Truchas (Fig. 5A) and Rancho Mike's Sky (Fig. 5B). Most sampling for trout was conducted at this locality due to its easy access and high abundance of fish.

Historical status: The Arroyo San Rafael was stocked twice with trout from Arroyo La Zanja by C. E. Utt. The first stocking was in 1938 when 16 trout were released into the stream about a mile below the intake of the Johnston ditch (a

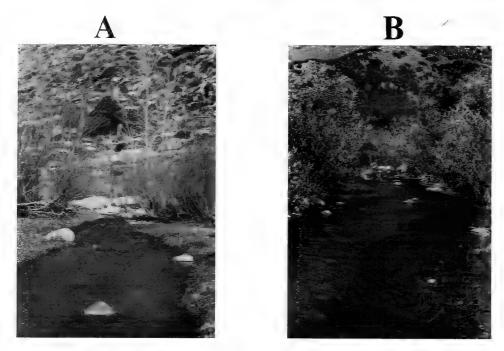


Fig. 5. (A) Arroyo San Rafael at Rancho Garet. (B) Arroyo San Rafael at Rancho Mike's Sky.

hydraulic mining venture). The second trout stocking occurred in the summer of 1939, with 14 trout being released at Rancho Garet.

Also at Arroyo San Rafael, Ruiz-Campos (1989) determined natural repopulation rates in 100 m stream segments through repeated removal by electrofishing. These results showed high rates of recolonization, mainly by YOY, reaching total recuperation in less than 10 weeks. Ruiz-Campos and Cota-Serrano (1992) described the seasonal diet and feeding ecology of the subspecies at this locality, which indicated a basically insectivorous diet and a specialized feeding strategy with regard to type and size of prey consumed.

Current status: During this investigation, 27 trout collecting trips were made to the Arroyo San Rafael between January 1987 and January 1994 (cf., Appendix 2 for sampling dates) with the main objectives of determining population density and structure. Observations on life history and habitat requirements have been recently described by Ruiz-Campos (1993). The average density of trout in 200 m sections along the stream through a seven year period is shown in Fig. 6. Trout density was relatively stable from January 1987 to August 1989 (ranging from 20 to 98 trout/200 m stream; mean = 48.8; Fig. 6A). However, between August 1989 and March 1993 trout density dropped to 0 to 14 trout/200 m stream (mean = 4.8; Fig. 6B), likely a consequence of the high mortality caused by a forest fire in August 1989. As a result of this event, the morphology of the stream was strongly modified due to accumulation of ash and sand, particularly in the large and deep pools (Fig. 7A). A gradual recovery in trout density was recorded from July 1993 to January 1994 (26 and 86 trout/200 m stream, respectively; Fig. 6B). A similar case of trout mortality resulting from delayed effects of fire by acute exposure to

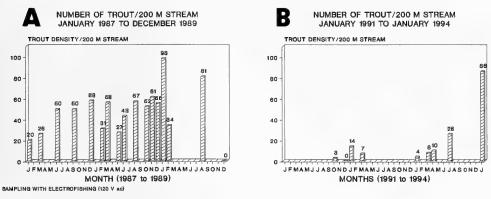


Fig. 6. Trout density per 200 m stream section in the Arroyo San Rafael, Sierra San Pedro Mártir, Baja California, México, from January 1987 to January 1994.

suspended sediment was observed in two streams of northwestern Wyoming (Bozek and Young 1994).

The length of the trout collected ranged form 34.2 to 240 mm (age, 0 to 4). Specimens <124 mm were the most abundant.

The stream at the locality of Rancho Mike's Sky is characterized by many large, deep (up to 2.0 m) pools alternating with riffle habitat. Dense riparian cover is provided mainly by Arroyo Willow, Fremont Cottonwood, and Western Sycamore. From October 1988 to December 1989, the average stream depth and discharge was variable, registering the highest values in winter (43.9 cm deep and a discharge of 2.204 m³/s) and the lowest in summer (28.2 cm deep and a discharge of 0.639 m³/s). In January 1993, the highest rainfall in the last 30 years was registered in the mediterranean region of Baja California, causing heavy flooding and strongly modifying stream morphologies (Fig. 7B). Trout density in the Arroyo San Rafael during that month was low (4 trout/200 m stream), increasing after one year to as high as 86 trout/200 m stream (Fig. 6B).

On March 12–13, 1994, the lower part of the Arroyo San Rafael was visually surveyed in an area 500 m upstream from its mouth to verify the possible occurrence of trout. None were observed in this segment. Unsuitable habitat conditions were noted, such as high siltation in the stream channel, average depth less than 30 cm, and lack of arboreal riparian vegetation.

Arroyo Vallecitos.—This stream is a tributary of the Arroyo San Rafael and reflects the usual highly fluctuating runoff patterns resulting from major discharges during the winter rainy season.

No records of occurrence or trout introduction at this locality were discovered in the literature.

On March 20, 1992, we surveyed a 100 m segment of the Arroyo Vallecitos. No trout were collected or seen. The average morphology and flow of the stream in the segment surveyed was as follows: 3.81 m wide, 12.0 cm deep, and a flow rate of 0.259 m³/s.

Another stream surveyed in the SSPM was the Arroyo San Telmo in three different localities: Rancho Meling [=San José], Ejido Sinaloa, and San Telmo.

No historical information was found concerning the presence or stocking of trout in this stream.



B



During the investigation of these sites no trout were seen, possibly due to poor habitat quality (e.g., low and variable flow, sparse cover, and heavy deposition of sand). Local residents reported that they have never seen or heard of trout in the stream.

Recommendations on Conservation and Management

The current conservation status of the San Pedro Mártir rainbow trout may be judged as stable. However, it should be noted that this is a consequence of the remoteness and inaccessibility of their distribution sites and not a result of the application of a conservation or management plan. These sites should be considered fragile ecosystems that may be endangered by anthropogenic activities. Therefore, it is fundamental that both in the short and long term, an integral ecosystem conservation and management plan should be established.

Some recommendations for future conservation and management of this subspecies, derived from the present study as well as from those recently described by Ruiz-Campos (1993), are as follows: (1) Because the type locality (Rancho San Antonio) in the Río Santo Domingo [=Arroyo San Antonio de Murillos] is situated outside the limits of the Parque Nacional de la Sierra San Pedro Mártir, it should be preserved as an area of protection for the endemic germplasm of this rainbow trout subspecies; (2) Strictly prohibit the introduction of exotic and non-native fishes or any other life form to the streams of the SSPM, which might harmfully interact with the endemic trout. The introduction of exotic and non-native fishes, mainly of congeneric or conspecific taxa, has caused numerous negative effects on native trout populations of the southwestern United States, such as competitive exclusion, hybridization, loss of genetic diversity, and decline of the native populations (Rinne and Minckley 1985; Rinne 1988a; Berg and Gall 1988; Leary 1991; Behnke 1992; Dowling and Childs 1992); (3) Regulated sport fishing of this trout may be practiced in those sites where it has traditionally occurred (e.g., San Rafael and La Grulla arroyos). It is suggested that the trout catch be limited to 160 mm SL (183 mm TL) or larger. This will permit individuals less than that size to reach sexual maturity with consequent spawning (Ruiz-Campos 1993); (4) Prohibit the taking of trout during its spawning period, which occurs between January and March (Ruiz-Campos 1993); and (5) Develop a habitat management plan that includes the conservation of both aquatic and riparian ecosystems. Regulations should be implemented to prevent alteration of these habitats by cattle grazing and other anthropogenic uses such as dam construction, logging and water diversion (Rinne 1988b; Marcus et al. 1990a, b; Contor and Platts 1991).

The future of *Oncorhynchus mykiss nelsoni* and its habitats will depend on careful planning and application of a holistic conservation and management program for the watersheds of the Sierra San Pedro Mártir. Such steps will ensure the continuity of this endemic subspecies which is a biological inheritance and an integral part of our own natural history.

Fig. 7. Modification of the morphology of the Arroyo San Rafael. (A) Siltation by ashes and sand after a forest fire in August 1989. (B) Erosion of stream channel and elimination of riparian vegetation cover by heavy flooding events in January 1993.

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Appendix 1. Collecting stations in the Sierra San Pedro Mártir, Baja California, México.

Station number	Name and coordinates	Elevation (m)	Sub- strate	Primary vegeta- tion*
1	Río San Rafael (lower part) 30°58′10″N, 116°16′15″W	<5	S	CSS
2	Arroyo San Rafael at Rancho Mike's Sky 31°06'35"N, 115°38'05"W	1219	S-G	CHA
3	Arroyo San Rafael at Rancho Garet 31°04′25″N, 115°36′05″W	1350	S-G	CHA
4	Arroyo Vallecitos at Vallecitos meadow 31°01'20"N, 115°28'15"W	2430	S-G	CON
5	Arroyo San Telmo at San Telmo town 30°58′25″N, 116°05′30″W	120	S	CSS
6	Arroyo San Telmo at Ejido Sinaloa 30°57′15″N, 115°59′40″W	130	S	CSS
7	Arroyo San Telmo [=San José] at Rancho San José 30°57'30"N, 115°44'30"W	640	S	CSS
8	Arroyo El Potrero at Rancho El Potrero 30°55'00"N, 115°38'45"W	950	S-G	CHA
9	Arroyo Santa Cruz at Rancho Santa Cruz 30°52'30"N, 115°37'50"W	860	S-G	CHA
10	Arroyo Santa Cruz (lower part) 30°51'40"N, 115°42'15"W	690	G	CHA
11	Arroyo Valladares at Rancho [Viejo] Valladares 30°52'15"N, 115°41'35"W	700	S	CHA
12	Arroyo Valladares at Rancho [Nuevo] Valladares 30°51'40"N, 115°42'15"W	690	S	CHA
13	Arroyo La Zanja ca. confluence with A. San Antonio 30°49′10″N, 115°37′35″W	565	S-G	CSS
14	Arroyo San Antonio de Murillos at R. San Antonio 30°49'05"N, 115°37'50"W	540	S-G	CSS
15	Arroyo San Antonio ca. confluence with A. La Zanja 30°49'05"N, 115°37'30"W	565	S-G	CSS
16	Arroyo La Grulla at La Grulla meadow 30°53'30"N, 115°29'00"W	2030	S-G	CON

^{*} Adjacent to riparian vegetation. Key to vegetation: CON = Coniferous forest, CSS = Coastal sage scrub, CHA = Chaparral.

Key to substrate: S = Sand, G = Gravel, S-G = Sand-gravel.

Appendix 2

Sampling dates in Arroyo San Rafael, Sierra San Pedro Mártir, Baja California, México. 1987: January 27, March 22, June 9, September 17–18 and December 5–6. 1988: February 11–12, March 26–27, May 7–8, June 29, August 20, October 5, November 5 and December 11. 1989: January 21–22, February 19, May 20, August 20 and December 10. 1991: October 3 and December 8. 1992: January 25 and March 18. 1993: January 31, March 6, April 25, and July 29. 1994: January 19.

Large-Scale Migrations of the Painted Lady Butterfly, Vanessa cardui (Lepidoptera: Nymphalidae), in Inyo County, California, during 1991

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Abstract. — Detailed observations on significantly large migrations of Vanessa cardui during 1991 in Inyo County, California, are presented, with special emphasis on their complex behavioral activities. The build up and mass exodus at a population center near Bishop are chronicled and provide insights into why some butterflies migrate. A directional shift from northward to southward migration occurred during the summer. The migration phenomenon in this species appears to be dependent upon larval stress subsequently influencing adult juvenile hormone levels. This behavior likely evolved during the Upper Miocene as an adaptation to avoid seasonally unfavorable arid conditions.

Vanessa cardui (Linnaeus), a regular seasonal migrant, experienced a dramatic population explosion between 1991 and 1993 in western North America, based upon our field observations, reports from various observers, the Lepidopterists' Society Season Summaries, and the Xerces Society's Fourth of July Butterfly Counts. Between 1987 and 1990, its migration activities had been minimal during widespread drought conditions. There was no prior indication that 1991 was destined to become a population explosion year other than its rather high abundance in Santa Cruz County, Arizona, during mid-August of 1990. Years of major V. cardui outbreaks in western North America appear to result from comparatively high winter rainfall in its northern Mexico source area, which in turn are correlated with, or closely follow, years of Pacific warm water intrusions brought on by El Niño and Namias-Sumner effects (Myres 1985). The longest recorded El Niño was present from early 1991 through late 1993 (various Science News and newspaper articles), the same period that produced an unprecedented three successive large migrations.

Background Information

In southern California, a very sparse migration of worn *V. cardui* proceeded northwesterly through Hemet and San Bernardino in mid-February 1991 and went WNW at Chuckwalla Valley in Riverside County in mid-March. In late March numerous individuals were migrating to the NW on the west side of the Salton Sea, with abundant adults basking, nectaring (especially on *Hyptis emoryi* Torr. (Lamiaceae), up to 15–20 per bush), and taking brief, random, non-directional flights near the ground in Anza-Borrego Desert State Park (J. P. Donahue in litt.). In the Apple Valley–Lucerne Valley area in early April they were common,

migrating WNW. Small larvae were in huge numbers on *Pectocarya recurvata* Jtn. and *Cryptantha* (Boraginaceae) in the Clipper Mountains of San Bernardino County, and large numbers of adults were reported from the south-central Mojave Desert in Riverside County, in mid-April. Many adults nectated on *Rhus trilobata* Nutt. ex T. & G. (Anacardiaceae) at Idyllwild, and a heavy migration flew north-westerly in San Gabriel Canyon and between Cajon Pass and Randsburg in late April. Also in late April, adults were common in the Greenhorn Mountains and near Idyllwild, while larvae were abundant on *Cryptantha* and *Salvia columbariae* Benth. (Lamiaceae) near Hemet. In early May in the San Jacinto Mountains, they were common and migrating to the NW, with very large numbers migrating northward at California City in Kern County and large numbers near Tehachapi Pass.

Migration records in Arizona during 1991 included a NW flight of V. cardui in Tucson in late March; in addition, large numbers were seen crossing the highway west of Phoenix in early April. In the spring, it was very common in central Arizona, with large numbers of adults and larvae observed in the Phoenix area over an extended period from mid-March to mid-May, whereas in most years when there is favorable development of desert vegetation, the primary period of activity there is mid-March to early April (K. Roever in litt.). A very wet March plus a cool April helped maintain foodplants much later than normal, such as annual lupine (Lupinus, Fabaceae), various borages, and introduced Malva (Malvaceae). Near Higley in Maricopa County on 24 March, 120-160 individuals/5 min/15 m migrated generally NE, then shifted abruptly to the SW between 12:30 and 1:00 PM (K. Roever in litt.). The reason for the shift in direction was not apparent, but definitely did not correlate with a reversal in wind direction. It migrated northward in early May at Prescott and Chino Valley, Yavapai County, and at Sun City, Maricopa County and migrated west at 300-400/5 min/15 m in Chino Valley on 2-3 April.

In southern Nevada, they first appeared in immense numbers in late April and continued into June. A massive northward migration was observed from Tonopah to Warm Springs in early May. Incredible numbers were widespread in northern Nevada in June and early July, decreasing somewhat later (still large numbers) in July into late August.

In Utah, very large numbers were observed in the Salt Lake City area on 4 May, many migrating northward.

In Colorado, migrating painted ladies were widespread, flying northeasterly in early May. It was the commonest butterfly at Florissant between late June and mid-July but did not migrate. Very large numbers were also reported in New Mexico.

A migration went northeasterly in South Dakota in early April, and there was an abundant spring migration in North Dakota.

Tens of thousands were observed along the Snake River in Baker County, Oregon, in late May, and in the Boise, Canyon, and Franklin Counties, Idaho. The migration was widespread in Oregon.

Migrations reached British Columbia, Alberta, Saskatchewan, and Manitoba in early to mid-May, with the strongest surge in Alberta and Manitoba. Adults were reported in mid-July in Ontario, Quebec, and Labrador. The butterfly was widespread and common during the summer in northeastern United States, as

well as being present in the Great Plains and Midwest. There was only sporadic representation in the Southeast, however.

The 1991 flight directions for spring migrations of V. cardui converge back to probable source areas in northwestern Mexico, with secondary centers in northern Baja California, the southern Mojave Desert, and the extreme northeastern Sonoran Desert. Heavy rains fell in southern Sonora and Sinaloa (approximately 20 in) during December of 1990 and January 1991, probably contributing to their population build ups. In Sinaloa the torrential rains led to flash flood devastation, while at the same time causing dams to burst, rivers to overflow their banks, and extensive crop damage.

J. R. Mori and R. E. Wells (in litt.) report that in April 1991 in Baja California, the desert areas north of a line 80 km S of Cataviña were very green and lush from heavy March rains, and that south of this line to Loreto (26° North latitude), heavy winter rains had produced a high stand of annuals that was rapidly drying out. They noted extremely sparse V. cardui migrants (flying generally northward) all the way down the Baja California peninsula to as far south as Santa Rosalía and San Lucas Bay in mid to late April, but not further south to Puerto Escondido. On 26 April large numbers were seen migrating northward (about 15–20 per minute crossing the highway within sight) 80 km S of Cataviña, with a huge migration flying NNW (hundreds crossing the highway within sight at any given moment) from about 40 km N of Cataviña (heaviest) to San Vicente (thinning out).

In prior years, several source areas for migratory butterflies have been identified for Mexico. In early April of 1949, at a promontory on the shore of Santa María Bay, Baja California Sur, thousands of *V. cardui* were emerging from pupae (Abbott 1951). Many flew south a short distance to the desert cliff edge, then flew back north to the emergence area. Although no migration was observed, they did migrate in California at about the same time that year. In mid-March of 1968, a *V. cardui* migration center was identified by E. S. Ross (in litt.) in Sonora, Mexico, between Hermosillo and Santa Ana. In that year, unusually early and abundant rains occurred in the region, involving a great build up of overcrowded, wandering larvae following host defoliation. The resultant adults simply took off NW in a huge migration, as per numerous records from intermediate points, that ultimately traversed the length of California from mid-March to mid-April, reaching southernmost northern California on 30 March and Medford, Oregon, in early April.

In some years, active populations of *V. cardui* are known to spend the winter in the Sierra Madre Oriental and the Chihuahuan Desert, with NE spring migrations across Texas (C. J. Durden in litt.). The species also occasionally overwinters in southwestern Arizona in December, commonly necataring on *Hyptis emoryi* in the desert southwest of Ajo (K. Roever in litt.).

Methods and Materials

Direction of flight was obtained by stepping into the path of a passing V. cardui and pointing a compass at the retreating butterfly. The number of butterflies involved in a migration was estimated by counting the individuals that crossed a measured line, set at right angles to the direction of flight, during an interval of time. Conversion to number/5 min/15 m provided a standard for comparison, and compass directions were converted to geographic directions in all instances.

All migration directions are expressed as the direction(s) that migrants were flying. Pacific Standard Time was used for dates preceding 7 April and following 27 October, and Pacific Daylight Time was used between those dates. Instar's at each site were estimated by measuring the lengths of a sampling of larvae and comparing these against standard instar lengths given by Hammad and Raafat (1972).

Typical migrators fly in rapid, non-stop, straight lines. When disturbed from rest, they all drift in the same direction, while non-migrators circle or re-land or move off in many directions. There appear to be several types of migration cessation. Either they settle down for the night but will readily drift in a preferred direction when disturbed, or, late in the season they show a declining tendency to migrate and spend more time nectaring on flowers, with little inclination to fly in a straight line when disturbed.

Inyo County Spring Migrations

The senior author closely monitored V. cardui activities in Inyo County during 1991 (see Figure 1). They were first observed on 23 February at Willow Creek, Saline Valley, 2300 ft (two, worn). They were first noticed at Big Pine, Owens Valley, 4000 ft, during 12 March-3 April in small numbers, nectaring at apricot blossoms or circling and alighting on the ground, but did not show a tendency to migrate. These were mostly small to medium-sized individuals with pale or faded coloration and powdery-white ventral surfaces, though some were larger with fairly bright colors. Possibly these had overwintered, since overwintering adults have been observed in Saline Valley from mid-December through February in 1977-1978, though a northern Mexico source cannot be discounted. During 24 February-11 March at Big Pine, none was seen at these blossoms, when the weather was often cool, cloudy, and breezy with few clear, sunny days. In early March, after a winter drought, it rained 3.8 in at Big Pine over a 2-3 day period and Bishop received 2.9 in of rain in March which later produced a sizable crop of Amsinckia in the Owens Valley. On 29-30 March, near Ridgecrest, numerous V. cardui were flying in all directions or circling about but were not migrating. Occasional migrants were seen at or near Big Pine during 3-23 April. On 18-19 April in Eureka Valley, occasional V. cardui were migrating in various directions (mainly NW and SW), circling about or landing during overcast weather.

The first appreciable wave of migrants entered the Owens Valley on 24 April and continued at about the same densities in Owens and Deep Spring Valleys to 2 May (4–19/5 min/15 m, with a surge of 48/5 min/15 m at midday flying NW–WNW on 24 April at Bishop). On 4–6 May the densities dramatically increased in the Owens Valley. On 4 May at 6400–7100 ft near Lone Pine, there were 184–230/5 min/15 m, flying N–NNE. On 5 May comparable numbers migrated across the northern Inyo Mountains (no counts made). On 6 May at 7500–9000 ft in the southern White Mountains, there were 98–211/5 min/15 m flying NNW–NNE, with lesser numbers below 7000 ft (22–82/5 min/15 m). In Fish Lake Valley in early May, on a fair day without much wind, a large migration went approximately N (S. Sawka pers. comm.). From 7–22 May, numbers of migrants considerably declined in the Big Pine and Bishop regions to 4–30/5 min/15 m. At Eureka Valley in mid-May, V. cardui first instar larvae were numerous on Baileya (Asteraceae) leaves. Migrating adults flew NNW there on 16 May at 3/5 min/15

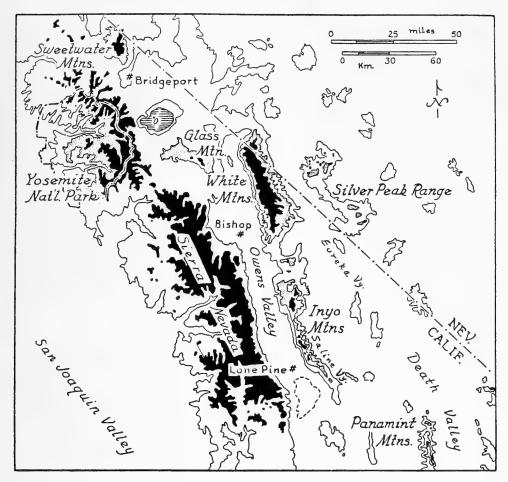


Fig. 1. Map of Inyo County and surrounding regions (modified from Johnson and Cicero 1986, Fig. 1).

m. On 17 May, they flew NNE at 6/5 min/15 m and also nectared on flowers of *Baileya*, *Dalea* (Fabaceae), *Encelia* (Asteraceae), and *Larrea* (Zygophyllaceae).

On 23 May at Santa Rita Flat, 6400–7200 ft, Inyo Mountains, migration again increased (38–116/5 min/15 m), flying N–NNW, although it was sparse in the Owens Valley (1–8/5 min/15 m), flying mostly NNE. In Eureka Valley on 25 May, many *V. cardui* were seen on flowers along with an occasional migrant, and occasional ones migrated in the Inyo Mountains. On 26 May at 9000–9200 ft in the White Mountains, the rate was 4–10/5 min/15 m, flying N–NNW. On 28–31 May, migration was extremely sparse in the Owens Valley, but on 2 June near Bishop, it suddenly increased to 8–36/5 min/15 m, flying primarily NNW. The latter flew from the direction of southern Owens Valley. Concurrently, near Barrel Springs (Mazourka Canyon, Inyo Mountains), there were numerous migrants at 5:15 PM under windy, cloudy conditions, many up to 50 ft high. The rate at 5:30 PM was 51–101/5 min/15 m, flying NW–NNW, when very large numbers were also on the many flowers of *Dalea* and *Encelia*. When disturbed by car along the

road at 6:30 PM, they rose up as a cloud and flew approximately N or NW in immense numbers (about 3427/5 min/15 m, a computed rate from one 13/7 sec/8 ft measurement), then resettled on the ground, on Artemisia (Asteraceae) and other shrubs, and on pinyon pines (even up around the 6-9 m high tops of the larger trees). By that time they had apparently settled for the night even though it was still daylight. On 3 June at Badger Flat, 9000 ft, Inyo Mountains, the rate was 20-43/5 min/15 m (7:30-8:05 AM), mainly NNW, yet almost ceased after 8:20 AM (2-4/5 min/15 m). At noon near Mazourka Canyon, many nectaring on Dalea and Encelia flew NW-NNW when disturbed. On 4 June at 4000-6000 ft in the White Mountains, many were migrating E-ESE, occasionally up to 8000 ft, with large numbers that showed no inclination to migrate at 5000 ft on flowers of Dalea and Encelia. From 12-21 June, migration was sparse in the Owens Valley and nearly ceased after that. On 22 June at Cedar Flat, 7300 ft, near Westgard Pass, rates increased (9-71/5 min/15 m), flying NNW-NNE during unstable weather. These flew 0.2-1 m above ground level. In the afternoon, there was a greater tendency for them to alight on flowers, bushes, trees, and on the ground. Many interactions were observed all day, such as one on the ground would fly up to a passing individual or two flying different directions would interact when they passed near one another.

Bishop Migration

Ovipositions during the 4-6 May migration most likely produced a 5-11 June mass exodus at the Bishop site since Egyptian V. cardui in early May averages 36 days from egg to adult emergence (Hammad and Raafat 1972), and the peak in migration from the south and the peak in local emergence corresponded with this time-schedule. Since the larvae at the Bishop site were the size of first instars by 13 May, the eggs would have been laid about 7-9 days earlier (in an egg-laying frenzy) using their minimum data, which would be 4-6 May. The few small larvae observed earlier at the Bishop site on 24 and 28 April were likely from one of the earlier flights. The length of time between egg deposition and adult eclosion would have been about 36 days, i.e., 4-6 May to 8-10 June. Also, both the 4-6 May and 5-11 June flights migrated at comparably high densities. The 5-11 June exodus reached maximum densities on 7-10 June. It is not known if the stock Hammad and Raafat used were migrant or non-migrant, but they report that V. cardui has eight genrations a year under laboratory conditions and that females oviposit between 420-686 eggs each (average = 507) in captivity. (On 4 May at Jerseydale, Mariposa County, a few females were seen to briefly oviposit in a frenzied manner on a composite, a legume, Lupinus, and Rumex (Polygonaceae) before resuming their migratory flight. Migrants sometimes paused briefly to nervously nectar at meadow flowers before resuming migration.)

The first adult *V. cardui* from the Bishop site began to migrate on 5 June. From 6–10 June, maximum counts of departing migrants consistently occurred between 7:30–8:00 AM, ½–1 hr after sunrise, with far fewer numbers between 7:00–7:30 AM and after 8:30 AM (4–56/5 min/15 m). Maximum numbers between 7:30–8:00 AM for five minutes over 15 m were: 7 June (128), 9 June (337), 10 June (220). From 10:30–1:30, rates were considerably reduced to 2–4/5 min/15 m. On 10 June the area was also monitored in the afternoon between 4:00–7:00 PM. The number of emigrants per 5 minute intervals over 15 m during this time was

Table 1. Weather summary for Bishop, California, November 1990-June 1991. P = precipitation in inches, Mn = minimum temperature (*F), Mx = maximum temperature (°F), T. = total precipitation for each month, T = trace. Source = annual summary of the National Oceanic and Atmospheric Administration.

June
×
May
pril Mn Mx
April P Mn
Mx X
March P Mn
February P Mn Mx
January P Mn Mx
December Mx
DQ a

23, 53, 18, 4, and 9, respectively. On 11 June, migration suddenly decreased just before 8:00 AM. The 1991 daily Bishop temperatures through June are given in Table 1.

Bishop Immatures

A 2½ sq mi area just west of Bishop was periodically surveyed between 24 April-11 June, where V. cardui larvae fed on Amsinckia tessellata Gray (Boraginaceae), the predominant foodplant in the Owens Valley. On 24 April the Amsinckia plants were 3-8 cm high with evidence of only one small larva. On 28 April they were 3-15 cm high, most less than 5 cm, with some coming into bloom, and one plant was found with webbing and another with a first instar larva. By 13 May larval numbers in the study are had dramatically increased to an estimated 15-45 million. The Amsinckia plants were luxuriant, 10-35 cm high, and in full bloom. Larvae were mostly first instars (a few second instars) and preferred to feed on the flower heads. On 19 May larvae were mostly second and third instars. On 28 May the larvae were fourth and fifth instars (mostly last instar), and in the morning many of them crawled over the ground in various directions but each along a straight line, primarily westward away from the sun. Amsinckia leaves on most plants had turned brown and brittle from desiccation. Some Amsinckia 50 cm high had green leaves remaining and contained up to over 100 larvae per plant. Cryptantha plants 5 cm high had up to 30 larvae per plant (mostly last instars). Some larvae were in large isolated shrubs (e.g., Artemisia) preparing to pupate (one pupa found), while dense groups of shrubs had none. Cooler than normal weather had benefited the larvae by preventing the plants from rapidly drying out. In some areas, the larvae had stripped the Amsinckia leaves and were eating the flower heads. On 30 May there were many pupae and many larvae about to pupate on an isolated Atriplex (Chenopodiaceae) shrub. On 5 June Amsinckia had mostly dried out and only 13 last instars were located on six plants. Many Amsinckia stems had had their outer layers eaten away. No larvae (except one) were crawling on the ground, and 32 pupae were located on five Amsinckia plants. One freshly emerged adult dried its wings at the base of a small shrub at 10:40 AM, and another one took its initial flight at 12:10 AM. By 7 June there were only a few last instars in the bushes, the vast majority now as pupae. Most pupae were in the foliage of shrubs and not on the denuded Amsinckia, and only two last instar larvae were crawling on the ground. Seven newly emerged adults were located between 9:20-9:30 AM. Three of these were observed for an hour and did not fly, instead perching with folded wings pointing toward or away from the sun for minimum light exposure. When disturbed, they flew only 1-3 m, with none showing a tendency to fly in a straight line. No flowers were evident in the fields of dried Amsinckia.

Larval behavior was monitored at the Bishop site during 28–31 May. Larvae were motionless, mostly on *Amsinckia*, all night. At 5:00–5:30 AM, larvae remained motionless on the *Amsinckia*. About 10 minutes after the 6:01 sunrise, some larvae began to move their heads about sluggishly. At 6:27 larvae began to move about a little on the plants. By 7:18 larvae were more active, fed, and a few began dropping off the plants and crawling on the ground in straight lines (all directions represented). By 8:08–8:30 most larvae were crawling on the ground,

with only a few remaining on the Amsinckia. Numbers on the ground reached a peak about 9:00-10:00 AM, then steadily declined until there were none by noon when they were back on the plants, and almost none were seen in the afternoon and at dusk on the ground. Between 10:05-10:30 AM on 28 May, numbers of larvae crawling on the ground in a 5 ft × 5 ft plot were 19, 14, 16, 7, and 4 in successive five minute intervals. With heat build up, larvae tended to climb back onto the Amsinckia to get off the hot ground and then remain there the rest of the day and overnight. Larvae on the ground moved faster as the heat increased. Those not finding shelter experienced heat stress, i.e., scrambling madly, often falling over on their sides, and becoming disoriented and dehydrated. Although larvae crawled on the ground in all directions, many tended to move westward away from the sun in the early morning and then between south and east at 10:35-11:00 AM. The larvae seemed to migrate due to the Amsinckia drying up. All sizes of larvae except first instars engaged in larval migration. On 4 June along Westgard Road east of Big Pine at 6000 ft, many Amsinckia plants had varioussized larvae on them but no larvae crawled on the ground at 9:00 AM. Here the Amsinckia was still in fairly good condition, i.e., mostly not dried out yet.

Distances travelled by 11 third to fifth instar larvae during five minute intervals were 1.5-6 m (average = 3.2 m). One larva covered 123 m in 1½ hrs, varying 24% in direction, though it displayed signs of heat stress. Larvae crawled more slowly over the ground in cooler weather on 31 May (1.4-2.8 m, four larvae, average 1.9 m, in five minutes).

Sometimes unidirectional larvae briefly investigated the Amsinckia plants they passed. Larvae that were physically turned in, or prodded to take, the opposite direction quickly returned to their original direction of travel. Larvae would slow their pace appreciably upon encountering shade. They deviated off their course toward nearby shady objects, such as a car or the observer, as ground temperatures rose. Taller objects attracted them more, and from further distance, than did smaller objects, especially with the medium-sized larvae. They would turn a complete circle if the observer walked around them and would follow him for 0.3-3.0 m, resuming their former directions if he then stepped back 2-4 m or crouched. If he crouched down, one larva heading toward him would immediately turn back to its original direction, but then turned back toward him if he stood up. When another object 0.2-0.6 m high was placed or moved around beside the observer when a larva was approaching him, it often confused them, one passing in between, but others seemed to select one object and head for it, ignoring the other. When approached closely from behind, however, larvae maintained their original directions. Other larval experiments at this site are reported elsewhere (Giuliani and Shields 1993).

A last instar larva that was preparing a web enclosure in an *Artemisia* was collected at the Bishop site on 5 June and kept indoors at room temperatures. It hung up to pupate on the lid of a container that afternoon, formed a pupa in the early afternoon of 6 June, and emerged as an adult in the early morning of 13 June (ca. 634 days as a pupa).

V. cardui larvae were found in the White Mountains during July and August on Sphaeralcea (Malvaceae) (6700–8800 ft), Cirsium (Asteraceae) (9800–10,100 ft), and Arnica (Asteraceae) (10,000–11,500 ft). Their rate of growth was slower with increasing altitude.

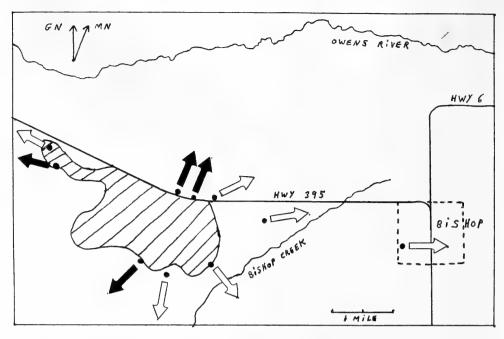


Fig. 2. Bishop emergence site, showing migration flight paths taken during mass exodus of newly-emerged *Vanessa cardui* adults. Cross-hatching = area of high-density hostplant (*Amsinckia*), black arrows = June 5-10, 1991 observations, light arrows = May 16-19, 1986 observations, GN = geographic north, MN = magnetic north.

Bishop Adults

At the Amsinckia site west of Bishop on 28–31 May, only one to three migrating adults were observed each day. During 5–11 June the vast majority of the pupae emerged and the adults migrated, with a maximum of 224–342/5 min/15 m on 9–10 June. These migrations radiated in almost all directions (except east) from the population center (see Figure 2), primarily during 7:00–10:00 AM, sometimes with a few continuing until 1:00 PM (5 June). Unlike "normal" migrators, these usually flew slowly, were easily distracted by other V. cardui flying nearby and flowers, and ceased migrating when the heat of the day built up, although lighter migration flights occurred in the late afternoon. The numbers considerably declined on 11 June during the hottest temperatures of the year (to then), when most migrators had already departed and few new ones were emerging to replace them.

In the late morning and during the afternoon, newly emerged adults congregated at flowers and in shrubs of *Chrysothamnus* (Asteraceae), *Atriplex*, and on the twigs of dead shrubs. Very small shrubs had almost none. These freshly emerged adults apparently waited until the following morning before migrating due to high midday and afternoon temperatures. Several freshly emerged (limp) adults displayed a strong tendency to climb up on vegetation. One of these nervously snapped its wings open and closed at each movement made by a nearby ant on two occasions. A passing car on 7 June at 11:30 AM caused huge numbers of freshly emerged individuals to rise into the air from the roadbanks before resettling, in an area

with fields of dried Amsinckia and no flowers. On 9 June at 7:38 AM, adults migrated to the NE-NNE at 342/5 min/15 m, and a passing car created a huge wave of them that flew in this direction. At 11:15 AM, huge numbers rose into the air from bushes when the car pulled up, quickly resettling in the bushes. At 1:15 PM each bush passed close to with the car on both sides of the road produced a cloud of V. cardui that quickly resettled on bushes. At 1:15 PM, over 1000 V. cardui were on shrubs such as Atriplex and Chrysothamnus in a 5000 sq ft area (ca. five million per sq mi), about 20-100 per shrub, mostly clustered on the shady side with folded wings pointed toward or away from the sun for minimum light exposure. These flew only short distances by circling about when disturbed. without a straight line flight, before quickly resettling on bushes. Some were on the ground in the shade beneath bushes. Occasionally one or two would leave a bush and drift NNE for a bit before landing, although almost no migrators were observed (2/5 min/15 m, going NNE). They remained in these bushes overnight. and at 11 PM when temperatures were still in the 70's flew, apparently short distances, when touched. Clouds of them also rose from bushes just east of Big Pine that afternoon. At 4 PM the yard at Big Pine was filled with V. cardui (40 on Encelia flowers, 3-4 times that number on shrubs, trees, and the ground). By 8 PM these were in the trees and larger shrubs, with occasional individuals still flying about and relanding. At other emergence areas in the Owens Valley at various unrecorded dates during the first half of June, butterflies also clustered on the shady side of shrubs or on flowers by midday and remained there until the next morning. When disturbed, these would rise up in large numbers. On 10 June at 6 AM they were perched in shrubs at the Bishop site and when touched would sluggishly open and close their wings, and there were not the great numbers seen here on shrubs at 1:15 PM on 9 June. On 11 June at 6:08 AM at the Bishop site, the passing car caused many to fly up from bushes that were in sun but not from bushes that were in shade.

Just after sunrise between 6:00–7:00 AM adults that had roosted in shrubs and bushes frequently had their wings open toward the sun to warm up ("basking," see Clench 1966), began to circle about and land on the ground, and made flights in a fixed direction before landing again. By 6:40 AM on 10 June there were more on the ground than in the bushes, with increasing numbers taking short flights heading north, and between 6:43–6:55 AM some suddenly flew north until lost from view.

Between 7:15–7:45 AM on 6–7 June, pairs rather frequently formed when individuals on the ground would rise up to interact with those flying over them, both then continuing on in the same direction and speed. Possibly this could be how migration "waves" originate. Some of the migrants would swerve off their straight flight here and there as they proceeded. Many were flying rather weakly or with little determination, although some were flying in straight lines fairly strongly. The 10 June migration was unusual in that as low numbers of migrants proceeded north, some went south between 4:00–6:45 PM while many others remained on flowers and bushes. After 10 June there were considerably fewer migrators in the Owens Valley.

Most migrators flew 0.3-2 m above the ground, though one was seen 9 m high. On 9 June occasional *V. cardui* were circling and drifting up to 60 m high but were not headed in a fixed direction. Many nectared at flowers when these were

available, such as *Dalea, Lycium* (Solanaceae), and several others, especially between 7:00–9:00 AM and around 4:00 PM.

Several mass emergences of *V. cardui* have been observed by K. Roever (in litt.), mainly in the central Maricopa (Phoenix) area of Arizona, since 1973. Adults would emerge from the chrysalis, dry their wings, and then launch directly into directional flight without expressing mating or feeding behavior in the immediate vicinity of emergence. On April 14, 1973, at a mass emergence site with lupines defoliated along Highway 95, 2–6 mi N of I-40 in Mohave County, Arizona, they fully expanded their wings by 7:30 AM (MST) with a heavy flight starting by 8 AM. From 8:30 to 8:35 AM they flew NNW at 900/5 min/15 m, with density about the same over a 15 mile drive north toward Oatman.

Adults at Flowers

In Inyo County during the first half of June, there were great abundances of adults nectaring at flowers in the vicinity of Big Pine and in the White and Inyo Mountains at low to moderate elevations (up to 6000 ft), especially on Encelia, Dalea, and Ailanthus (Simarubaceae). These reached a peak on 2-12 June, then gradually decreased in the Owens Valley during the second half of June until only occasional singletons were observed at Big Pine during latest June and July, perhaps due to summer heat. At their peak, large to very large numbers would visit flowers. Nectaring occurred especially between 8:00-10:00 AM and in the last afternoon until about 8:00 PM, though sometimes this period extended to early afternoon (19 June) or even all day (13 June). Except in Mazourka Canyon on 3 June at noon, where a large migration had been in progress on 2 June, these showed no tendency to migrate when disturbed, preferring instead to circle about before returning to the flowers. On 16 June at Big Pine, a migration going west showed no tendency to alight on flowers, and nectaring adults did not interact with the migrators except to briefly circle about from flowers. The nectaring V. cardui appeared to come from all over Owens Valley, as they were emerging everywhere Amsinckia was growing on the valley floor. Large numbers on flowers were also noted on 17-21 June at 5200-7500 ft above the floor of Owens Valley on either side. W. D. Patterson (in litt.) reports that during 2-5 June, V. cardui adults were very common in the desert north of Bishop, with numbers flying northward in the Benton Hot Springs/Benton area of Mono County. Elsewhere they varied from abundant to scarce and appeared to be sedentary and absorbed in nectaring. They were abundant and nectaring into the lower part of Westgard Pass and at 5000-6000 ft in the Inyo Mountains. At Santa Rita Flat, 6500 ft, Inyo Mountains, great swarms were nectaring at yellow composites. Above Westgard Pass and on the west side of Owens Valley at 5000-5500 ft, they were present but only in fair to low numbers.

Amsinckia

In 1991, Amsinckia was the dominant annual plant in the Owens Valley and formed vast fields. No rain fell from September 1990 through February 1991, unique for Owens Valley, while sufficient rains in March caused the Amsinckia to germinate. It tended to grow in open areas and not where there was extensive shrub growth. Though it was found up to over 7000 ft in elevation, it was not common above the valley floor (4000 ft). Amsinckia was dense in places on the

west side of the valley from Bishop to Big Pine and was scarce on the east side (although dense in one 2 sq mi area east of Big Pine where two 5 ft \times 5 ft plots had 94 and 140 larvae on 21 May), and extended on down to Lone Pine. It also extended into much of Round Valley and sparingly north of the Owens River. Virtually everywhere *Amsinckia* was found, *V. cardui* larval impact was evident (up to 100 larvae per plant on 28 May). Our estimate of 100 million larvae is very conservative and does not take into account their use of foodplants other than *Amsinckia*.

The emergence site monitored in 1991 is located in the Owens Valley 5–10 km west of downtown Bishop, 4300–4500 ft in elevation. The main area is 2 × 3 km, with a ½ × 2 km westward extension. The plant was very limited west, north, and east of this area. In 1986, Amsinckia was confined primarily to this emergence site. No Amsinckia was found in Owens Valley in 1987–1990 due to drought, and the open ground at the Bishop site remained barren. In 1986 and 1991, the Bishop site had essentially the same area and density of Amsinckia, although in 1986 the Amsinckia boundary there encompassed slightly less territory and it germinated in December instead of March. The site was open ground dominated by Amsinckia, with Artemisia, Chrysothamnus, and Atriplex in scattered clumps. In the past, the area had been altered by agriculture and overgrazing.

Angiosperms Utilized

The following is a list of *V. cardui* larval hostplants from Inyo County in 1991. Larvae were consistently found feeding on these. Most of the plant identifications were made by Mary DeDecker.

Asteraceae

Baileya pleniradiata Harv. & Gray Lactuca serriola L. Cirsium drummondii T. & G. Tetradymia axillaria A. Nels. Arnica parryi sonnei (Greene) Maguire

Boraginaceae

Amsinckia tessellata—the main, preferred hostplant Pectocarya heterocarpa (Jtn.) Jtn.

Cryptantha barbigera (Gray) Greene

C. confertiflora (Greene) Pays.

C. micrantha (Torr.) Jtn.

C. pterocarya (Torr.) Greene

C. recurvata Cov.

C. utahensis (Gray) Greene

Fabaceae

Lupinus excubitus Jones

Malvaceae

Malva neglecta Wallr.

Sphaeralcea ambigua ambigua Gray S. a. rosacea (M. & J.) Kearn.

Preffered adult nectar sources in Inyo County in 1991 were the following:

Asteraceae

Baileya pleniradiata Chrysothamnus nauseosus (Pall.) Britton Encelia virginensis actonii (Elmer) Keck—especially

Brassicaceae

Stanleya elata Jones

Fabaceae

Dalea fremontii Torr.—especially

Rosaceae

Prunus armeniaca L.—cultivated P. andersonii Gray—especially

Simarubaceae

Ailanthus altissima (Mill.)-introduced Tree of Heaven

Solanaceae

Lycium sp.

Tamaricaceae

Tamarix sp.

Zygophyllaceae

Larrea divaricata Cav.

Predators and Parasites

Some predation on *V. cardui* was observed in Inyo County in 1991, although few natural enemies seemed to be present. These included a large *Calosoma* sp. (Carabidae) eating larvae, a large asilid fly twice capturing adults, an unidentified wasp carrying a last instar larva back to its ground hole, black harvester ants attacking and carrying off one larva, crows eating many larvae, and a flock of starlings probably hunting pupae. Also, English sparrows ate the bodies on car grills. A tachinid larva was parasitic in a few *V. cardui* pupae, and a small wasp larva was rather frequently parasitic on small *V. cardui* larvae above 7000 ft in the White Mountains in late summer.

Shift in Direction and Return Flight

V. cardui disappeared from lower elevations by the end of June. Migratory flights continued above 9000 ft in the White Mountains into early September at low rates (up to 1/5 min/15 m). No such flights were seen in the Sierra Nevada above Owens Valley at that time. Their migration directions abruptly shifted from

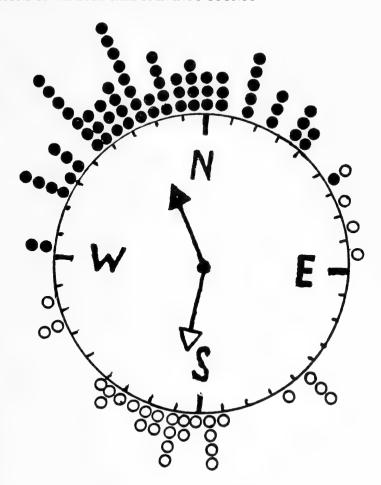


Fig. 3. Circle diagram of sudden change in individual flight directions from northwesterly to southerly of *Vanessa cardui* migrators in the White Mountains above 9000 ft. Black dots = June 12–30, 1991, light dots = July 10–30, 1991, arrows = average (median) flight direction for each period. All directions are geographic. Each dot represents one measured migrator.

northwesterly to southerly sometime between 1–9 July (see Figure 3). Migrators flew in all directions (no preferred direction observed) on 4 July at 9200–10,300 ft in the White Mountains.

One of us (D. G.) observed predominantly SW flights in eastern Oregon in early August and at Cour d'Alene, Idaho, during the latter half of August.

At Jerseydale in late August, occasional *V. cardui* migrated SW. From 31 August to 15 October they were common to very common there (fresh to worn), nectaring at *Cirsium*, with occasional ones migrating SW–SSE. In late October to early November, their numbers steadily decreased, with the last worn individual of the season observed there on 15 November.

On 17 September in Eureka Valley, there were some fourth and fifth instar larvae left and many empty webbings with fifth instar frass on *Sphaeralcea ambigua* following recent rains, with occasional adults migrating mostly SW-WSW at 1/5 min/15 m. At 5000 ft in the Dry Mountains on the same day, worn *V*.

cardui adults were numerous on Encelia flowers, with mostly fresh ones higher in elevation on Chrysothamnus flowers.

P. Cherubini (in litt.) noted a large S-SW movement of *V. cardui* in early September, beginning about 1 September, in Placerville, the Sacramento Valley, and the area around Petaluma and Sebastopol, with thousands nectaring on yard *Buddleja* (Buddlejaceae) on 14–15 September at Placerville.

On 19 October occasional migrators went ESE-E on Mt. Tamalpais and S-ESE at Alpine Lake in Marin County. On 20 October they migrated SE-E at 14/5 min/15 m on the Point Reyes Peninsula. The Baja California peninsula appeared devoid of *V. cardui* in October except for several around Cataviña on 14-15 October (J. R. Mori pers. comm.). Many adults nectared on *Petalonyx* (Loasaceae) in the Kelso Dunes of San Bernardino County on 29 September, and fresh to worn adults were common on *Lepidospartum* (Asteraceae) in San Jacinto Valley of Riverside County on 16 October.

In September to mid-October in Owens Valley, occasional *V. cardui* were seen migrating mostly S-SW, as residents, or nectaring on *Chrysothamnus nauseosus*. During early November, only single *V. cardui* were resident at Big Pine (last seen there on 9 November), and only two were sighted in November in the White Mountains (on 13 November at 7200 ft and 25 November at 8500 ft). The last *V. cardui* to appear that season were observed in Saline Valley on 27 November (13 between 1100–1700 ft) and 27–31 December (three between 2300–2400 ft). At Hemet in Riverside County, worn adults nectared at yard *Lantana* (Verbenaceae) on 24 November (five or six) and were last observed there on 26 December (one, worn).

Migration Dynamics

Between 28 April and 9 June, we made observations of *V. cardui* migrations in the Ovens Valley region and at Jerseydale (3500 ft, Mariposa County) on a daily basis. The largest migrations occurred on days that were clear and sunny (warm to hot), with calm, breezy, or gusty wind conditions. None migrated during cold temperatures, though sometimes individuals were seen that were not migrating. None was observed migrating on drizzly or rainy days. In the Owens Valley region on 9–10 May under cold, cloudy, and windy conditions, many *V. cardui* were observed on the ground, probably for warmth (see Clench 1966), and these did not migrate. The same behavior was observed while driving down the Lead Canyon road to the Saline Valley road on 3 May when conditions were mostly cloudy with a light wind and cooler than normal, and at Jerseydale on 2 May in cool, overcast weather. Temperature seemed to be the main factor in limiting flights.

Migrants sometimes flew in strong gusty winds on cool days. In Owens Valley there were two migration periods. The first occurred from mid-April to mid-May and consisted of immigrants from the south. The second was by local emergers during the first half of June. During the 28 April to 9 June period, migrations were observed for 86% of the days in Owens Valley and 79% at Jerseydale. On 51% of the days in Owens Valley and 42% at Jerseydale, migrations were greater than 1/5 min/15 m. The low numbers in the Owens Valley during the latter half of May appeared to be due to the migration from the south ending rather than weather-caused.

The dates when rates exceeded 1/5 min/15 m at Jerseydale corresponded to dates that they were above or well above 1/5 min/15 m in the Owens Valley during 28 April–9 June. On those dates where we had same day data for both places, the Owens Valley rates averaged $2\frac{1}{2}-12 \text{ times}$ greater than the Jerseydale rates (6 May = $3 \times$, 7 May = $9 \times$, 12 May = $2\frac{1}{2} \times$, 15 May = $3 \times$, 2 June = $12 \times$), if the 4 May Lone Pine date ($43\frac{1}{2} \times$) is excluded. The highest rates during the 43-day period occurred in both places on 6 May (22-211/5 min/15 m in Owens Valley, 34-44/5 min/15 m at Jerseydale). On eight days, rates exceeded or greatly exceeded 1/5 min/15 m in the Owens Valley but not at Jerseydale even though the weather was favorable on those days at Jerseydale.

The predominant direction of the migrators at both Big Pine and Jerseydale in May was N to NNW. They migrated in all directions at Big Pine in June. Big Pine is located 87 air mi ESE of Jerseydale, on the opposite side of the Sierra Nevada. Thus the source of the Jerseydale migrants could not have been Owens Valley and instead was in the direction of the southern San Joaquin Valley to Baja California. In Inyo County, migration directions averaged NNW in May and early June and S in July.

We computed flight speeds on a few migrators. On 6 May near Jerseydale in mid-morning during warm, calm weather, 10 were clocked at 15–20 mph by driving a car at their speed and reading the speedometer. On 4 May near Lone Pine in the late morning in clear, cool conditions with decreasing winds that occasionally gusted, 22 were clocked at 12–26 mph (mean = 16 mph, median = 15 mph) by using a stopwatch to time them over measured distances. On 30 April at noon on a ridge SW of Bishop during clear, cool weather with a strong wind blowing crosswise to their flight, three were timed at 10, 12, and 16 mph.

At Jerseydale the migrations usually began about 9:30 AM and lasted until about 5:00 PM in May and early June. In the Owens Valley region, however, migrations began about 7:00 AM and lasted until about 6:10 PM in May and early June. The Bishop exodus flight on 5–11 June began about 6:30–6:50 AM and lasted until about 6:50 PM, with an early afternoon hiatus.

In the Owens Valley and at Jerseydale on 4–6 May, the flight was characterized by some large fresh individuals with many medium to small-sized ones. At Jerseydale, however, this flight actually began on 3 May with a 5 May lull. The numbers were reduced in both places before and after these dates. *V. cardui* ceased migrating at Jerseydale in mid-June with the onset of hot weather.

Several attempts were made to determine migration directions at 500 to 1000 ft elevational intervals on the same day. On 4 May along Horseshoe Meadow road SW of Lone Pine, *V. cardui* migrated N-NE and N-NNE between 5100–9100 ft in the afternoon under cool, clear, calm to breezy conditions, shifting to NW (and E) at 9400 ft and E at 9600 ft. Wind directions were variable. They avoided an area that was in shadow at 7100 ft at 5:30 PM, with migration ending at 6:05 PM that day. On 6 May in the White Mountains, they migrated N-NNE between 5000–9000 ft in mid-morning, then went N-NNW between 7000–8500 ft from 11 AM to 1 PM, and NW-WNW at 6000 ft at 1:30 PM. Winds were light to strong and gusty, and varied in direction. At Vista in the White Mountains, 9200 ft, 10:15 AM, a stream of migrators was funnelled up a steep canyon by strong, gusty winds from the WSW, at 425/5 min/15 m going N-NE.

Discussion

Migration of Vanessa cardui, a non-diapausing species, allows it to redistribute a significant part of its populations to more seasonally favorable environments over a large area. It appears incapable of surviving both summer and winter at any one place (Larsen 1976), e.g., the hot summer in Egypt or the cold winter in Canada. Spring migrations of V. cardui are likely due to high densities of starving, stressed larvae migrating on the ground in search of suitable foodplants, which in the adult stage becomes expressed as changes in behavior (e.g., gregariousness, heightened activity, and migration), reproduction, and hormonal levels following emergence. Perhaps only those larvae that engage in crawling behavior will migrate as adults. It has been experimentally determined that last instar lepidopteran larvae reared in crowded conditions are more resistant to starvation than are those reared in isolation (Iwao 1962). Large numbers of V. cardui larvae per plant hasten the deterioration of their foodplants, coupled with a more rapid desiccation of annuals like Amsinckia compared to perennials. Larvae crawled in straight lines away from hostplants because they were no longer suitable food sources, not because of excessive larval density. When various taxa of lepidopterous larvae were reared in crowded conditions, they developed more rapidly, had a higher fat content, developed polyphagous feeding habits, increased feeding activity, were more active, nervous, aggressive, and cannibalistic, and pupated more simultaneously than did solitary larvae (Long 1953; Iwao 1962). At the Bishop site, crowded V. cardui larvae similarly displayed elevated activity, nervousness, some cannibalism, and pupated relatively simultaneously. Migrant V. cardui, at eclosion, have a very large fat-body reserve and undeveloped reproductive organs (cf. Williams 1925; Herman and Dallmann 1981). No matings whatsoever were observed at the Bishop emergence site or the June nectaring aggregations. In Australian Vanessa kershawi McCoy, a close relative of V. cardui, laboratory experiments suggest that short daylengths greatly affect the sex ratio in favor of females, thus potentially enchancing the colonizing ability of early spring migrants (James 1987).

A key factor in Lepidoptera migration is juvenile hormone (JH). JH in insects is known to regulate feeding, growth, development, metamorphosis, reproduction, diapause, and behavior (Bowers 1991). Wild-caught, fall-migrating V. cardui adults had low levels of JH in their haemolymph, preventing reproductive maturation (adult reproductive diapause), with significant reproductive maturation occurring when JH was injected (Herman and Dallmann 1981). In lepidopterous larvae reared under crowded conditions, haemolymph titers of JH are reduced and result in a more rapid generation time compared with isolated larvae (Yagi 1976). In some insects, it is known that JH levels decline during starvation and are elevated by nutrition (Benz 1972; Novak 1975; Rankin 1978). A few plants are known to contain antijuvenile hormones (AJH) which lower the insect's JH levels (Bowers 1991). However, some species of Boraginaceae examined for AJH's proved negative (W. S. Bowers in litt.), and AJH's probably have little influence on migratory V. cardui since it utilizes such a wide variety of larval hostplants. The corpus allatum (CA), which produces JH, is posteriorally connected to the brain and embryonically arises "as ectodermal invaginations in the area between the mandibular and maxillary pleurites" (Novak 1975, p. 127). Nervousness is known to inhibit CA activity in phytophagous insects (Novak 1975). JH is synthesized in the endoplasmic reticulum and is absorbed and dissolved by lipid droplets that are released into the haemolymph via gradual extrusion through the surface of the CA (Slama et al. 1974, p. 27; Novak 1975, p. 127). Adipokinetic hormone in *V. cardui* metabolizes fat-body lipid reserves by releasing haemolymph-circulating diglyceride lipids, thus providing the fuel necessary for its migration flights (cf. Herman and Dallmann 1981, Herman 1993).

The delay in reproductive maturation means that migrating adults are able to widely disperse, thus escaping adverse climates and deteriorating foodplants in the emergence area, before mating and oviposition can begin (McDonald and Cole 1991). Nectaring at flowers along the migration route is the most likely cause of elevating JH levels in V. cardui which induces eventual reproductive maturation. This behavior was directly observed in the central Mojave Desert in mid-April of 1973, when many V. cardui adults both migrated and nectared in the afternoon and avidly nectared in the early morning on wildflowers carpeting the desert (Shields 1974). Also, Shapiro (1980) has found that return migrations of northern California V. cardui, which frequently nectar, contain females with large fat-bodies and reproductive immaturity early in the fall, with females reaching reproductive maturity later in the fall. It has been experimentally determined that amino acids obtained from nectar-feeding are utilized in gamete formation by adult butterflies, with nectar sugars increasing total egg production (Murphy et al. 1983). Also, nectar sugars replenish the flight fuel after lipid reserves are depleted (DeVries and Dudley 1990).

The migration phenomenon in *V. cardui* most likely evolved as a means of escaping seasonally unfavorable arid conditions, which reached a Neogene maximum during late Upper Miocene times in western North America (see Axelrod 1980, pp. 101–103). This would by phylogenetically possible since a close ancestor of *V. cardui* already existed by lower Middle Miocene times, in the North Caucasus (Nekrutenko 1965).

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Research Notes

Salinity Tolerance of *Cletocamptus deitersi* (Richard 1897) and its Presence in the Salton Sea

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The Salton Sea supports a limited diversity of aquatic invertebrates, and until recently only one copepod species, the cyclopoid *Apocyclops dengizicus*, had been reported from it (Dexter 1993). The presence of harpacticoid copepods has not been reported in the scientific literature, but at least two species have been found within the Salton Sea. In 1983 I. E. Bayly and S. H. Hurlbert collected a harpacticoid in shallow water (salinity 36–38 g/L) at the north end of the Salton Sea. This species was identified as *Nitocra dubia* by R. Hammond (in litt. to S. H. Hurlbert).

In 1990 I began salinity tolerance studies on *Apocyclops dengizicus*. Plankton tows collected in Oct. 1990 from Red Hill Marina, Salton Sea (salinity 43 g/L) in water approximately 1 m deep were used to establish cultures at various salinities (Dexter 1993). Within 60 days, in cultures maintained at 73 g/L a harpacticoid copepod became very abundant, while *A. dengizicus* became scarce. This harpacticoid was not present in cultures from the same source maintained at lower salinities. I hypothesize that at 73 g/L a few individuals avoided predation by *Apocyclops dengizicus*, and increased in density as the numbers of *A. dengizicus* declined through time at this high salinity.

This new harpacticoid was identified by R. H. Hammond as *Cletocamptus bicolor*, a species which has been synonymized by Yeatman (1963) with *C. deitersi*. Fleeger (personal communication) confirmed that the Salton Sea *Cletocamptus* is *C. deitersi*. *C. deitersi* is widely distributed throughout the world (Chandler and Fleeger 1987, Dussart and Defaye 1990, Fleeger 1980, Lang 1948, Yeatman 1963). It is reported from North America (Louisiana, Massachusetts, Texas), Central America (Guatemala, Nicaragua), the Caribbean (Bermuda, Cuba, Haiti), South America (Argentina, Ecuador, Uruguay), Hawaii, China, Australia, Ethiopia, and Israel. Habitats for this species include brackish coastal ponds, mangroves, estuaries, salt marshes, inland bays, saline lakes, freshwater lakes, and freshwater rivers. *C. deitersi* is characterized as an errant deposit feeder which grazes algae and detritus attached to sediment particles (Chandler and Fleeger 1987).

Water collected at the Salton Sea was evaporated outdoors until a salinity of 136 g/L was obtained. This water was filtered through a 35 μ m mesh net and diluted with de-ionized water to obtain the desired salinities. Cultures of 0.5 g/L salinity were produced by combining Salton Sea water, de-ionized water, and filtered pond water (as source of phytoplankton). Salinity was determined with a Reichert-Jung refractometer, and final salinity determined using correction factors for Salton Sea ionic compositions.

Harpacticoid copepods collected during Oct. 1990 were separated from cyclo-

poids by maintenance at salinities between 68–73 g/L which killed the cyclopoids. Approximately 100 ml of concentrated harpacticoid culture was introduced into aerated plastic containers with 1.9 L of Salton Sea water adjusted to various salinities. Copepods were introduced without acclimation, and often without replication.

A series of culture experiments were run. A total of 18 salinities were used ranging from 0.5 to 119 g/L. Culture salinity and number of replications (in parentheses) were: 0.5 (4), 1 (2), 6 (1), 13 (1), 17 (1), 34 (1), 45 (1), 62 (1), 68 (1), 74 (1), 80 (1), 85 (4), 90 (1), 96(2), 102 (4), 107 (4), 113 (1) and 119 (2) g/L.

Salinities were monitored every 15 days and adjusted by addition of de-ionized water. Phytoplankton was present at all salinities and its growth was encouraged with approximately 0.2 grams biweekly of fish food pellets (Pet Co., Koi's Choice). At 30, 60, 90, and 120 days, each culture was gently filtered through a 35 μ m mesh net, examined under a dissecting microscope for abundance and presence of life history stages, and returned to its respective container.

C. deitersi cultures at salinities from 0.5 to 80 g/L supported relatively high densities of individuals of all life history stages (nauplii, copepodites, males, females, and gravid females) throughout the duration of the 120 day experiment (Table 1). C. deitersi cultured at salinities between 85 to 96 g/L steadily declined in density, but some individuals were alive at the end of 120 days. Mating was observed at salinities from 0.5 to 107 g/L, but apparently was unsuccessful at salinities greater than 85 g/L. Copulating pairs remained attached for at least several hours. Reproduction was continuous during the 3 year period this species was maintained in laboratory cultures at salinities between 20 to 60 g/L.

Harpacticoids are considered an important food source for early stages of benthic fish and are often used in aquaculture systems to provide food for hatchery fish. The ease with which *C. deitersi* is cultured in the laboratory, at various salinities, without the presence of sediment, suggests it as a good candidate for this purpose.

The cosmopolitan distribution of this species suggests its ability to tolerate a wide variety of habitats, temperatures, and salinities. But such a distribution could also indicate that a number of morphologically indistinguishable sibling species are present. This study showed that the Salton Sea population of *C. deitersi* is very tolerant of a wide range of salinities in culture, from basically fresh water to high salinities. This favorable attribute may be of particular importance to this species, given that the salinity of the Salton Sea may reach 90 g/L by the year 2010 (Black 1983) if mandated water conservation programs are followed. The presence of this species within the Salton Sea is possibly a result of deliberate introduction of the seagrass *Diplanthera wighti* from Texas by California Fish and Game in 1957, although flora and fauna were also introduced from the Gulf of California and from the California coast (Linsley and Carpelan 1961).

A. dengizicus is the dominant copepod within the Salton Sea and normally there would be little interaction between this planktonic species and the benthic C. deitersi; the sediment habitat of the latter would limit or prevent predation. A. dengizicus is an effective predator of naupliar stages of Artemia in culture conditions (Hammer and Hurlbert 1992), and on C. deitersi in laboratory cultures without sediment. However, the upper limit of salinity tolerance differs in these species. Reproduction in A. dengizicus becomes limited at salinities exceeding 57

Life history stage	Salinity g/liter	Abundance ¹ at			
		30 days	60 days	90 days	120 days
Gravid females	0.5, 1, 6, 13, 17, 34, 45, 62, 68, 74, 80 85, 90	+++	+++	+++	+++
	96, 102, 107	+	0	0	0
	113, 119	0	0	0	0
Nauplii	0.5, 1, 6, 13, 17, 34, 45, 62, 68, 74, 80 85, 90	+++ ++	+++ +	+++	+++ 0
	96, 102, 107	+	0	0	0
	113, 119	0	0	0	0
Copepodids	0.5, 1, 6, 13, 17, 34, 45, 62, 68, 74, 80	+++	+++	+++	+++
	85, 90 96	++	++	+	+
	102, 107	+	+	+	0
	113	+	0	0	0
	119	0	0	0	0

Table 1. Salinity tolerance of Cletocamptus deitersi.

g/L (Dexter 1993), while *C. deitersi* appears unaffected in salinities up to 80 g/L. I predict that *C. deitersi* will become more abundant in the shallow water plankton and benthos as salinities increase at the Salton Sea.

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¹ Abundance categories are denoted as follows: 0, not seen; +, 1-5/liter; ++, 6-20/liter; +++, >20/liter.

First Record of *Madracis* sp. cf. M. pharensis (Heller, 1868) on Continental Eastern Pacific Shores

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The scleractinian coral *Madracis* Milne Edwards and Haime, 1848 is worldwide in distribution and has a geologic range of Upper Cretaceous to Recent (Colgan 1990). In the eastern Pacific Ocean it has been recorded for the Eocene of Washington (U.S.A.) and Chiapas (México) (Durham 1942; Frost and Langenheim 1974), but otherwise is known only from the Recent.

There are two nominal species of *Madracis* reported in the eastern Pacific. *Madracis asperula* Milne Edwards and Haime, 1850, was found at Islas Galápagos, Ecuador (0°N) (Durham and Barnard 1952). The second species, originally identified as *Madracis* sp., was collected at Galápagos and Isla Gorgona, Colombia (5°N) (Durham and Barnard 1952). Later, these specimens and several others found at Islas Galápagos and Rocas Alijos, México (24°N), were identified as *M. pharensis* (Heller 1868) by Wells (1983) or as *Madracis* sp. cf. *M. pharensis* (Cairns 1991; Wilson in press). *M. pharensis* was originally known from the eastern Atlantic and Mediterranean Sea, but had also been reported in Bahamas, Jamaica, Netherland Antilles, Panamá, Belize, Colombia and Brasil (Laborel 1967 fide Zibrowius 1980; Porter 1972; Wells 1973; Laborel 1974; Erhardt and Werding 1975; Reed 1985; Jackson et al. 1985; Kobluk and Lisenko 1987; van Moorsel 1988). Some of these records had been taken as dubious by Zibrowius (1980) because the true degree of morphological variability of American coralla is unknown.

This paper presents the first record of *Madracis* sp. cf. *M. pharensis* on the western continental shores of America. The specimens were collected in October, 1991 at the Cabo Pulmo reef, east coast of Baja California Sur, México (23.5°N, 109.5°W). This is the northernmost reef in the eastern Pacific and has been described elsewhere (Squires 1959; Brusca and Thomson 1975; Reyes Bonilla 1993). The coral fauna of the reef consists of 10 species of hermatypic corals and one ahermatype, *Tubastraea coccinea* Lesson, 1829 (Reyes Bonilla 1993). Voucher specimens are deposited in the Museo de Historia Natural de la Universidad Autómoma de Baja California Sur (MHN-UABCS) (La Paz, B.C.S., México) and in the Invertebrate Paleontology Section, Natural History Museum of Los Angeles County (Los Angeles, CA, U.S.A.).

The coralla of Madracis sp. cf. M. pharensis were collected at a depth of 16 m

from crevices in a stone wall located in the outer central section of the reef, locally known as "Los Cantiles." The larger coralla were growing under a large (>40 cm largest diameter) colony of *Pavona gigantea* Verrill, 1869. Other small coralla were seen, but not collected, on the reef substrate (granite) at 3 m depth, in the south section of the reef. Elsewhere in the eastern Pacific (Galápagos, Gorgona, Rocas Alijos), this form was found at depths from 24 to 343 m, whereas in the Atlantic, some finds were as shallow as 2 m (Durham and Barnard 1952; Zibrowius 1980; Wells 1983; Cairns 1991; Wilson in press).

Wells (1983) and Cairns (1991) agree that in the Pacific, the southern distributional limit of *M. pharensis* or *Madracis* sp. cf. *M. pharensis* is Isla Gorgona, Colombia, based on a specimen figured by Durham and Barnard (1952) but they have overlooked another record of the species from off the coast of Chile (25°44′S, 85°25′W) at Nazca Ridge. Several corolla were found, apparently live, on a fossil (Pleistocene?) *Porites* dredged from a reported depth of 210 to 227 m (Durham 1980). The coral was identified as *Stylophora* sp. (?) (Allison et al. 1967), and reidentified as *Madracis* sp. cf. *M. pharensis* by John W. Wells in 1974 (Durham 1980, p. 69). Later studies have shown that the actual depth of the guyot where the corals were dredged is 167 m and it was dated at surface level from 29.2 to 7.2 m.y. ago (Newman and Foster 1983).

The collection deposited at the MHN-UABCS consists of 27 corolla, most of them with 3 to 10 corallites. The largest one (23 mm in diameter) has 90 corallites, and probably was younger than a year old, since the extension rate of M. pharensis is 0.7 to 13.3 mm/month in the Caribbean (van Moorstel 1988). All of the colonies are plocoid and encrusting, growing as a calcareous lamina on carbonated surfaces. The calices are 2.06 mm in diameter (N = 15; SE = 0.11), polygonal and have 10 septa in the first cycle, which are exsert in most of the corallites. The secondary septa are absent or reduced to a few irregular spines on the calicular wall, but in one corallum they are well developed and conspicuous. When they occur, the secondary septa are exsert and costae are present. Most of the calices have a central, styliform columella, fused near the basal plate with a series of spines or paliform lobes, which are separated by a notch from the septa. The intercalicular coenosteum is 0.2 mm long in average and has a spinose surface.

Looking at the main skeletal characters (styliform columella, paliform lobes, septa exsert, polygonal calices), the specimens from Cabo Pulmo are similar to the ones described in the literature, and so may be considered *M. pharensis* or its eastern Pacific form. Notwithstanding, Wilson (in press) noticed a recurrent difference in the secondary septa among Atlantic and Pacific specimens of the nominal species. Most of the corallites figured by Zibrowius (1980) and collected in the Atlantic Ocean and the Mediterranean Sea, do have distinct secondary septa even if the corallum is small. The ones from Galápagos (figured in Wells 1983 and Cairns 1991), Rocas Alijos (Wilson in press) and Cabo Pulmo have only traces of secondary septa.

The paucity of skeletal elements in this genera has forced taxonomists to look for very general differences to separate species. For example, the species *M. kirbyi* Veron and Pichon, 1976 was differentiated from *M. pharensis* because of the absence of secondary septa of the former species (Veron and Pichon 1976; Veron 1986). Similarly, Wells (1973) and Zlatarski and Martínez Estalella (1982) separated species of *Madracis* on the basis of the secondary septa and the growth

form of the corallum. Considering that the first character is different among *M. pharensis* and the *Madracis* specimens from the eastern Pacific, we believe that there is enough evidence to support Wilson and even to suggest that the eastern Pacific *Madracis* is a different species.

To conclude, the current distributional range of *Madracis* sp. cf. *M. pharensis* in the eastern Pacific is from Rocas Alijos (24°N) and Cabo Pulmo (23°N) to Nasca Ridge (25°S). A direct examination of the specimens collected at Pulmo and Alijos, together with comparisons of the figured specimens from Islas Galápagos and Isla Gorgona, allow us to suggest that the skeletal differences among *M. pharensis* and *Madracis* sp. cf. *M. pharensis* are important and consistent enough that they may represent two different species.

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Distribution and Host for Four Symbiotic Crustaceans of the Mexican Pacific (Stomatopoda and Decapoda)

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Collecting efforts during 1990–1994 in the Mexican Pacific resulted in the discovery of new hosts and/or range extensions for four species of symbiotic crustaceans. The specimens have been deposited in the Invertebrate Collection of the Facultad de Ciencias, Universidad Autónoma de Baja California. Abbreviations are: BC, Baja California; BCS, Baja California Sur; GC, Gulf of California.

Order Stomatopoda Family Nannosquillidae Alachosquilla digueti (Coutière 1905)

Previous distribution. — From Guaymas, Sonora, and Cabo San Miguel, BC (GC) to Isla Taboga, Panama (Hendrickx and Salgado-Barragán 1991).

Material examined. — 1 male, beach at Rancho Punta Estrella, km 13 San Felipe-Puertecitos road, San Felipe, BC (lat 30°55′N, long 114°45′W); tidal pool, free-living.

Proposed common name. - Pacific dwarf squilla.

Remarks.—Because it features two dark spots on the telson, the Atlantic species A. floridensis Manning, is considered distinct from A. digueti, a single spot species (Schotte and Manning 1993). Our specimen agrees with this, but specimens of digueti from the Gulf of California studied by Hendrickx and Salgado-Barragán (1991, fig. 39D, pl. 30E) also possess two spots on the telson. Additional study is necessary to decide whether these two species are synonyms or not, as suggested by Manning (1963, 1974). Alachosquilla digueti has been recorded as a commensal in the burrow of Balanoglossus, along with a polynoid worm, Lepidasthenia digueti Gravier (Coutière 1905; Schmitt 1940).

Order Decapoda Family Alpheidae Leptalpheus mexicanus Ríos and Carvacho 1983

Previous distribution and host.—Known only from the type locality, Estuary of the Mulegé River, BCS (GC); in burrows of the mud shrimp *Upogebia dawsoni* Williams (Ríos and Carvacho 1983).

Material examined. — 1 male, 3 females, Mangrove at El Conchalito, Ensenada La Paz, in front of Centro Interdisciplinario de Ciencias Marinas—Instituto Politécnico Nacional, La Paz Bay, La Paz, BCS (lat 24°10′N, long 110°25′W), 4 June 1992; in burrows of *U. dawsoni*.

Proposed common name. - Mexican pistol shrimp.

Remarks.—Ríos (1992) and Wicksten and Hendrickx (1992), based on a personal communication, recorded L. mexicanus from the Colombian Pacific. Because this species is taxonomically poorly known we recommend that material be re-examined to confirm this range extension. Leptalpheus mexicanus was collected in burrows of Upogebia dawsoni constructed in a sandy-mud bottom. Other burrowing species collected in El Conchalito were the goneplacid crab Malacoplax californiensis (Lockington) and the fiddler crab Uca latimanus (Rathbun) but L. mexicanus was not found associated with these species.

Family Pinnotheridae Juxtafabia mulinarum (Rathbun 1918)

Distribution and previous hosts.—Santa Clara, Sonora, (GC), México to Costa Rica, in the bivalves *Chione californiensis* (Broderip), *C. fluctifraga* (Sowerby), *C. tumens* (Verril), *Polymesoda inflata* (Phillipi), *Protothaca grata* (Say) and *Tagelus affinis* (C.B.Adams) (Campos 1993).

Material examined and new host.—1 female (hard stage), La Paz Bay, in front of Hotel Grand Baja, La Paz, BCS (lat 24°10′N, long 110°25′W), July-August 1991; in the clam Laevicardium elatum (Sowerby).

Common name. - Clam Crab (Campos 1993).

Remarks.—The clam also hosted a juvenile of the Pacific Pen shrimp Pontonia pinnae Lockington (see below). The general morphology of the female in hard stage is almost identical to the male in hard stage described by Campos (1993), including the fusion of the abdominal somites 4–5. Presence of gonopods and a wider abdominal somite 3 allows recognition of male.

Family Palaeomonidae Pontonia pinnae Lockington 1878

Distribution and previous host.—Upper GC to Colombia and west coast of BC to Bahia Tortugas, BCS; in the Pen Shells *Pinna rugosa* (Sowerby) and *Atrina tuberculosa* (Sowerby) (Campos-González 1988; Campos et al. 1992; Lemaitre and Alvarez-León 1992).

Material examined and new hosts.—1 juvenile, Bahía de la Paz, in front of Hotel Grand Baja, La Paz, BCS, August 1989; in the clam Laevicardium elatum.—5 juveniles, Espiritu Santo Island, BCS (lat 25°30′N, long 110°21′W), 19 September 1991; in the clam Megapitaria aurantica (Sowerby).

Proposed common name. - Pacific Pen shrimp.

Remarks.—As this represents a first record of *P. pinnae* in species of clams (Cardiidae and Veneridae), it should be noted that all shrimps were juveniles and that these clams could serve only as occasional hosts.

Acknowledgments

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COVER: Arroyo San Antonio de Murillos ca. Rancho San Antonio, Sierra San Pedro Mártir, Baja California, México. June 17, 1992. Photograph by Gorgonio Ruiz-Campos.