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## A New Species of *Lepeophtheirus* (Copepoda; Caligidae) Parasitic on Three Kelpfish Species (Clinidae) from the Southern California Coast

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**Abstract.**—A new copepod species, *Lepeophtheirus schaadti* n. sp., is established based on female and male specimens obtained from the Giant Kelpfish, *Heterostichus rostratus* Girard, 1854, and Striped Kelpfish, *Gibbonsia metzi* Hubbs, 1927, captured at Inner Cabrillo Beach in southern California, U.S.A. In addition, comparisons with copepod specimens identified by Wilson (1935) as *L. parviventris* Wilson, 1905 from the Spotted Kelpfish, *Gibbonsia elegans* (Cooper, 1864), in Newport Bay, California, revealed they are conspecific with *L. schaadti* n. sp. The new species differs from its congeners by a combination of characters that include: female with a genital complex that is more than half the length of the cephalothoracic shield and with posterolateral lobes, an abdomen that is composed of one somite and is less than one-quarter the length of the genital complex, a maxillulary dentiform process bearing a thin ridge on the inner tine and lacking a basal knob, no myxal process on the maxilliped, apically rounded tines on the sternal furca, the spine on the first exopodal segment of leg 3 inserted distally on the basal swelling, a 3-segmented leg 4 exopod, and a broad inner lobe of leg 5 that does not extend beyond the posterior margin of the genital complex; and male with three accessory claws on the antennal endopod and no myxal process on the maxilliped. *L. schaadti* n. sp. represents the first account of an ectoparasitic species from the Striped Kelpfish and Spotted Kelpfish, as well as the fourth ectoparasitic species reported from the Giant Kelpfish.

Members of the copepod family Caligidae Burmeister, 1835, commonly known as sea lice, are predominantly external parasites of marine fishes (Dojiri and Ho 2013). Among the 30 valid caligid genera, *Lepeophtheirus* von Nordmann, 1832 is one of the more speciose genera, with 121 valid species and 2 recognized subspecies (Boxshall and Walter 2016). *Lepeophtheirus* parasitizes marine teleosts worldwide, but is more diverse in temperate latitudes (Kabata 1979). One species, *Lepeophtheirus salmonis* (Krøyer, 1837) sensu lato, is the most pathogenic ectoparasite on farmed salmonids in the northern hemisphere (Johnson et al. 2004; Costello 2006). Presently, 17 species of *Lepeophtheirus* have been reported from 16 fish families along the California coast, from San Francisco Bay in the north to La Jolla in the south of the state (Table 1). Recent samples of Giant Kelpfish (*Heterostichus rostratus* Girard, 1854) and Striped Kelpfish (*Gibbonsia metzi* Hubbs, 1927) (Clinidae Swainson, 1839) collected within the Port of Los Angeles during Cabrillo Marine Aquarium's Inner Cabrillo Beach Survey (ICBS) were infected with an unidentified species of *Lepeophtheirus*. The ICBS is a long-term, tri-annual survey designed to monitor the abundance and diversity of the invertebrates and



Table 1. Fish hosts and locality records for species of *Lepeophtheirus* reported from California, U.S.A.

Copepod species	Host family	Host species	Locality	Reference
<i>Lepeophtheirus</i> sp.	Kyphosidae	<i>Medialuna californiensis</i> (Steindachner, 1876)	Off La Jolla	Hobson (1971)
	Labridae	<i>Oxyjulis californica</i> (Günther, 1861)	Off La Jolla	Hobson (1971)
	Pomacentridae	<i>Hypsypops rubicundus</i> (Girard, 1854) (as <i>Hypsypops rubicunda</i> )	Off La Jolla	Hobson (1971)
	Sciaenidae	<i>Geyonemius lineatus</i> (Ayres, 1855)	Southern California	Love and Moser (1983)
	Sciaenidae	<i>Menticirrhus undulatus</i> (Girard, 1854)	Southern California	Love and Moser (1983)
	Scorpaenidae	<i>Sebastes paucispinis</i> Ayres, 1854	Southern California	Love and Moser (1983)
	Paralichthyidae	<i>Paralichthys californicus</i> (Ayres, 1859)	Anaheim Bay	Ho (1972a)
<i>Lepeophtheirus bifidus</i> Fraser, 1920	Pleuronectidae	<i>Pleuronichthys guttulatus</i> Girard, 1856 (as <i>Hypsopsetta guttulata</i> )	Anaheim Bay	Ho (1975)
	Embiotocidae	<i>Cymatogaster aggregata</i> Gibbons, 1854	Southern California	Love and Moser (1983)
<i>Lepeophtheirus bifurcatus</i> Wilson, 1905	Embiotocidae	<i>Phanerodon furcatus</i> Girard, 1854	Southern California	Love and Moser (1983)
	Paralichthyidae	<i>Paralichthys californicus</i> (Ayres, 1859)	Santa Monica Bay	Kalman (2006)
	Pleuronectidae	<i>Pleuronichthys verticalis</i> Jordan & Gilbert, 1880	Santa Monica Bay	Kalman (2006)
	Pleuronectidae	<i>Psettiichthys melanositicus</i> Girard, 1854	San Francisco Bay	Wilson (1908)
<i>Lepeophtheirus brachyurus</i> Heller, 1865	Scorpaenidae	<i>Scorpaena guttata</i> Girard, 1854	Off La Jolla	Wilson (1908)
<i>Lepeophtheirus constrictus</i> Wilson, 1908	Serranidae	<i>Paralabrax clathratus</i> (Girard, 1854)	Southern California	Love and Moser (1983)
	Serranidae	<i>Paralabrax maculatofasciatus</i> (Steindachner, 1868)	Off La Jolla	Wilson (1908)
	Serranidae	<i>Paralabrax nebulifer</i> (Girard, 1854)	Southern California	Love and Moser (1983)
<i>Lepeophtheirus longitabdominis</i> Shiino, 1960	Sciaenidae	<i>Arctoscion nobilis</i> (Ayres, 1860) (as <i>Cynoscion nobilis</i> )	Off La Jolla	Shiino (1960)
	Polyprionidae	<i>Stereolepis gigas</i> Ayres, 1859	Off La Jolla	Wilson (1908)
<i>Lepeophtheirus longipes</i> Wilson 1905	Scorpaenidae	<i>Sebastes serriceps</i> (Jordan & Gilbert, 1880)	Off La Jolla	Hobson (1971)
	Serranidae	<i>Paralabrax clathratus</i> (Girard, 1854)	Catalina Island	Wilson (1921)
	Molidae	<i>Mola mola</i> (Linnaeus, 1758)	Santa Catalina Island	Wilson (1908)
<i>Lepeophtheirus nordmanni</i> (Milne Edwards, 1840)			Southern California	Wilson (1908) <sup>a</sup>
			Monterey Bay	Wilson (1935)

Table 1. Continued.

Copepod species	Host family	Host species	Locality	Reference
<i>Lepeophtheirus parviventris</i> Wilson, 1905	Clinidae	<i>Heterostichus rostratus</i> Girard, 1854 <sup>b</sup>	Newport Bay	Wilson (1935) <sup>b</sup>
	Labridae	<i>Halichoeres semicinctus</i> (Ayres, 1859) (as <i>Iridio semicinctus</i> )	Southern California	Wilson (1924) <sup>c</sup>
<i>Lepeophtheirus parvus</i> Wilson, 1908	Scorpaenidae	<i>Sebastes rubrivinctus</i> (Jordan & Gilbert, 1880) (as <i>Sebastes rubrivinctus</i> )	Off Santa Barbara Island	Wilson (1908) <sup>c</sup>
	Urotrygonidae	<i>Urobatis halleri</i> (Cooper, 1863) (as <i>Urolophus halleri</i> )	California	Wilson (1924) <sup>d</sup>
	Embiotocidae	<i>Cymatogaster aggregata</i> Gibbons, 1854	Southern California	Love and Moser (1983)
	Labridae	<i>Damalichthys vacca</i> (Girard, 1855) <i>Semicossyphus pulcher</i> (Ayres, 1854) (as <i>Pimelometopon pulcher</i> and <i>P. pulchrum</i> )	Southern California Off San Diego	Love and Moser (1983) Wilson (1908); Shiino (1963)
<i>Lepeophtheirus paulus</i> Cressey, 1969	Scorpaenidae	<i>Sebastes serriceps</i> (Jordan & Gilbert, 1880) (as <i>Sebastes serriceps</i> )	Off La Jolla Off La Jolla	Hobson (1971) Cressey (1969)
<i>Lepeophtheirus pravipes</i> Wilson, 1912	Hexagrammidae	<i>Ophiodon elongatus</i> Girard, 1854	Off San Diego	Shiino (1965) <sup>e</sup>
	Scorpaenidae	<i>Scorpaena guttata</i> Girard, 1854	Off Pacific Grove	Wilson (1935)
<i>Lepeophtheirus remiopsis</i> Dojiri, 1979	Barachoididae	<i>Porichthys notatus</i> Girard, 1854	Off Huntington Beach	Dojiri (1979)
	Paralichthyidae	<i>Hippoglossina stomata</i> Eigenmann & Eigenmann, 1890	Off Huntington Beach Santa Monica Bay	Dojiri (1979) Kalman (2006)
	Paralichthyidae	<i>Xystreurys liolepis</i> Jordan & Gilbert, 1880	Santa Monica Bay	Kalman (2006)
	Pleuronectidae	<i>Parophrys vetulus</i> Girard, 1854	Off Huntington Beach Santa Monica Bay	Dojiri (1979) Kalman (2006)
<i>Lepeophtheirus rotundipes</i> Dojiri, 1979	Pleuronectidae	<i>Pleuronichthys verticalis</i> Jordan & Gilbert, 1880	Off Huntington Beach Santa Monica Bay	Dojiri (1979) Kalman (2006)
	Cottidae	<i>Chitonotus pugetensis</i> (Steindachner, 1876)	Off Huntington Beach	Dojiri (1979)
	Paralichthyidae	<i>Citharichthys stigmaceus</i> Jordan & Gilbert, 1882	Off Huntington Beach	Dojiri (1979)
<i>Lepeophtheirus rotundipes</i> Dojiri, 1979	Scorpaenidae	<i>Scorpaena guttata</i> Girard, 1854	Off Huntington Beach Santa Monica Bay	Dojiri (1979) Kalman (2006)

Table 1. Continued.

Copepod species	Host family	Host species	Locality	Reference
<i>Lepeophtheirus salmonis oncorhynchi</i> Skern-Mauritzen, Torrissen and Glover, 2014	Salmonidae	<i>Oncorhynchus tshawytscha</i> (Walbaum, 1792)	Monterey Bay	Wilson (1908) <sup>f</sup>
<i>Lepeophtheirus spatha</i> Dojiri and Brantley, 1991	Paralichthyidae	<i>Paralichthys californicus</i> (Ayres, 1859)	Santa Monica Bay	Dojiri and Brantley (1991); Kalman (2006)
<i>Lepeophtheirus thompsoni</i> Baird, 1850	Sciaenidae	<i>Atractoscion nobilis</i> (Ayres, 1860) (as <i>Cynoscion nobilis</i> )	Off La Jolla	Wilson (1908)

<sup>a</sup> Reported as *L. insignis*.

<sup>b</sup> Specimens were reported as *L. parviventris*, but examination of these specimens revealed they are *L. schaadti* n. sp. Furthermore, the same specimens were reported from *Heterostichus rostratus*, but *Gibbonsia evides* (= *Gibbonsia elegans*) was handwritten on the vial label.

<sup>c</sup> Specimens were reported as *L. parviventris*, but examination of these specimens revealed they are not conspecific with *L. parviventris*.

<sup>d</sup> Reported from *U. halleri* held in an aquarium at the marine station of the University of Southern California, at Venice, California.

<sup>e</sup> Reported as *L. trifidus*.

<sup>f</sup> Reported as *L. salmonis*.

fishes living in subtidal eelgrass beds off Inner Cabrillo Beach. Subsequent examination of the unidentified *Lepeophtheirus* specimens revealed they were not conspecific with *Lepeophtheirus parviventris* Wilson, 1905, a species previously reported by Wilson (1935) from the Giant Kelpfish in Newport Bay, California. Indeed, the *Lepeophtheirus* specimens from Inner Cabrillo Beach, as well as those of Wilson (1935), represent an undescribed species, which is described in detail herein.

### Materials and Methods

Nearly all copepod specimens of the new taxon were obtained from *Heterostichus rostratus* samples that were collected in beach seines at three stations along Inner Cabrillo Beach during the 2011–2014 ICBS. Only two copepod specimens were obtained from one individual of *Gibbonsia metzi* captured in a winter 2011 ICBS. Copepod samples were preserved in 70% ethanol upon removal from the host. Copepod specimens were later soaked in lactophenol prior to examination using an Olympus SZX10 dissection microscope and an Olympus BX53 compound microscope equipped with differential interference contrast optics. Selected specimens were also measured intact using an ocular micrometer and/or dissected and examined according to the wooden slide procedure of Humes and Gooding (1964). In the description, length measurements are provided first, followed by width measurements; all measurements given are expressed as the mean followed by the range in parentheses. Pencil drawings of the copepod body and appendages were made with the aid of a drawing tube. Drawings were subsequently inked in with Sakura Pigma Micron™ pens on 110 g/m<sup>2</sup> tracing paper, digitized with a CanoScan LiDE 500F scanner, and assembled into figure plates using Adobe Photoshop. Morphological terminology follows Huys and Boxshall (1991) and Dojiri and Ho (2013). Fish names and classifications conform to Page et al. (2013). Type material and voucher specimens of the new taxon are deposited at the Crustacea Department of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, U.S.A., and Cabrillo Marine Aquarium (CMA), San Pedro, California, U.S.A.

Type material and voucher specimens of *L. parviventris* deposited by Wilson (1905, 1908, 1924, 1935) in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., were also examined for comparative purposes: syntypes comprising 22 females, 15 males, and 11 juveniles (USNM 42064), ex *Gadus macrocephalus* Tilesius, 1810 (*Gadidae* Rafinesque, 1810), Chignik Bay, Alaska, 1903; 2 females and 1 male (USNM 69798), ex skin of *Gibbonsia evides* (Jordan & Gilbert, 1883) (= *Gibbonsia elegans* (Cooper, 1864)) (as *Heterostichus rostratus*), Newport Bay, California, 1934; 5 females and 1 male (USNM 38566), ex *Sebastes rubrivinctus* (Jordan & Gilbert, 1880) (as *Sebastes rubrivinctus* (Jordan & Gilbert, 1880)) (*Scorpaenidae* Risso, 1827), Station 4417, off Santa Barbara Island, 29 fathoms, April 12, 1904; 1 female (USNM 53491), ex *Halichoeres semicinctus* (Ayres, 1859) (as *Iridio semicinctus* (Ayres, 1859)) (*Labridae* Cuvier, 1816), southern California, April 12, 1913.

### Results

#### *Lepeophtheirus schaadti* n. sp. (Figs. 1–6)

Type material. Holotype female (LACM CR-2011-3), allotype male (LACM CR-2011-4), and 1 male and 2 female paratypes (CMA 2017.04.0002), ex *Heterostichus rostratus* (222 mm SL), Station 2 (33°42'38.3"N, 118°16'58.5"W), off Inner Cabrillo Beach, San Pedro, California, U.S.A., February 5, 2011.

Other material examined. From Station 1 (33°42'42.6"N, 118°16'59.1"W), off Inner Cabrillo Beach, San Pedro, California, U.S.A.: 10 females (7 with an unidentified species of *Udonella* Johnston, 1835 (*Monogenea*) attached to the genital complex) and 4 males (3 with *Udonella* sp.

attached to the genital complex) (CMA 2017.04.0006), ex *H. rostratus* (330 mm SL), October 10, 2014; 2 females (each with *Udonella* sp. attached to the genital complex and egg sacs) (CMA 2017.04.0005), ex *H. rostratus* (169 mm SL), October 11, 2014; 3 females (LACM MBPC 17851), ex *H. rostratus* (193 mm SL), October 11, 2014; 1 female and 1 male (LACM MBPC 17852), ex *H. rostratus* (197 mm SL), October 11, 2014. From Station 2 (33°42'38.3"N, 118°16'58.5"W), off Inner Cabrillo Beach, San Pedro, California, U.S.A.: 1 female and 1 male (CMA 2017.04.0014), ex *Gibbonsia metzi* (110 mm SL), February 5, 2011; 1 female (CMA 2017.04.0003), ex *H. rostratus* (170 mm SL), February 5, 2011; 1 female and 1 male (CMA 2017.04.0004), ex *H. rostratus* (120 mm SL), February 5, 2011; 1 female and 1 male (CMA 2017.04.0010), ex *H. rostratus* (86 mm SL), October 28, 2011; 1 female (CMA 2017.04.0011), ex *H. rostratus* (182 mm SL), October 28, 2011; 2 females and 2 males (CMA 2017.04.0012), ex *H. rostratus* (163 mm SL), October 28, 2011; 1 female and 2 males (CMA 2017.04.0013), ex *H. rostratus* (178 mm SL), October 28, 2011; 4 females (CMA 2017.04.0008), ex *H. rostratus* (200 mm SL), October 17, 2013; 1 female (CMA 2017.04.0009), ex *H. rostratus* (245 mm SL), October 17, 2013. From Station 3 (33°42'35.5"N, 118°16'51.3"W), off Inner Cabrillo Beach, San Pedro, California, U.S.A.: 1 female (dissected and mounted on glass slide) and 3 males (1 male partially dissected and mounted on glass slide) (CMA 2017.04.0007), ex *H. rostratus* (260 mm SL), June 10, 2013.

Description of adult female. Body (Figure 1A) 4.08 (3.85–4.25) mm long (excluding caudal setae) ( $n=7$ ). Cephalothoracic shield subcircular, nearly as long as wide [2.19 (2.05–2.35)  $\times$  2.11 (1.98–2.33) mm], with well-developed paired frontal plates, posterior margin of thoracic zone extending beyond posterior limit of lateral zone, and hyaline membrane along frontal and lateral rims. Free fourth pedigerous somite about three times wider than long [209 (170–230)  $\times$  609 (560–645)  $\mu\text{m}$ ] and indistinctly separated from genital complex. Genital complex large, more than half the length of cephalothoracic shield, marginally wider than long [1.41 (1.30–1.55)  $\times$  1.52 (1.38–1.78) mm], with nearly parallel lateral margins and protruded posterolateral corners. Abdomen (Fig. 1B) composed of 1 somite, 247 (220–280)  $\times$  416 (370–460)  $\mu\text{m}$ , widest anteriorly, and indistinctly separated from genital complex. Caudal ramus (Fig. 1C) slightly longer than wide [111 (105–120)  $\times$  99 (90–110)  $\mu\text{m}$ ], with 6 plumose setae (seta I absent) and short row of setules along inner margin. Egg sacs (Fig. 1A) uniseriate.

Antennule (Fig. 1D) 2-segmented. Proximal segment longer than distal segment, bearing 1 tiny semispherical knob and 1 bifid process on posterodistal corner and 27 setae (25 hirsute, 2 naked) along anterior margin. Distal segment cylindrical, bearing 12 setae (2 setae near posterodistal corner share a common base) and 2 aesthetascs.

Antenna (Fig. 2A) 3-segmented, comprising coxa, basis and 1-segmented endopod incorporating distal claw. Coxa with long, apically rounded process on posterolateral corner. Basis stout, with corrugated surface on protruded, inner distal corner and 1 large, outer distal adhesion pad on dorsal surface. Endopod long, uncinuate, bearing 2 naked setae.

Postantennal process (Fig. 2A) with small bump midway on anterior margin of basal section, pair of setulose papillae on base, 1 setulose papilla posterior to base, and recurved, apically rounded hook.

Mandible (Fig. 2B) modified into elongate stylet bearing distolateral hyaline membrane and 12 distomedial teeth (1 blunt, 11 sharp).

Maxillule (Fig. 2A) composed of trisetose papilla and bifid dentiform process. Sclerite anterior to papilla with posteriorly-directed triangular process. Tines on dentiform process subequal, with thin ridge on inner tine.

Postoral process (Fig. 2A) small, triangular.



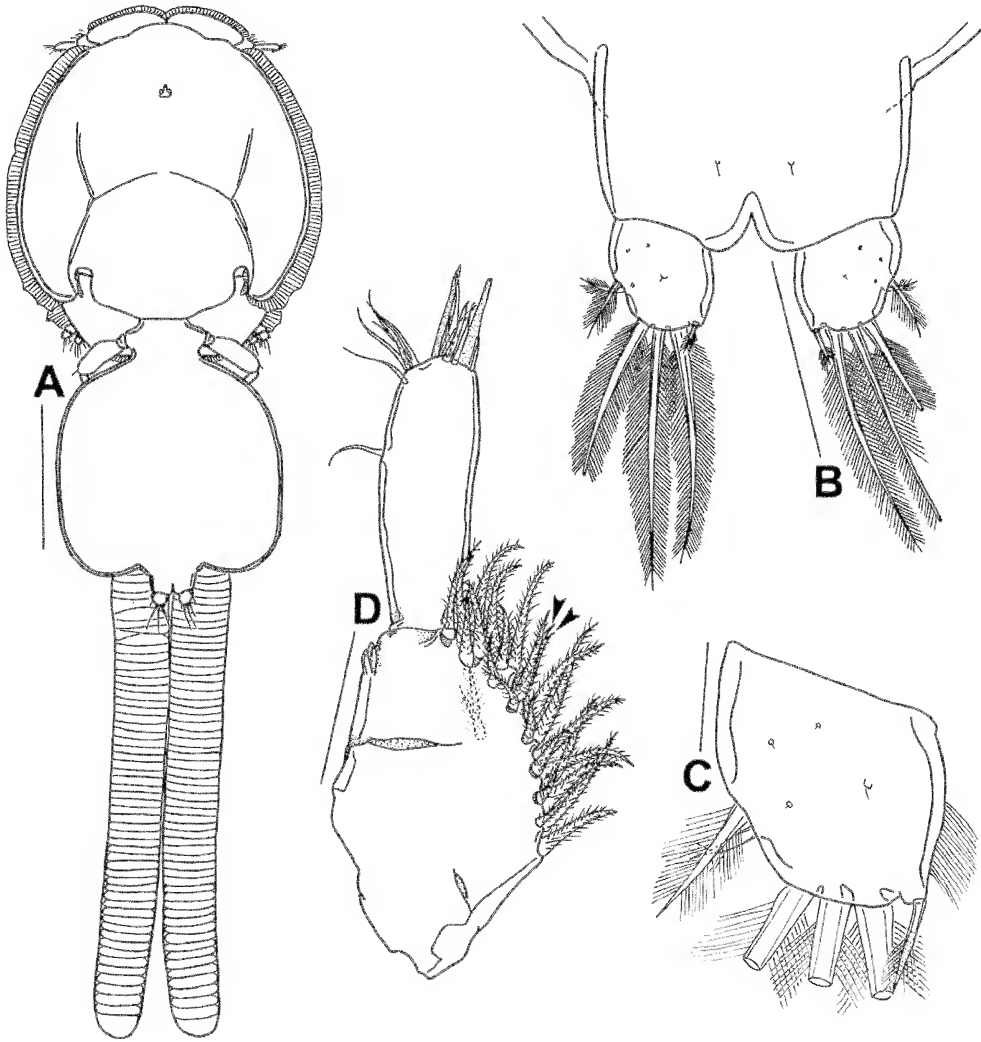


Fig 1. *Lepeophtheirus schaadti* n. sp., adult female. A) Habitus, dorsal; B) Abdomen and caudal rami, dorsal; C) Right caudal ramus, dorsal; D) Right antennule (arrowheads indicate naked setae on proximal segment), ventral. Scale bars: 1.00 mm for A; 200  $\mu\text{m}$  for B; 50  $\mu\text{m}$  for C; 100  $\mu\text{m}$  for D.

Maxilla (Fig. 2C), brachiform, 2-segmented, composed of elongate, unarmed syncoxa and slender basis. Basis with large flabellum and long apical calamus and shorter apical canna; calamus furnished with finely serrated membranes; canna with finely serrated posterior margin.

Maxilliped (Fig. 2D) large, subchelate, 3-segmented, comprising long protopod (corpus) and subchela consisting of free endopodal segment (shaft) and claw. Protopod with 2 large patches of denticles near inner margin and small patch of denticles on distolateral corner. Shaft unarmed. Claw with long, naked basal seta and 2 thin ridges and fine striations distally.

Tines of sternal furca (Fig. 2E) longer than box, slightly divergent, and apically rounded; shallow T-shaped depression present, situated anterior to base of box.

Legs 1 to 3 (Figs. 3A–B and 4A) biramous; leg 4 (Fig. 4C) uniramous. Armature formula of legs 1–4 is shown in Table 2.

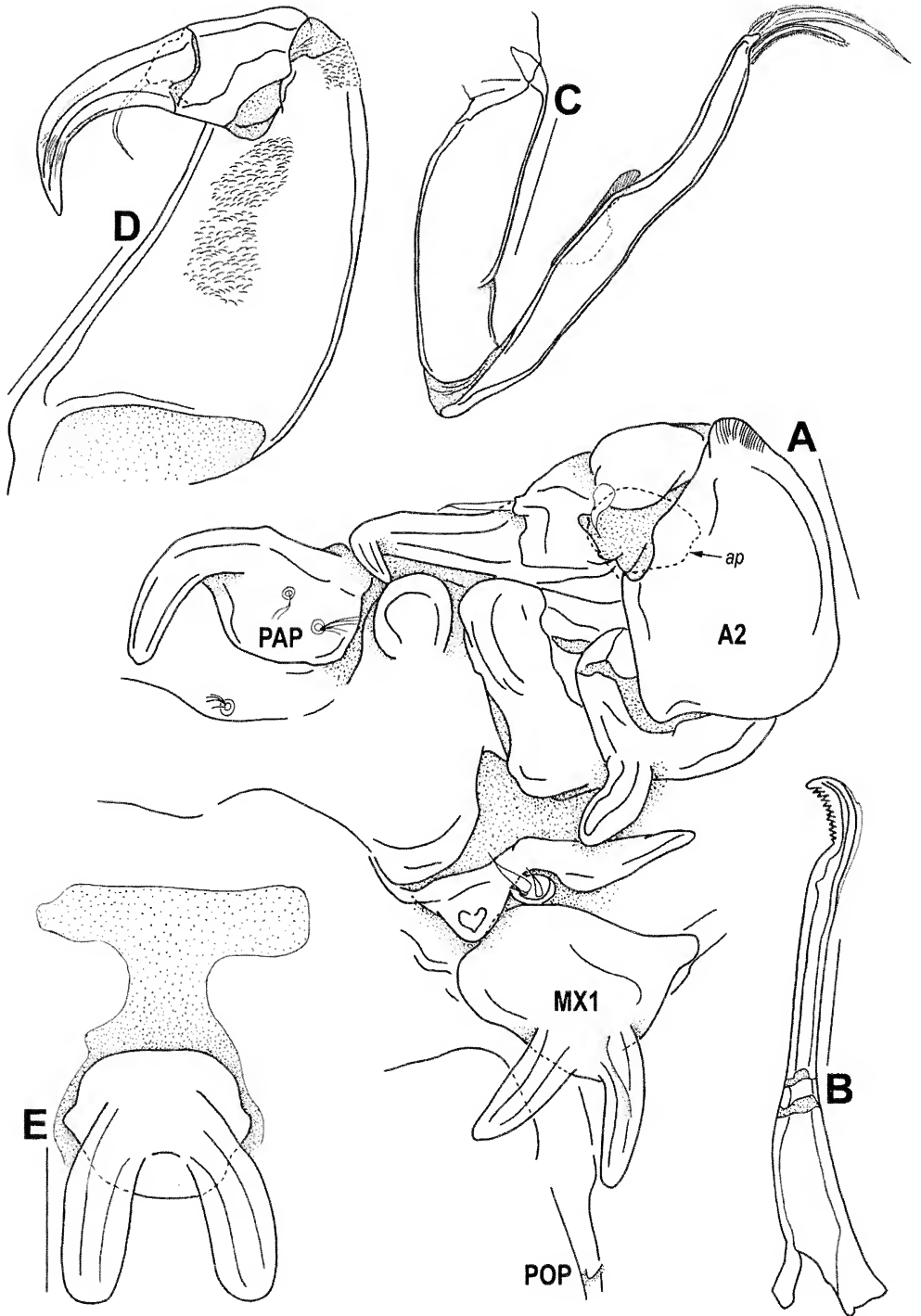


Fig 2. *Lepeophtheirus schaadti* n. sp., adult female. A) Right antenna (A2) (ap = adhesion pad), postantennal process (PAP), maxillule (MX1) and postoral process (POP), ventral; B) Left mandible, posterior; C) Right maxilla, anterior; D) Right maxilliped, anterior; E) Sternal furca, ventral. Scale bars: 100  $\mu\text{m}$  for A, E; 50  $\mu\text{m}$  for B; 150  $\mu\text{m}$  for C, D.

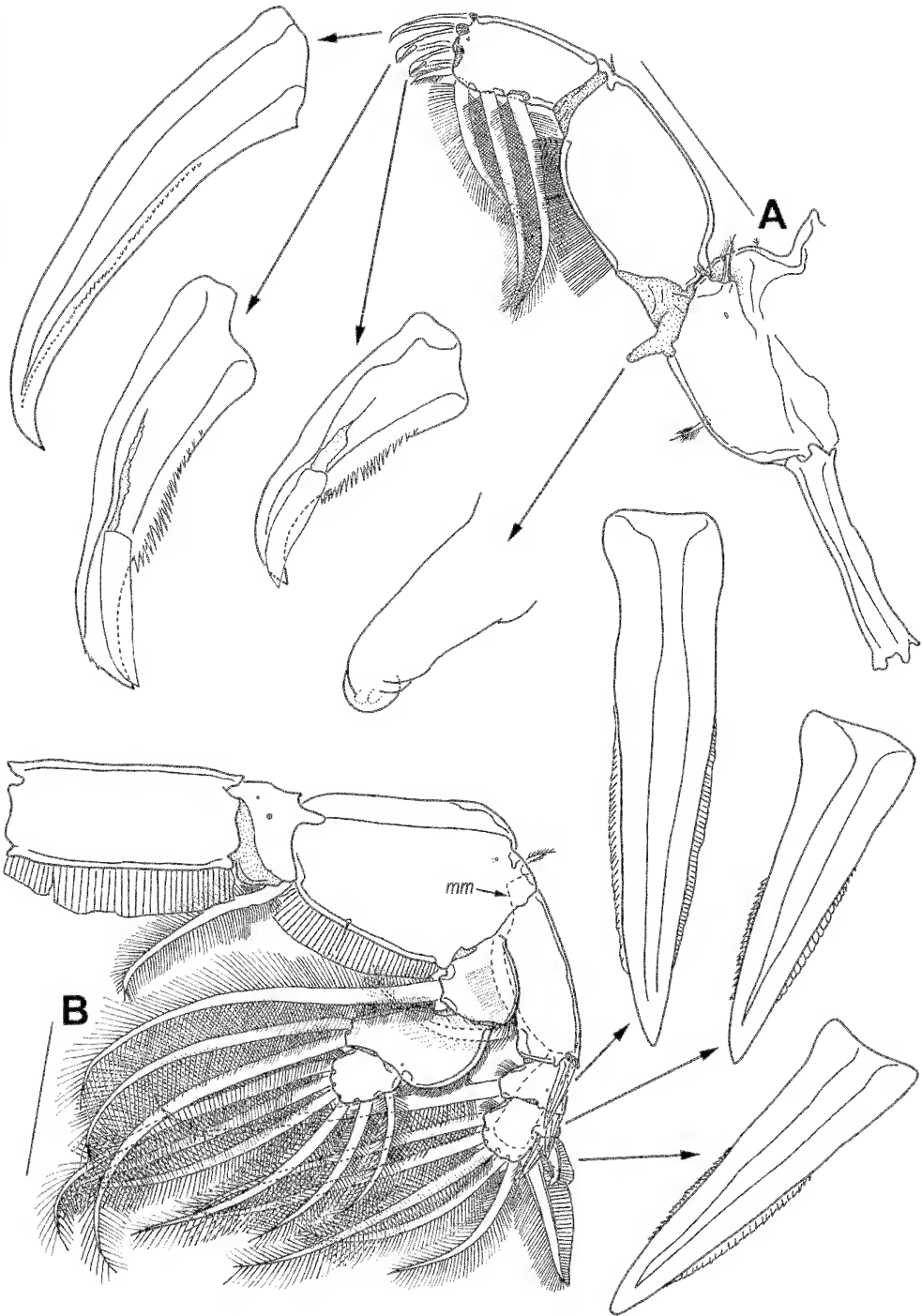


Fig 3. *Lepeophtheirus schaadti* n. sp., adult female. A) Right leg 1 with detail of endopod and apical spines on second exopodal segment, anterior; B) Left leg 2 (mm = marginal membrane) with detail of outer spine on first and second exopodal segments and proximalmost outer spine on third exopodal segment, anterior. Scale bars: 200  $\mu$ m for A, B.

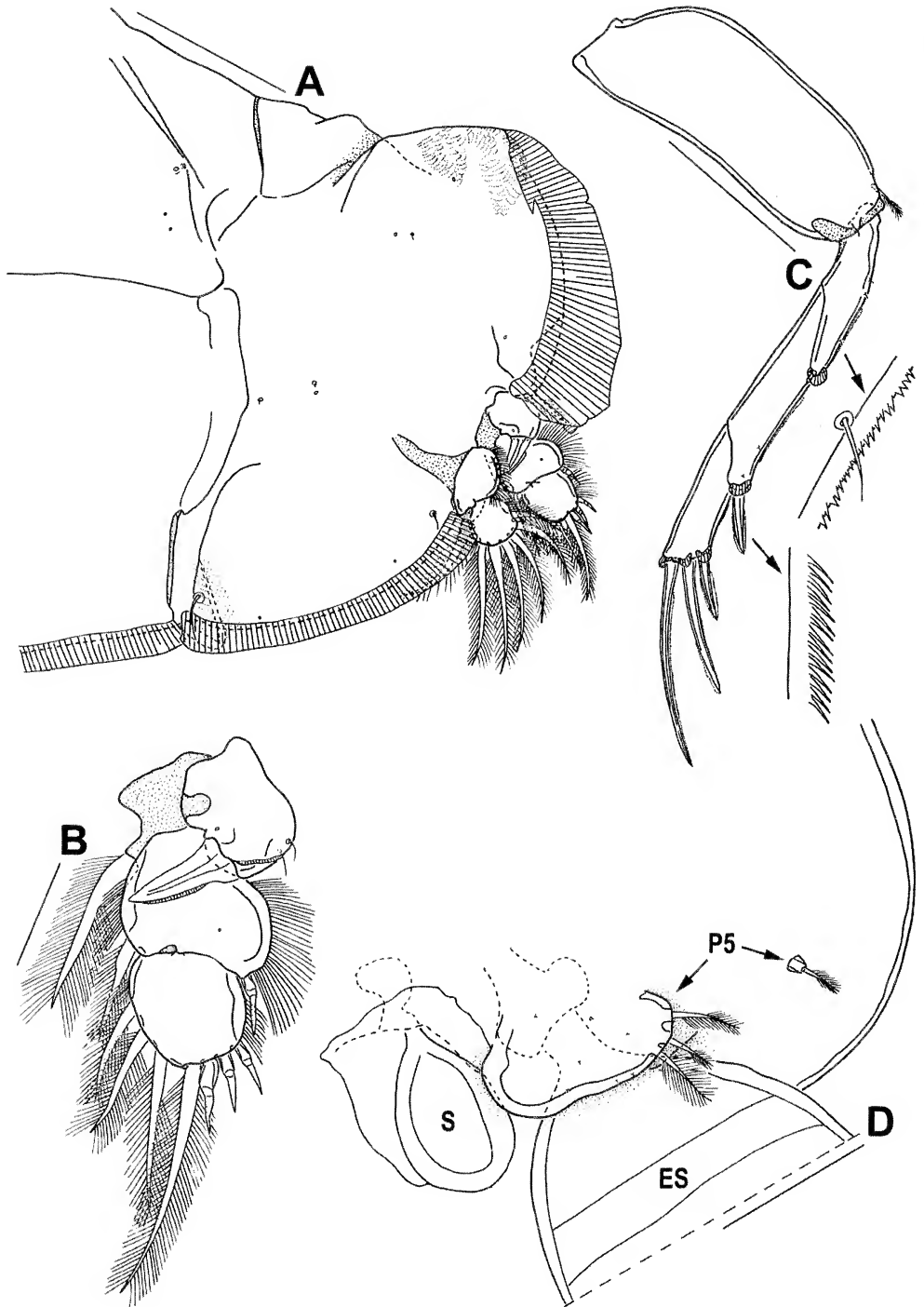


Fig 4. *Lepeophtheirus schaadti* n. sp., adult female. A) Left leg 3, ventral; B) Left leg 3 exopod, ventral; C) Left leg 4 with detail of serrations along outer margin of first exopodal segment and fine teeth along outer margin of spine on second exopodal segment, anterior; D) Left leg 5 (P5), spermatophore (S) and egg sac (ES), ventral. Scale bars: 200  $\mu$ m for A, C, D; 50  $\mu$ m for B.

Table 2. Armature on legs 1-4 (Roman numerals = spines; Arabic numerals = setae).

	Coxa	Basis	Exopod	Endopod
Leg 1*	0-0	1-1	I-0; 0,III + 1,3	vestigial
Leg 2	0-1	1-0	I-1; I-1; II,1,5	0-1; 0-2; 6
Leg 3*	0-1	1-0	I-1; I-1; II,1,4	0-1; 6
Leg 4*	0-0	1-0	I-0; I-0; II,1,0	absent

\* Although the coxa and basis are fused to form a protopod in this leg, these segments are treated separately in this Table.

Leg 1 (Fig. 3A) intercoxal sclerite naked and elongate. Protopod with 1 outer and 1 inner plumose setae, 1 proximolateral setulose papilla, and 1 mid-lateral pore. First exopodal segment with 1 small, naked outer spine and inner row of setules. Second exopodal segment with 4 apical elements (3 spines, 1 seta), 3 inner plumose setae, tiny inflated process near apical margin, and pectinate membrane at base of each apical spine; outer apical spine with row of tiny denticles on anterior and posterior sides (denticles on posterior side not drawn); middle and inner apical spines each with serrations on anterior and posterior sides (serrations on posterior side not drawn) and an accessory process; apical seta plumose, shorter than outer apical spine. Endopod digitiform, bearing 2 elements apically.

Leg 2 (Fig. 3B) intercoxal sclerite subquadrate, with large hyaline membrane along distal margin. Coxa with 1 inner plumose seta and 2 pores on anterior surface. Basis with 1 outer short, plumose seta, 1 minute pore near outer margin, 1 inner sensillum, and large hyaline membrane along inner margin. Exopod 3-segmented, with large hyaline membrane covering dorsal surface of ramus. First segment with 1 inner plumose seta, inner row of setules, and pectinate membrane at base of large outer spine; latter with sclerotized flange along outer margin and fine serrations along inner margin. Second segment with 1 inner plumose seta, inner row of setules, 1 outer serrate spine, and 1 minute pore on anterior surface. Third segment with inner row of setules, 5 inner plumose setae, 3 outer spines, and 1 minute pore near lateral margin; proximal outer spine with serrated margins; middle outer spine with hyaline membrane along both margins; outer distal spine with hyaline membrane along outer margin and row of setules along inner margin. Endopod 3-segmented. First segment with 1 inner plumose seta and row of setules on distolateral corner. Second segment with 2 inner plumose setae, row of setules along inner and outer margins, and 1 minute pore on anterior surface. Third segment with 6 plumose setae and short row of setules along proximolateral and proximomedial margins.

Leg 3 (Fig. 4A) protopod large, modified to form apron, with 1 outer plumose seta situated near base of exopod, 1 inner plumose seta near large intercoxal sclerite, 1 proximolateral corrugated pad on dorsal surface, 3 marginal membranes, minute pores scattered on ventral surface, and 2 unequal sensilla along posterior margin. Exopod (Fig. 4B) 3-segmented. First segment with 1 inner plumose seta, 1 apical spine reflexed over second segment and furnished with sclerotized flange along outer margin, and 1 minute pore, several sensilla and sclerotized flange on outer basal swelling. Second segment with 1 outer naked spine, 1 inner plumose seta, 1 minute pore, and setules along lateral and medial margins. Third segment with 4 plumose setae, 3 naked spines, and setules along proximal margins. Endopod 2-segmented. First segment with 1 inner plumose seta and outer row of setules. Second segment with 6 plumose setae and setules along outer and inner margins.

Leg 4 (Fig. 4C) protopod with 1 distolateral plumose seta. First exopodal segment with pectinate membrane at base of small, outer naked spine and serrations and several sensilla

along outer margin. Second exopodal segment similar to first segment but with much larger outer spine furnished with pectinate margins. Third exopodal segment with 3 apical pectinate spines, pectinate membrane at base of each spine, and tiny serrations along outer margin; spines progressively increase in length from outer to inner apical margin.

Leg 5 (Fig. 4D) vestigial, comprised of small setiferous papilla and broad trisetose lobe on posteroventral surface of genital complex.

Leg 6 (not figured) rudimentary, represented by unarmed genital operculum at gonopore opening.

Description of adult male. Body (Fig. 5A) 2.64 (2.53–2.78) mm long (excluding caudal setae) ( $n=4$ ). Cephalothoracic shield slightly longer than wide [ $1.73$  (1.65–1.83)  $\times$   $1.62$  (1.58–1.65) mm], ornamented as in female. Free fourth pedigerous somite wider than long [ $170$  (160–180)  $\times$   $406$  (385–420)  $\mu\text{m}$ ]. Genital complex wider than long [ $448$  (420–470)  $\times$   $514$  (490–540)  $\mu\text{m}$ ]. Abdomen composed of 1 somite,  $210$  (210–210)  $\times$   $268$  (260–275)  $\mu\text{m}$ , narrowed at junction with genital complex. Caudal ramus longer than wide [ $120$  (110–130)  $\times$   $110$  (100–115)  $\mu\text{m}$ ], armed as in female.

All limbs as in female, except for the following. Antennule (Fig. 5B) with 29 setae (27 hirsute, 2 naked) on proximal segment. Antenna (Fig. 5C–E) 3-segmented, comprising coxa, basis, and 1-segmented endopod incorporating distal claw. Coxa with large corrugated pad along outer margin on posterior side and fine striations on inner distal margin on anterior side. Basis with 1 large and 1 small corrugated pad on posterior side and 3 unequal corrugated pads on anterior side. Endopod forming robust terminal claw with sclerotized flange on posterior side and bearing 2 naked setae and 3 accessory claws. Maxillule (Fig. 5F) with hyaline digitiform process medial to bifid dentiform process. Postoral process (Fig. 5F) elongate and corrugated. Maxilliped (Fig. 6A) lacking small patch of denticles on distolateral corner of protopod and fine apical striations on claw. Weakly sclerotized adhesion pad (Fig. 6B) present, situated anterior to sternal furca. Leg 5 (Fig. 6C) lobate, bearing 2 plumose and 2 unipinnate setae. Leg 6 (Fig. 6C) forming genital operculum, armed distally with 1 pinnate and 2 plumose setae.

Variability. Female specimen from *H. rostratus* captured at Station 3 without row of setules along inner margin of caudal rami (Fig. 1B) and with one apically bifurcate seta on distal endopodal segment of right leg 3 (Fig. 6D).

Attachment site. Body surface.

Prevalence and mean intensity. From a total of 655 Giant Kelpfish that were inspected for *Lepeophtherius* infections between June 2011 and February 2013, 233 *L. schaadti* n. sp. were removed from 86 fish (prevalence = 13.1%; mean intensity = 2.71). By contrast, from a total of 2716 Striped Kelpfish captured within the same time period at Inner Cabrillo Beach, only two *L. schaadti* n. sp. were recovered from one fish (prevalence = 0.04%; mean intensity = 2).

Etymology. This species is named in honor of Mike Schaadt, the Director of the Cabrillo Marine Aquarium.

Remarks. Examination of Wilson's (1908, 1924) *Lepeophtherius* specimens from the Flag Rockfish, *Sebastes rubrivinctus*, and Rock Wrasse, *Halichoeres semicinctus*, captured in California waters revealed they are not conspecific with *L. parviventris*. More importantly, examination of Wilson's (1935) *Lepeophtherius* specimens from Newport Bay, California, revealed they are conspecific with *L. schaadti* n. sp. and the host was the Spotted Kelpfish, *Gibbonsia elegans*, rather than the Giant Kelpfish, as indicated on the vial label.

*L. schaadti* n. sp. resembles *L. elegans* Gusev, 1951, *L. hexagrammi* Gusev, 1951, and *L. hospitalis* Fraser, 1920 by having in the female a genital complex that is at least half the length of the cephalothoracic shield (including frontal plates) and with small, rounded posterolateral lobes, a 1-segmented abdomen that is less than one-quarter the length of the genital complex, a

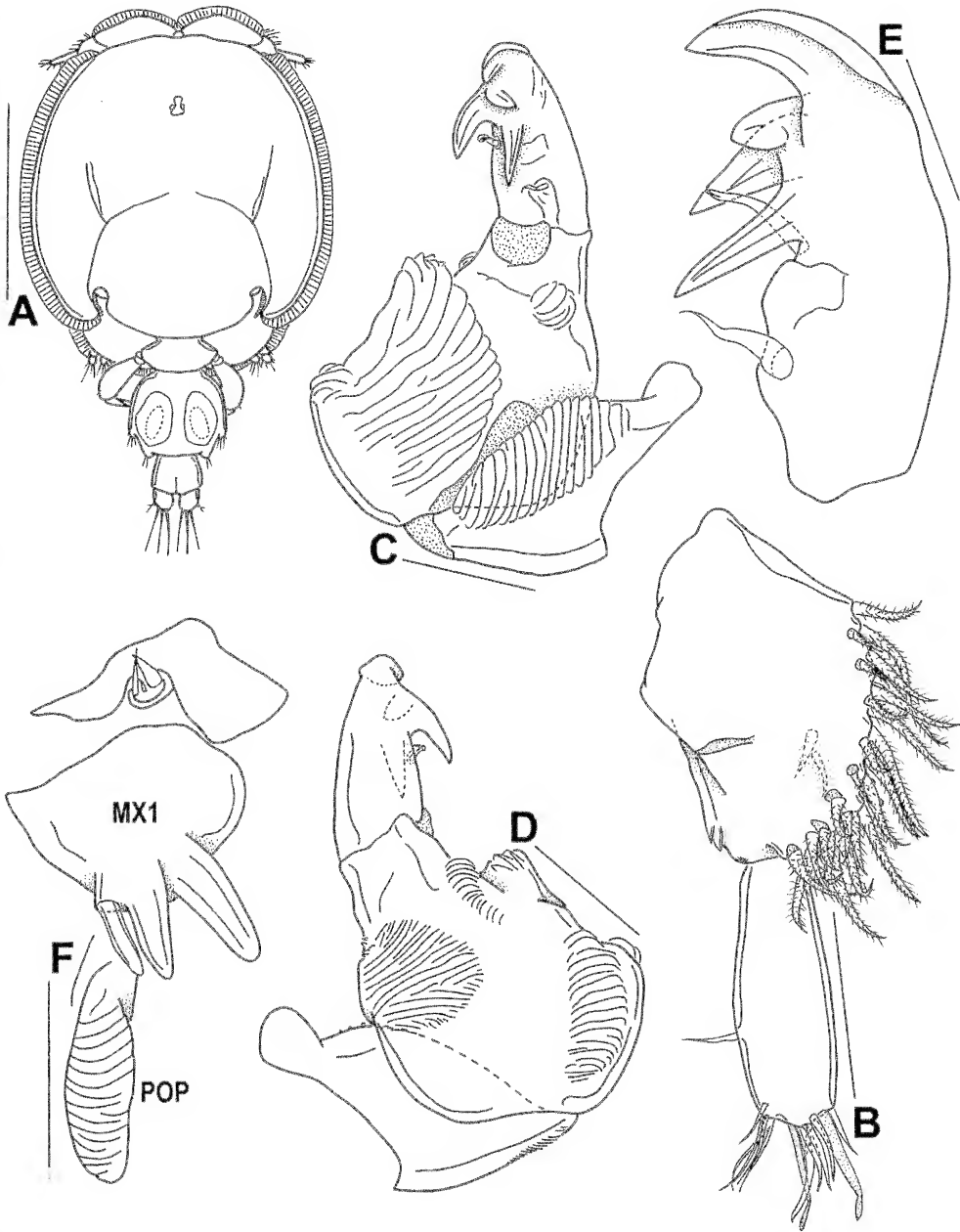


Fig 5. *Lepeophtheirus schaadti* n. sp., adult male. A) Habitus, dorsal; B) Left antennule, ventral; C) Left antenna, posteromedial; D) Left antenna, anterolateral; E) Distal endopodal segment of left antenna, posterior; F) Left maxillule (MX1) and postoral process (POP), ventral. Scale bars: 1.00 mm for A; 100  $\mu$ m for B, C, D, F; 50  $\mu$ m for E.

maxillule with two large tines on the dentiform process, a maxilliped without a myxal process, a pair of non-bifid tines on the sternal furca, the spine on the first exopodal segment of leg 3 inserted distally on the basal swelling, a 3-segmented leg 4 exopod, and the inner lobe of leg 5 not protruding beyond the posterior margin of the genital complex.

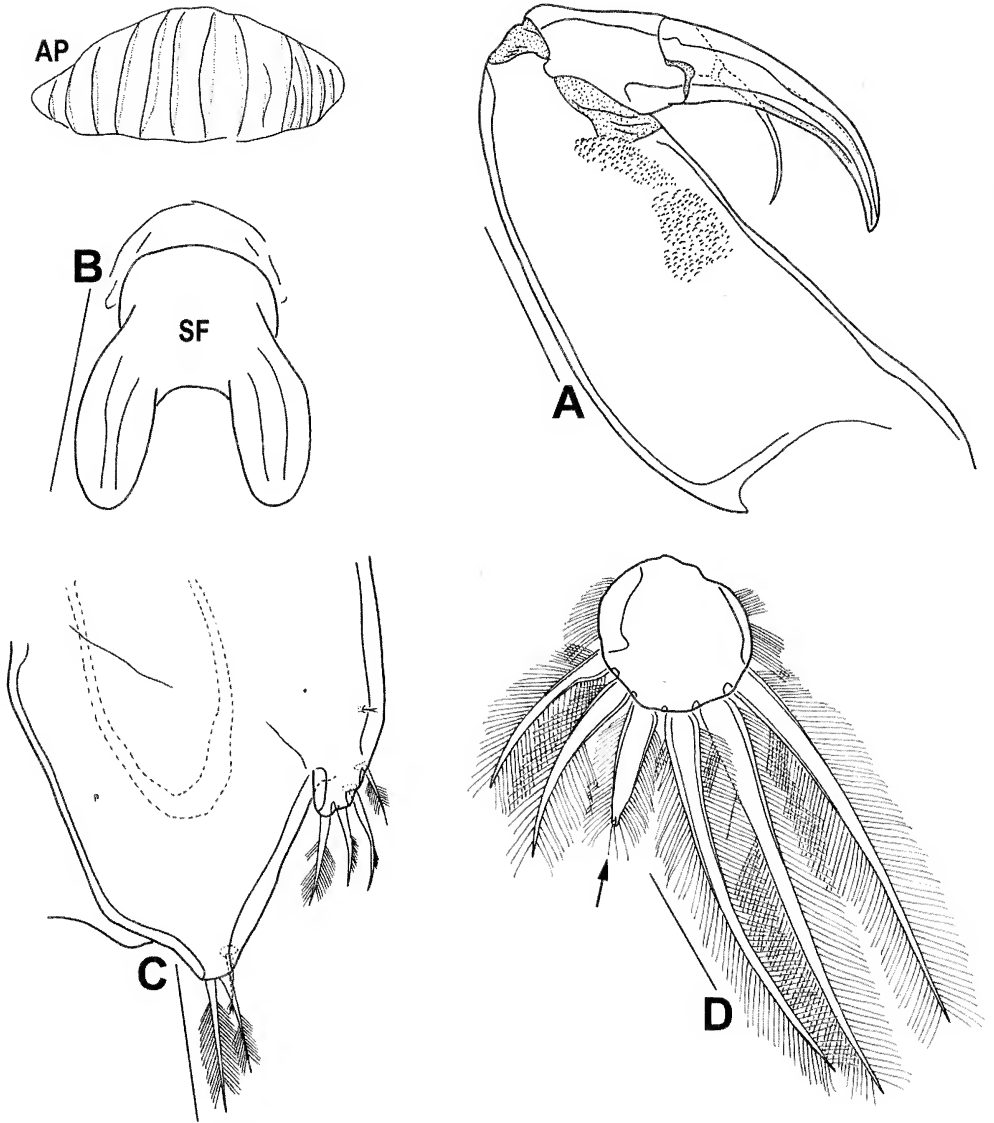


Fig 6. *Lepeophtheirus schaadti* n. sp., adult male (A–C) and adult female (D). A) Left maxilliped, anterior; B) Sternal furca (SF) and adherence pad (AP), ventral; C) Left legs 5 (P5) and 6 (P6), ventral; D) Distal endopodal segment of right leg 3 (arrow indicates abnormal seta), ventral. Scale bars: 100  $\mu$ m for A, B, C; 50  $\mu$ m for D.

*L. elegans* can be distinguished from *L. schaadti* n. sp. by having a smooth inner distal corner on the basis of the female antenna, pointed tines and no ridge on the inner tine of the dentiform process of the female maxillule, no denticles on the outer distal corner of the protopod of the female maxilliped, pointed tines on the female sternal furca, a subtriangular inner lobe on the female leg 5, no accessory claws on the endopod of the male antenna, and a large, cone-shaped myxal process on the protopod of the male maxilliped.

*L. hexagrammi* can be differentiated from *L. schaadti* n. sp. by the presence of a smooth inner distal corner on the basis of the female antenna, a broader and less recurved hook on the postantennal process of both sexes, both an outer basal knob and a ridge on both tines on the



dentiform process of the female maxillule, more tapered tines on the female sternal furca, one accessory claw on the endopod of the male antenna, and a large, cone-shaped myxal process on the protopod of the male maxilliped.

*L. hospitalis* can be discerned from *L. schaadti* n. sp. by having a pointed and less recurved hook on the postantennal process of both sexes, a basal semispherical knob on the dentiform process of the maxillule of both sexes, broad flanges on the pointed tines of the female sternal furca, a subtriangular inner lobe on the female leg 5, and two accessory claws on the endopod of the male antenna.

### Discussion and Conclusions

The discovery of *L. schaadti* n. sp. represents the first account of an ectoparasitic species from the Striped Kelpfish and Spotted Kelpfish, as well as the fourth ectoparasitic species reported from the Giant Kelpfish. The copepods *Chondracanthus heterostichi* Ho, 1972 and *C. horridus* Heller, 1865 (Chondracanthidae Milne Edwards, 1840) and the leech *Heptacyclus cabrilloi* Burrenson, Kalman Passarelli & Kim, 2012 (Piscicolidae Johnston, 1865) were previously recorded from the Giant Kelpfish (Wilson 1935; Ho 1972b; Burrenson et al. 2012). It must be noted, however, that Wilson's record of *C. horridus* on the Giant Kelpfish requires verification, as *C. horridus* was originally described from the Black Goby, *Gobius niger* Linnaeus, 1758 (as *Gobius jozo* Linnaeus, 1758) (Gobiidae Cuvier, 1816), from the Mediterranean Sea (Heller 1865).

In this study, 13.1% of the Giant Kelpfish were infected with *L. schaadti* n. sp. as compared to only 0.04% of the Striped Kelpfish. These disparate infection levels suggest that the Giant Kelpfish is a more common host of *L. schaadti* n. sp. at Inner Cabrillo Beach. It remains to be determined how common *L. schaadti* n. sp. is throughout the geographical range of its kelpfish hosts, including the Spotted Kelpfish.

From 2011 to 2014, 20 individuals of *L. schaadti* n. sp. were infected with the hyperparasitic monogene *Udonella* sp. (Udonellidae Taschenberg, 1879). Nearly all *Udonella* specimens were attached to the external surface of the copepod's genital complex, with a few on the cephalothorax and egg sacs. In California, *Udonella caligorum* Johnston, 1835 has been reported from the copepods *Trebius caudatus* Krøyer, 1838 and *T. latifurcatus* Wilson, 1921 (Trebiidae Wilson, 1905) parasitic on the Bat Ray, *Myliobatis californica* Gill, 1865 (Myliobatidae Bonaparte, 1835); on the Curlfin Sole, *Pleuronichthys decurrens* Jordan & Gilbert, 1881 (Pleuronectidae Rafinesque, 1815); and on the isopod *Elthusa vulgaris* (Stimpson, 1857) (as *Lironeca vulgaris* Stimpson, 1857) (Cymothoidae Leach, 1818) parasitic on the Sand Sole, *Psettichthys melanostictus* Girard, 1854 (Pleuronectidae) (Love and Moser, 1983). Identification of the *Udonella* material is currently underway and will be dealt with in detail elsewhere.

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## Habitat Use and Behavior of the East Pacific Green Turtle, *Chelonia mydas*, in an Urbanized System

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**Abstract.**—Green sea turtles, *Chelonia mydas*, are known to inhabit populated and often urbanized areas. To understand turtle habitat use and behavior within these unique habitats, seven juvenile green turtles were fitted with acoustic transmitters (September 2012 – August 2014), of which two transmitters included an accelerometer (AP transmitter). One individual fitted with an AP transmitter was tracked using a passive acoustic array in an urbanized river, the San Gabriel River, Long Beach, CA (33°45' N, 118°05' W). Three additional turtles in this river and three turtles (one with AP transmitter) in a restored estuary (33°44' N, 118°03' W) in southern California were actively tracked for two non-consecutive 24-h periods. Those fitted with AP transmitters indicated that turtles were less active at night ( $0.58 \pm 0.56$  m/s<sup>2</sup> and  $0.50 \pm 0.63$  m/s<sup>2</sup>) than during the day ( $0.86 \pm 0.63$  m/s<sup>2</sup> and  $0.78 \pm 0.60$  m/s<sup>2</sup>) at both sites. Activity data and corresponding movements of the actively tracked turtle fitted with the AP transmitter were used to infer resting periods for other tracked individuals. Turtles rested near bridge pilings and runoff outflows in the river to potentially shelter from tidal flow. Turtles used significantly larger daily areas in the urbanized river ( $0.046 \pm 0.023$  km<sup>2</sup>) where resources may be patchier and less abundant, compared to turtles in the estuary ( $0.024 \pm 0.012$  km<sup>2</sup>) where large, dense eelgrass beds are present. Based on the habitat use and behaviors of green sea turtles, it appears that some green sea turtles are able to make use of both highly developed and restored habitats and likely benefit from certain aspects of development.

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Green sea turtles, *Chelonia mydas*, have been listed and protected in the United States under the Endangered Species Act (ESA) since 1978 (FWS and NMFS, 80 FR 15271). Through decades of research and assessment programs, populations have increased throughout different areas of the world (Chaloupka and Limpus 2001, Godley et al. 2001, Balazs and Chaloupka 2004). Specifically, the east Pacific green sea turtle (hereafter referred to as green turtle) population has shown signs of recovery through an increase in nesting females in Michoacán, Mexico (largest nesting aggregation in the population), likely a result of nesting beach protection in 1979 in Mexico coupled with a reduction in poaching in foraging areas (Seminoff et al. 2015).

As this green turtle population continues to increase, we expect turtle abundance to increase at the edges of their range and new individuals to expand the population range as far as their thermal tolerance will allow. Currently, the northern residential limit of this population is the heavily urbanized region of southern California. In California, roughly 90% of the natural wetlands and

riparian habitat have been destroyed or altered in some way (Allen and Feddema 1996, Smith 1999, Ackerman and Stein 2007). Adult green turtles use these types of coastal habitats to forage, while juveniles use them for up to 20 years where they feed on various species of algae, eelgrasses, and invertebrates until they reach maturity at approximately 30 years of age (Musick and Limpus 1997, Seminoff et al. 2002b, Goshe et al. 2010). Therefore, due to the reduction of natural suitable habitat, individuals may seek out these urbanized estuarine environments in search of food and refuge. However, few studies have investigated how green turtles use these types of urban habitats (Renaud et al. 1995, MacDonald et al. 2012, MacDonald et al. 2013).

Anecdotal evidence suggested that an unknown number of green turtles have been observed within anthropogenically-altered habitats further north of their previously known residential range within the east Pacific (San Diego Bay, CA) at Long Beach and Seal Beach, CA for at least the last 50 years in smaller numbers (D. Lawson, pers. comm.). This aggregation of green turtles seems to have increased (D. Lawson, pers. comm.) and primarily been observed inhabiting the San Gabriel River, a highly urbanized river that is channelized with rocky levees and lined with two electric generating plants (herein referred to as “power plants”). Despite this increase in green turtle presence, the river lacks eelgrass (Merkel & Associates Unpub. data), which is a major green turtle food source. In addition, green turtles have been found in the more “natural” Seal Beach National Wildlife Refuge (SBNWR) composed of some restored habitat, including shallow saltwater basins and tidal channels that were dredged out as part of restoration project. Specifically, green turtles have been observed within a smaller eelgrass covered, recently restored, dredged saltwater basin called the 7<sup>th</sup> St. Basin (Jirik and Lowe 2012).

Further, previous passive acoustic telemetry monitoring has indicated that juvenile green turtles likely remain in the river year around, while some individuals spend the warmer months in the basin (Crear et al. 2016); however, based on the low positional accuracy (50 – 600 m) of passive tracking it is unclear how green turtles are selecting for microhabitats within these altered environments. As a result of the anthropogenic changes made to coastal habitats, we expect to see a change in prey density and an influence in foraging habitat use, which should in turn, directly influence green turtle area use and habitat selection. For example, in the San Gabriel River green turtles have to rely on prey items like algae and invertebrates because the river lacks eelgrass. As a result of this missing resource, green turtles might be expected to use more of the river in search of prey compared to a habitat that has an abundance of eelgrass (e.g. SBNWR) (Whiting and Miller 1998, Seminoff et al. 2002a, Makowski et al. 2006, Seminoff and Jones 2006). Individuals in altered areas may also undergo behaviors that are often observed in natural habitats, like displaying higher activity levels during the day (possibly foraging) (Heithaus et al. 2002, Makowski et al. 2006, Blumenthal et al. 2010). Green turtles may also adapt to the presence of various manmade hard structures (i.e. rocky levees) by resting, a behavior that has been observed along natural vertical features to avoid predation and tidal currents (Shaver 1994, Makowski et al. 2006, Seminoff et al. 2006). These behaviors have not been addressed in green turtles that inhabit urbanized habitats.

These study sites present a unique opportunity to understand how green turtles use habitats in a heavily urbanized environment (the San Gabriel River) compared to an adjacent, restored, more “natural” environment (SBNWR). Based on diel differences in habitat use and movements of green turtles and the differences between the two sites, it was hypothesized that green turtles would: 1) use smaller activity spaces, move shorter distances, and travel more slowly within the smaller, eelgrass-covered 7<sup>th</sup> St. Basin, 2) exhibit more resting behavior at night by moving less at both sites, and 3) display a behavior indicative of resting while associating with hard structures within the river at night. Understanding how a recovering threatened species behaves

in an altered environment compared to a restored one will inform management as to the best habitats to protect or restore, ensuring populations continue to increase.

### Materials and Methods

The San Gabriel River (33°45' N, 118°05' W; estuarine region) is a highly urbanized river, lined with concrete and channelized near the mouth (Stein 2007), that discharges into the Pacific Ocean between Long Beach, CA and Seal Beach, CA (O'Brien et al. 2011). The concrete portion extends from upriver to approximately six km upstream from the mouth of the river (i.e. green turtles cannot access upstream of six km from the mouth of the river because the river is lined by concrete and too shallow). Where the concrete portion ends, depth increases to approximately four meters, providing 0.51 km<sup>2</sup> of estuarine river habitat (Fig. 1). The substrata along this stretch of river consists of mostly fine sediments; however, hard structures like rocky levees and runoff outflows from the two power plant systems line either side (Merkel & Associates Unpub. data). This highly urbanized river supports multiple species of fish, mollusks, arthropods, polychaetes, and marine algae either as infauna within the muddy substratum or as epifauna among the hard structures (Turner and Strachan 1969). Many of these species often serve as prey for juvenile green turtles (Blumenthal et al. 2010, Carrión-Cortez et al. 2010). Although there is a diverse benthic community in the San Gabriel River, there are no eelgrass beds (Merkel & Associates Unpub. data), which are thought to be an important food source and common habitat component in some areas where green turtles forage (Musick and Limpus 1997).

Unlike the highly urbanized San Gabriel River, the SBNWR (33°44' N, 118°03' W) is a 14-km<sup>2</sup> estuary surrounded by the Seal Beach Naval Weapons Station and is inaccessible to the public (Fig. 1). SBNWR has four restored dredged estuarine basins which connect to Anaheim Bay through a network of dredged channels (Jirik and Lowe 2012) (Fig. 1). Green turtles have been observed in one of the restored basins (7<sup>th</sup> Street Basin: 0.15 km<sup>2</sup>; less than a third of the San Gabriel River) since 2008 (K. Jirik, pers. comm.). A concrete culvert (1.5 × 2.4 × 12.0 m) dampens tidal flow in and out of the 7<sup>th</sup> St. Basin and animals are able to swim freely through the culvert except during strong tidal changes (Jirik and Lowe 2012). Depth is relatively uniform and shallow (<3 m) throughout the basin; therefore, water temperatures within the 7<sup>th</sup> St. Basin get warmer than the adjacent natural estuary in the summer, but become colder in the winter (Jirik and Lowe 2012). In fact, green turtles have only been observed in the 7<sup>th</sup> St. Basin during the warmer months (Crear et al. 2016; K. Gilligan, pers. comm.). A muddy substratum is uniformly distributed throughout the 7<sup>th</sup> St. Basin; however, unlike the San Gabriel River, large patches of eelgrass (*Zostera marina* and *Enteromorpha* spp.) cover over 40% of the basin (Merkel & Associates Unpub. data).

Green turtles were caught using entanglement nets (set time: 1-5 hrs; checked nets < 30 mins; net length: 50-150 m; mesh size: 0.3 m) in the San Gabriel River and 7<sup>th</sup> St. Basin approximately every three months from June 2012 to August 2014 (Fig. 1). When green turtles were caught, they were removed from the net, kept on the boat (San Gabriel River) or brought to shore (7<sup>th</sup> St. Basin) for work up. Straight carapace length (SCL, ± 0.1 cm) was measured and each turtle was weighed (± 1.0 kg), tagged with an Inconel flipper tag (Style 681, National Band and Tag Company, KY), and injected with an internal passive integrative transponder (PIT) tag (Avid, Norco, CA). A subsample of individuals was fitted with a continuous acoustic transmitter (V13-1L, 13 × 45 mm, frequencies: 60-84 kHz, continuous pulse rate 2000 ms, power output: 153 dB, 12 g in air, VEMCO Ltd). Transmitters were attached to the carapace using a fiberglass cloth and resin laminate (Balazs et al. 1996). Upon completion, all turtles were released at the capture location within 1.5 hrs.

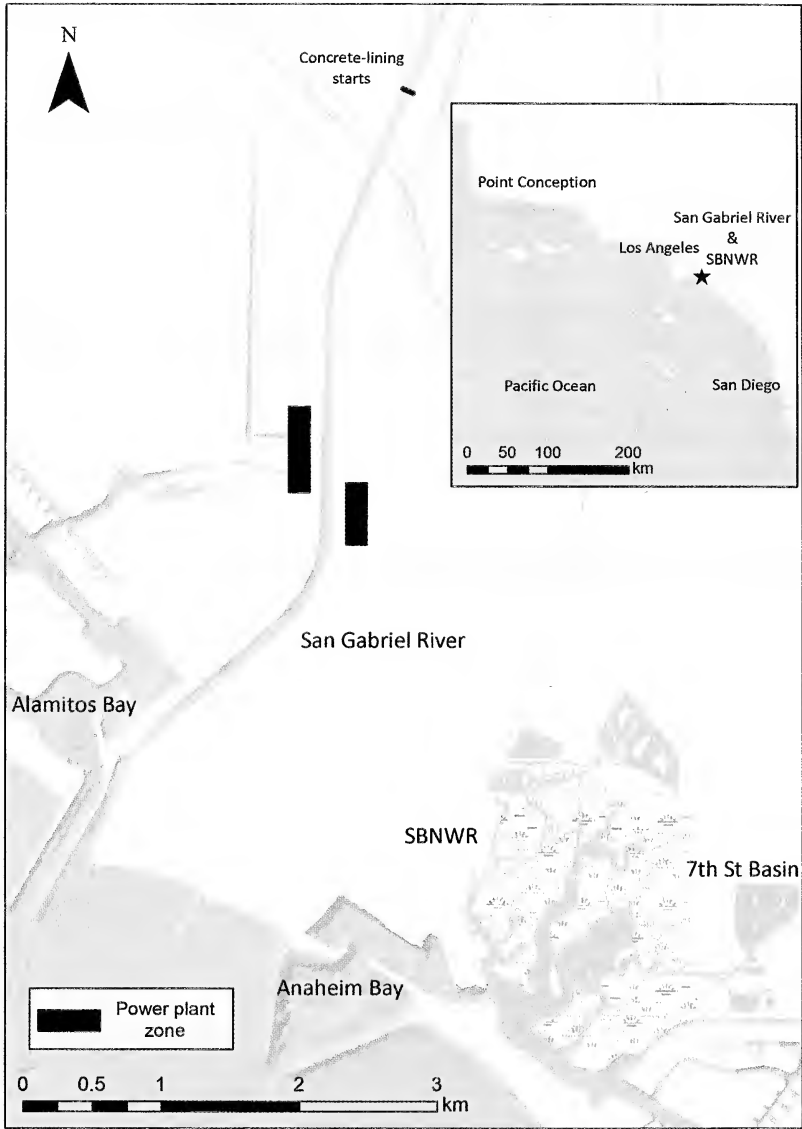


Fig. 1. Map of the San Gabriel River and 7<sup>th</sup> St. Basin within the Seal Beach National Wildlife Refuge (SBNWR). Concrete-lining begins at 6 km from the river mouth and continues upstream.

Tagged green turtles were actively tracked for two non-consecutive 24-h periods at least a day following capture and release in order to avoid behavioral changes due to capture stress. Individuals were tracked from a 4.3-m aluminum boat using a directional hydrophone (VH110, VEMCO Ltd, Bedford, Nova Scotia) and an acoustic tracking receiver (VR100, VEMCO Ltd). The VR100 records the gain, time, date, latitude and longitude, and signal strength of each detection. At 10 min intervals, VR100 positional data with the highest signal strength above 80 dBs under a gain of zero were selected for inclusion in the data set, except in areas where the attenuation of the transmitter's signal was altered due to the turbulence from the power plants discharged water. Due to this attenuation, if the turtle was in the discharge outflow all received

signal strengths were kept. If a tracked turtle was detected moving into the power plant discharged outflow in the San Gabriel River and the signal was lost, a fixed position corresponding to the opening of the closest discharge station was recorded. All VR100 detections at 10-min intervals that followed the previous criteria were considered valid geolocations. Some intervals between geolocations were greater than 10 min due to the time required for replacing tracking personnel; therefore, the number of geolocations varied for each track.

Transmitters were range-tested to determine the distance the VR100 (at a gain of zero) must be from the transmitter on the turtle in order to get an accurate location of the turtle at various locations within the study sites. To do this, the researcher made several passes by a transmitter suspended midwater, while using the directional hydrophone and VR100 to measure signal strength. The range-test assessed the signal strength from 0-150 m away from multiple directions. The results of the range test indicated that the tracker would need to be within 10 m of the tagged turtle in order to receive a signal strength of 80 dB or higher; however, this distance significantly decreased in power plant discharge locations.

Accelerometer and pressure sensing (AP) coded acoustic transmitters were fitted to the carapace of two individuals to determine when turtles were resting. An AP transmitter initially transmits its unique ID and pressure value, then measures acceleration on three axes (X,Y,Z) at 5 Hz over a given time period (T), calculates the root mean squared (RMS;  $m/s^2$ ) for the three axes, and then transmits the RMS value. This value represents the average acceleration over the three axes and the general activity index of the animal in this study (O'Toole et al. 2011). The shallow depth of both sites made it difficult to use any of the depth data provided by the AP transmitter. One of the two turtles fitted with an AP transmitter (V13AP-1L, 13 × 44 mm, frequencies: 69 kHz, pulse rate 15 s, T: 12 s, estimated battery life: 104 days, power output: 153 dB, 12.3 g in air, VEMCO Ltd) was included in the subsample of turtles actively tracked in the 7<sup>th</sup> St. Basin, for which acceleration was acquired in real time via the VR100 with an associated signal strength. The second individual tagged with an AP transmitter (V13AP-1L, 13 × 44 mm, frequencies: 69 kHz, random pulse rate 40-80 s, T: 37 s, estimated battery life: 203 days, power output: 153 dB, 12.3 g in air, VEMCO Ltd) was detected and archived by a passive acoustic array from a concurrent study (15 VR2W acoustic receivers, VEMCO Ltd), in which receivers were spaced 300–600 m apart within the San Gabriel River from the river mouth to the concrete lined portion of the river (Crear et al. 2016). Horizontal movements of this individual were included in Crear et al. (2016), while this study incorporated only the individual's acceleration values.

Using the valid VR100 geolocation data every 10-min, localized convex hulls (LoCoHs) were created for each individual 24-h track to determine daily activity use and core area use in R (v. 3.2.3, R Core Team, 2015) using the *adehabitatHR*, *adehabitatHS*, *fields*, and *maptools* packages (Calenge 2006, Bivand and Lewin-Koh 2013, Furrer et al. 2013). LoCoHs were used due to their ability to handle geomorphological boundaries (e.g. river and estuary boundaries) when constructing utilization distributions (Getz and Wilmer 2004, Getz et al. 2007). Adaptive or *a*-LoCoH method was used in which a hull is constructed around each reference point and nearby points, where the sum of the distances between nearby points and the reference point equals *a*. The value of *a* is selected for each individual based on the distance that individual traveled during that track. The hulls are then merged together from smallest to largest (Getz et al. 2007). The area in which 95% of the hulls were merged represented green turtle daily area use, while the area in which 50% of the hulls were merged represented green turtle core area use. In order to take into account the differences in the number of geolocations acquired among tracks and possibility of autocorrelation, bootstrapping was done for each track, where only a subset of geolocations was randomly selected. Linear mixed effects models were used to

compare daily and core area use sizes from each green turtle track between the two sites with turtle and individual track as random effects in the R package lme4 (Bates et al. 2013). Both core and daily area use sizes were log transformed in order to achieve equal variances. A likelihood ratio test was used to compare each model to the model without site. Core and daily area use LoCoHs from each track were mapped in ArcGIS 10.2.

To determine when periods of resting occurred, first passage time (FPT) was used. FPT is the time required for an animal to cross a circle of a given radius, where movements become more tortuous the longer it takes an animal to cross the circle (Fauchald and Tveraa 2003, Papastamatiou et al. 2012). This type of analysis is typically used to determine periods of area-restricted search (ARS); however, higher FPT values are indicative of resting; therefore, we referred to it as area-restricted-use (ARU). The circle radius or the spatial scale of ARU selected was 25 m for the analysis because it was thought that a turtle resting on the bottom, followed by the individual ascending to the surface for a breath, then descending back down to possibly a new area would not exceed a circle with a radius of 25 m. It is important to note that 25 m is greater than the errors in the geolocations, which ensured that we were analyzing turtle movements, not geolocation error. FPT analysis was conducted on each track for each individual using adehabitatLT package in R (Calenge 2006). To validate high periods of FPT corresponding with resting (ARU), a Pearson's product-moment correlation was conducted between FPT values from the actively tracked turtle fitted with an AP transmitter and the corresponding RMS acceleration values (see Results). Based on the relationship between RMS acceleration and FPT data and observations in the field, when an FPT value was greater than 4000 sec (67 mins), the turtle was assumed to be resting and undergoing ARU. Each point was assigned a "yes" or "no" for resting or not based on the FPT value at that point. This threshold was used on all tracked individuals in order to predict periods of resting. To determine whether turtles spent more time resting during the day or at night or between sites, a generalized linear mixed effects model with a binomial distribution was used with turtle as the random effect. A likelihood ratio test was then used to compare the full model to models without each factor (diel period and site).

To provide support for ARU and resting behavior results for different diel periods between sites, various movement metrics were quantified. The total distance traveled and rate of movement (ROM) were determined for day, night, and the complete track. Total distance traveled was determined by summing the distances between each subsequent 10 min geolocations. ROM was calculated as the distance traveled between two consecutive geolocations, divided by the time taken by the green turtle to swim between the two geolocations. Pearson's product-moment correlations were conducted to test for a negative correlation between all combined FPT and ROM values from the river tracks and all combined FPT and ROM values from the basin tracks. In addition, to determine if the distance traveled and ROM differed between day and night or between the two sites, linear mixed effects models were used with individual green turtle as a random effect in R v. 3.0.1 using the nlme package (Pinheiro et al. 2013). ROM values were  $\log(x + 1)$  transformed in order to achieve equal variance. All statistics were evaluated at significance levels of  $\alpha = 0.05$ .

Substrate type and eelgrass presence or absence were characterized in both the San Gabriel River and the SBNWR using interferometric sidescan sonar with dual antenna differential GPS by Merkel & Associates (Unpub. data). Ground-truthing was completed at both sites using a combination of visual surveys from shore, snorkel, SCUBA, ROV, and drop camera verification (Merkel & Associates Unpub. data). Substrate type was divided into six groups in the San Gabriel River: non-vegetated soft bottom, mixed rubble/soft bottom, rubble/hard bottom, engineered structures (bridge pilings, cement discharge structures, runoff outflows), debris, and



Table 1. Summary of size, tracking duration and tracking location for the six green turtles tracked. Turtle 2 was fitted with an AP transmitter and actively tracked for nonconsecutive 24-hs periods. Turtle 7 was fitted with an AP transmitter and monitored by the acoustic array in the San Gabriel River for 69 days. SCL = straight carapace length; Duration of tracks = the combined hours of the two nonconsecutive tracks; SGR = San Gabriel River.

Turtle No.	SCL (cm)	Mass (kg)	Date Tagged	1 <sup>st</sup> Track Date	2 <sup>nd</sup> Track Date	Duration of Tracks (h)	Site Tagged/ Tracked
1	66.3	42	8-Aug-12	28-Sep-12	16-Nov-12	45	SGR
2	56.8	20	10-Jul-13	15-Jul-13	29-Jul-13	48	SBNWR
3	61.4	27	2-Feb-14	14-Feb-14	21-Mar-14	48	SGR
4	74.3	52	29-May-14	6-Jun-14	13-Jun-14	48	SGR
5	67.1	45	5-Aug-14	11-Aug-14	15-Aug-14	48	SBNWR
6	50.8	41	6-Aug-14	18-Aug-14	23-Aug-14	48	SBNWR
7	54.8	23	28-Aug-13	-	-	-	SGR

intertidal sand beach. Within the SBNWR, substrate types were divided up into vegetated and non-vegetated (Merkel & Associates Unpub. data).

To quantify habitat use, habitat selection index (HSI) was used to determine green turtle preference or avoidance of non-vegetated soft bottom, mixed rubble/soft bottom, hard rubble, engineered structures, debris, and intertidal sand beach in the San Gabriel River. Habitat selection index was also used to determine green turtle preference or avoidance of the culvert in the 7<sup>th</sup> St. Basin. A 100 m buffer was made around the culvert to indicate affinity to habitat around the culvert. The area near the culvert was separated into non-vegetated areas (culvert/non-vegetated) and eelgrass covered areas (culvert/eelgrass) based on the presence or absence of eelgrass. The area away from the culvert was also separated into non-vegetated areas (no culvert/non-vegetated) and eelgrass covered areas (no culvert/eelgrass). Based on the criteria determined in Topping et al. (2005), HSI was calculated by taking the percent of the individual's geolocations over a given habitat (habitat use) divided by the percent of each available habitat within the river or the basin (habitat availability). HSI values  $> 1$  and  $< 1$  indicate preference and avoidance, respectively, of a particular habitat type. HSI values were calculated for each habitat type for each turtle during the day, night, and 24-h period, as well as for periods when the turtle was assumed resting (determined through FPT analysis). Habitat selection was analyzed at each site using a chi-square test for each individual turtle. Once a chi-squared value was determined for each individual, chi-squared values were summed to get an overall chi-squared statistic. HSI were calculated in ArcGIS 10.2.

## Results

Six juvenile green turtles were tracked for two nonconsecutive 24-h periods (three in the San Gabriel River and three in the 7<sup>th</sup> St. Basin) between September 2012 and August 2014 (Table 1). No green turtles left the San Gabriel River while they were tracked; however, one green turtle exited the 7<sup>th</sup> St. Basin through the culvert, but remained close to the basin and did not travel to any other area in SBNWR for the remainder of the study. The fewest geolocations for a track were 81; therefore, each LoCoH run was created using 81 randomly selected geolocations from each individual 24-h track. The difference in green turtle core area use (50%) was not significant (Likelihood-ratio test,  $\chi^2 = 3.70$ ,  $p = 0.055$ ) between the San Gabriel River and the 7<sup>th</sup> St. Basin at an  $\alpha = 0.05$  due to the large variability among individuals. The mean for the river (mean  $\pm$  SE) ( $11811 \pm 270 \text{ m}^2$ ; Fig. 2 a-c) was over twice that for the 7<sup>th</sup> St. Basin ( $5113 \pm 127 \text{ m}^2$ ; Fig. 2d). There was a significant difference in daily area use (95%) between the two

Table 2. Percent of time individuals rested during the day and night over each 24-hs track. Tracks where % Resting was 0 is indicative of the individual not exhibiting resting behavior. SGR = San Gabriel River

Turtle #	Track	Location Tracked	% Resting	
			Night	Day
1	1	SGR	100	2
1	2	SGR	69	37
2	1	7 <sup>th</sup> St. Basin	28.6	21.7
2	2	7 <sup>th</sup> St. Basin	73.2	1.5
3	1	SGR	53.7	25
3	2	SGR	15.2	42.9
4	1	SGR	0	0
4	2	SGR	0	0
5	1	7 <sup>th</sup> St. Basin	0	3.3
5	2	7 <sup>th</sup> St. Basin	20	11.9
6	1	7 <sup>th</sup> St. Basin	0	0
6	2	7 <sup>th</sup> St. Basin	24	0

sites (San Gabriel River:  $46552 \pm 943 \text{ m}^2$ ; 7<sup>th</sup> St. Basin:  $23789 \pm 539 \text{ m}^2$ ) (Likelihood-ratio test,  $\chi^2 = 4.51$ ,  $p = 0.034$ ). No overlap occurred among the locations of the core areas of individuals within the San Gabriel River (Fig. 2a-c). At the 7<sup>th</sup> St. Basin, Turtle 2 and Turtle 5 had a 2.5% overlap and Turtle 5 and Turtle 6 had a 21.7% overlap (Fig. 2d). The locations of core areas between the two tracks of an individual varied as well, with five of six turtles showing no overlap in the core areas of their two tracks (Fig. 2a-d). Turtle 6 exhibited a small amount of overlap (19.6%) in core area between its two tracks in the 7<sup>th</sup> St. Basin (Fig. 2d).

Turtle 2, which was fitted with an AP transmitter and actively tracked twice within the 7<sup>th</sup> St. Basin showed a higher mean acceleration during the day ( $0.79 \pm 0.015 \text{ m/s}^2$ ) compared to at night ( $0.47 \pm 0.018 \text{ m/s}^2$ ) (Fig. 3a). Turtle 7, which was also tagged with an AP transmitter, was monitored and acceleration data was archived for 69 days by the passive acoustic array within the San Gabriel River (Crear et al. 2016). Mean acceleration for Turtle 7 in the river was higher during the day ( $0.86 \pm 0.0074 \text{ m/s}^2$ ) compared to during the night ( $0.58 \pm 0.0076 \text{ m/s}^2$ ). Further, the distribution of acceleration values differed between day and night with a high frequency of acceleration values from 0.0-0.1  $\text{m/s}^2$  at night and 0.4-1.0  $\text{m/s}^2$  during the day (Fig. 3b).

There was a significant negative correlation between FPT values and acceleration values (Pearson's product-moment correlation,  $p < 0.05$ ;  $r = -0.19$ ) for the turtle tracked in the 7<sup>th</sup> St. Basin for two 24-h periods (Fig. 3a). This result validated the relationship between high periods of FPT and resting (ARU). In addition, there was a significant negative correlation between FPT values and ROM values for all individuals in the river (Pearson's product-moment correlation,  $p < 0.001$ ;  $r = -0.36$ ) and 7<sup>th</sup> St. Basin (Pearson's product-moment correlation,  $p < 0.001$ ;  $r = -0.41$ ) (Fig. 4b,d). Based on the 4000 sec threshold, resting occurred on 75% of the tracks (Table 2). Turtles appeared to rest for a significantly greater proportion of time during the night (33.0%) compared to during the day (11.7%) ( $\chi^2 = 82.50$ ,  $p < 0.001$ ); however, there was no difference in the proportion of time spent resting between the two sites (Likelihood-ratio test,  $\chi^2 = 0.0002$ ,  $p = 0.99$ ).

All tracked turtles traveled further and had a higher mean ROM during the day than at night (ANOVA,  $F_{1,17} = 30.16$ ,  $p < 0.001$ ,  $F_{1,1266} = 131.66$ ,  $p < 0.001$ ); however, there was no

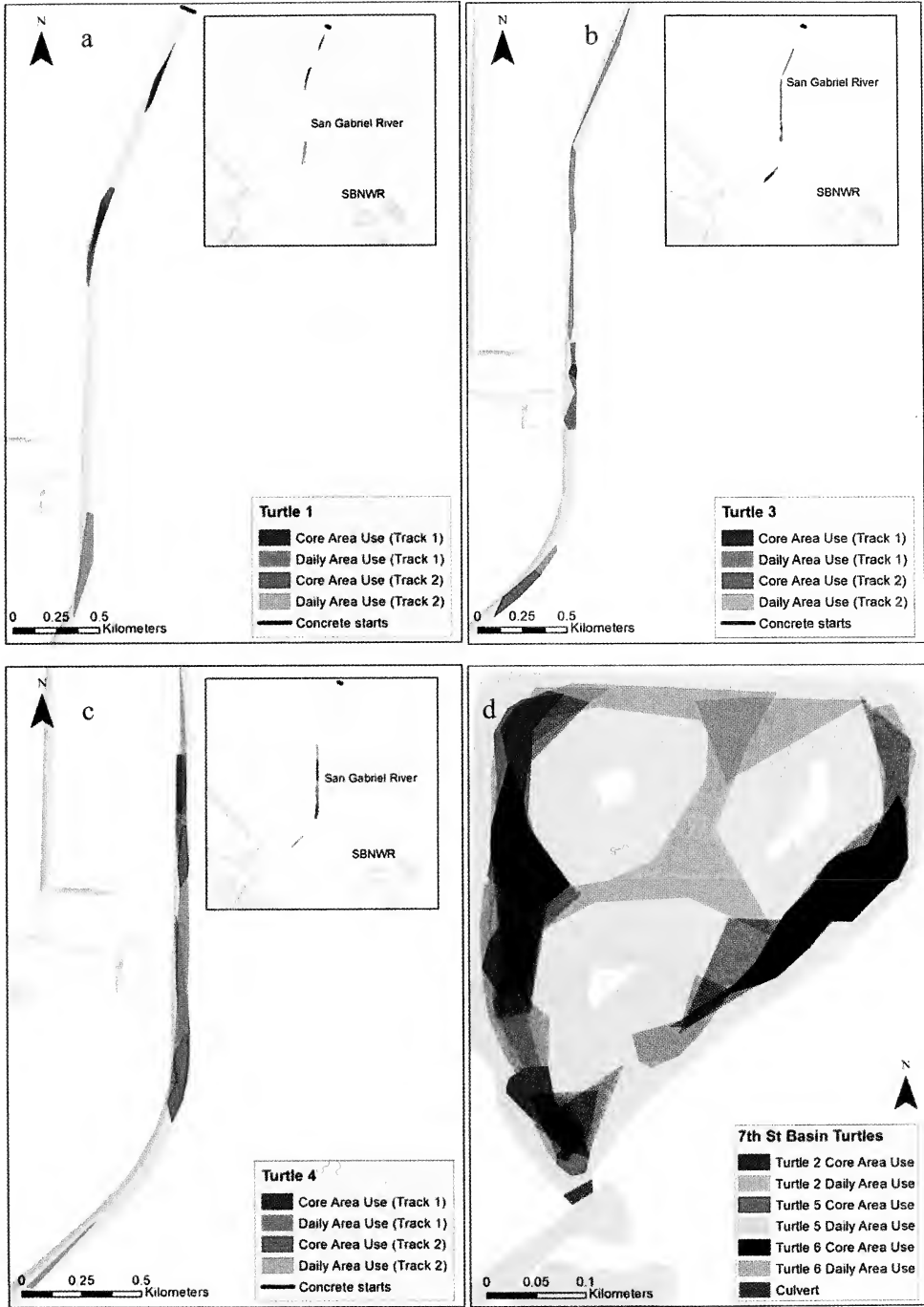


Fig. 2. Core areas and daily areas created by LoCoHs of both tracks of (a) Turtle 1, (b) Turtle 3, and (c) Turtle 4 in the San Gabriel River and (d) both tracks of Turtles 2, 5, and 6 in the 7<sup>th</sup> St. Basin. The lightest shade of blue represents the water and the white in the center of the basin represents the three islands.

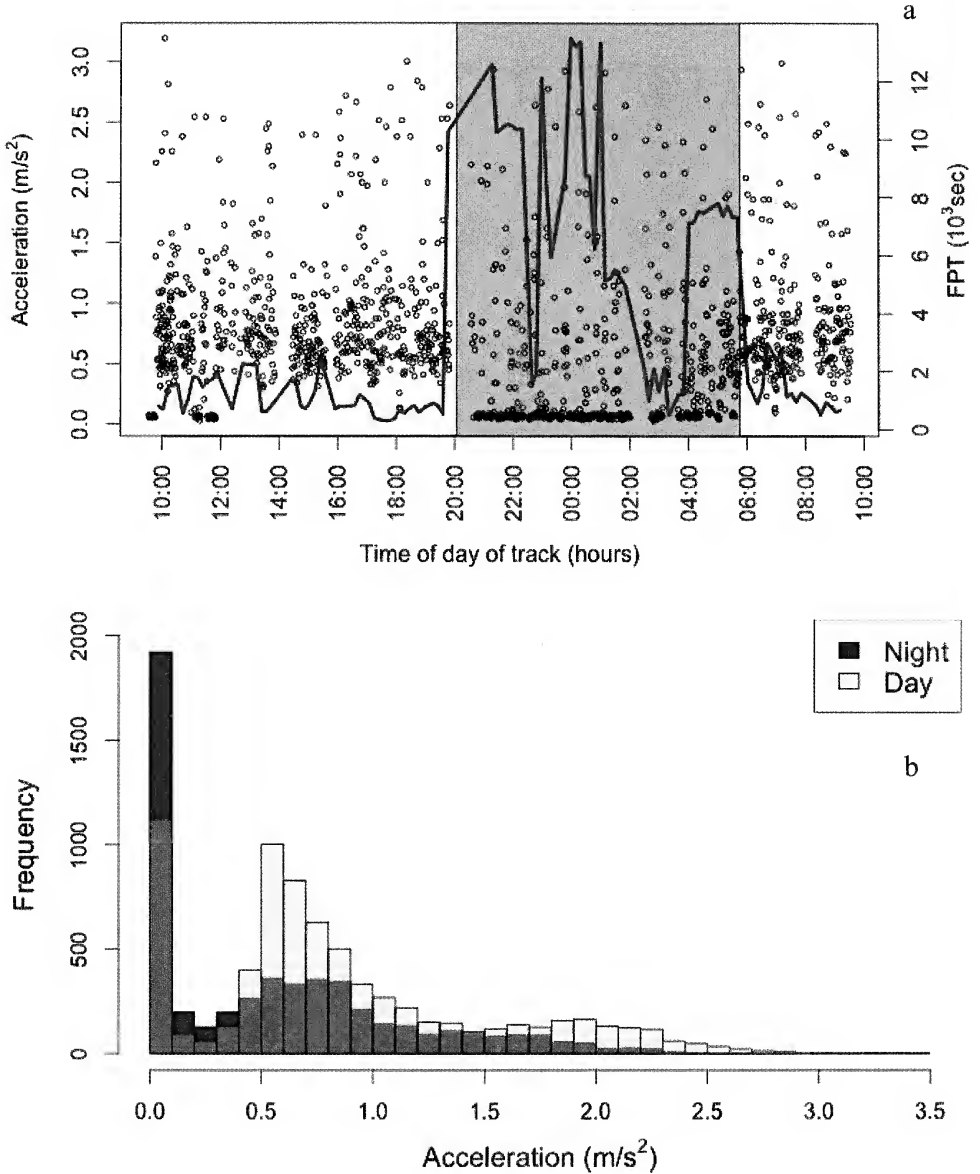


Fig. 3. (a) Raw acceleration (circles) values from the second track of Turtle 2 overlaid by FPT (red line) values. The grey box represents the period between sunset and sunrise on the date of the track. (b) Distribution of all acceleration values during the night and day for Turtle 7 monitored for 69 days by the acoustic array in the San Gabriel River. The middle blue shade indicates where the two histograms overlap.

significant difference in distance traveled (ANOVA,  $F_{1,4} = 0.14$ ,  $p = 0.73$ ) or ROM (ANOVA,  $F_{1,4} = 0.10$ ,  $p = 0.77$ ) for turtles tracked between sites (Table 3).

Actively tracked turtles had unique habitat preferences within both sites. However, turtles only appeared to show a diel difference in HSI at one habitat type (culvert/eelgrass in the 7<sup>th</sup> St. Basin: day:  $0.67 \pm 0.04$ ; night:  $2.62 \pm 1.34$ ); therefore, only 24-h HSI was used for each track. In the river, green turtles exhibited the greatest mean HSI and highest selection for

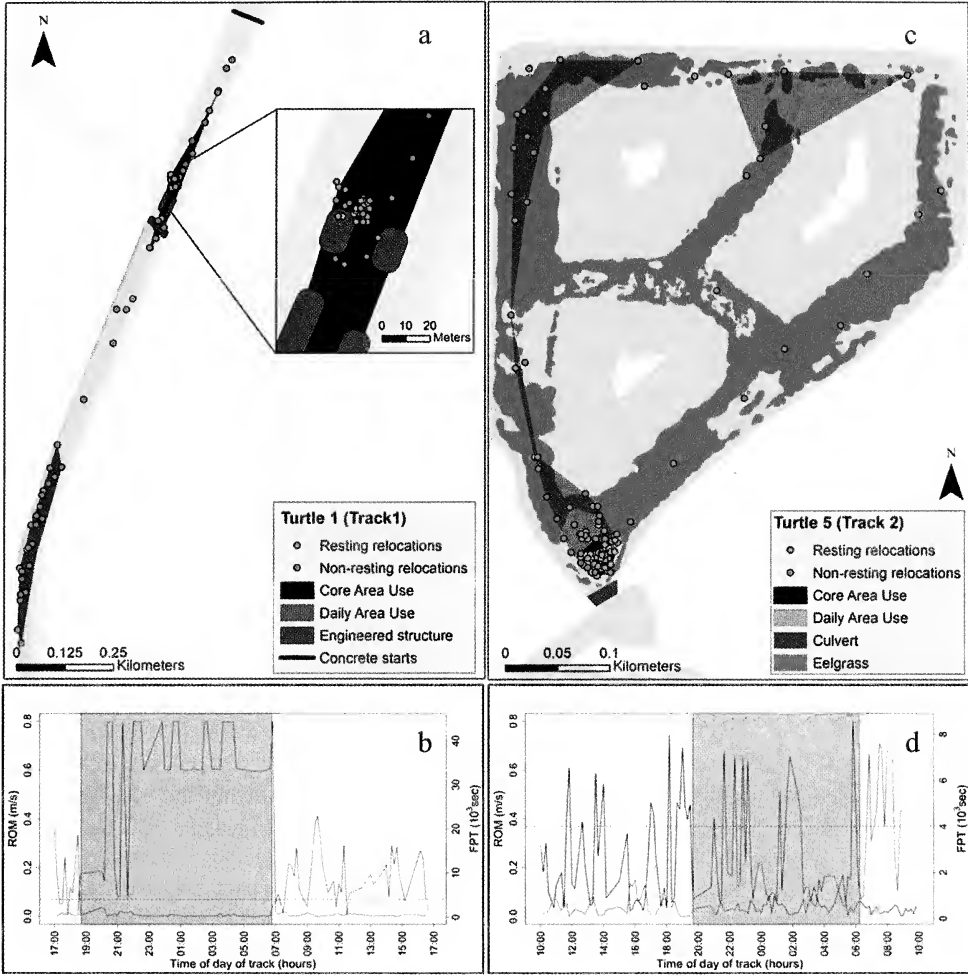


Fig. 4. (a) Resting and non-resting geolocations of the first track of Turtle 1 in the San Gabriel River with an enlarged inset of the area where resting occurred and (c) second track of Turtle 5 in the 7<sup>th</sup> St. Basin. Plots represent the ROM (black line) and FPT (red line) values against the time of day of (b) the first track of Turtle 1 and (d) second track of Turtle 5. The blue dashed line represents the 4000 second threshold, where FPT values greater than 4000 seconds indicates periods of resting.

engineered structures ( $2.99 \pm 0.76$ ), followed by non-vegetated substratum ( $1.11 \pm 0.04$ ), while not selecting for mixed rubble/soft substratum ( $0.63 \pm 0.24$ ) and hard rubble ( $0.29 \pm 0.08$ ) (Chi-squared test,  $\chi^2 = 149.09$ ,  $p < 0.001$ ). While resting in the river, turtles selected areas associated with engineered structures ( $3.56 \pm 0.33$ ) followed by non-vegetated substratum ( $1.06 \pm 0.05$ ), while not selecting for hard rubble ( $0.35 \pm 0.29$ ) and mixed rubble/soft substratum ( $0.32 \pm 0.32$ ) (Chi-squared test,  $\chi^2 = 57.34$ ,  $p < 0.001$ ; Fig. 4a). In the 7<sup>th</sup> St. Basin, green turtles displayed the greatest mean HSI and highest selection for culvert/non-vegetated ( $6.10 \pm 3.14$ ), followed by culvert/eelgrass ( $1.57 \pm 0.61$ ) and no culvert/eelgrass ( $1.36 \pm 0.19$ ), while not selecting for no culvert/non-vegetated ( $0.44 \pm 0.10$ ) (Chi-squared test,  $\chi^2 = 919.09$ ,  $p < 0.001$ ). While resting in the basin, turtles selected areas associated most often with culvert/non-vegetated ( $11.59 \pm 9.24$ ), followed by culvert/eelgrass ( $2.34 \pm 1.58$ ) and no culvert/eelgrass

Table 3. Mean and standard error of rate of movement (ROM) and distance traveled for the six active tracks at each site during the day, night and 24-h periods. SGR = San Gabriel River

Metric	Site	Day	Night	24 hours
ROM	SGR	0.15 ± 0.008	0.06 ± 0.006	0.11 ± 0.005
(m/s)	7th St. Basin	0.12 ± 0.006	0.06 ± 0.004	0.09 ± 0.004
Distance Traveled	SGR	6.29 ± 3.73	2.22 ± 0.79	8.51 ± 1.43
(km)	7th St. Basin	4.67 ± 0.77	2.42 ± 0.70	7.08 ± 0.95

(1.28 ± 0.70), while not selecting for no culvert/non-vegetated (0.18 ± 0.13) (Chi-squared test,  $\chi^2 = 564.12$ ,  $p < 0.001$ ; Fig. 4c).

### Discussion

This study is the first study to look at green turtle habitat use at this fine of scale (10 min intervals) for a continuous 24-hs, particularly within an urbanized habitat. In addition, by coupling both horizontal movements and activity we were able to more accurately infer behavior (i.e. resting) than is typically possible using a single data source (e.g. dive profiles). This study is also one of the few studies that have directly compared habitat use and behavior between two very different habitats (urbanized river vs. restored estuary).

We identified how green turtles behave and use habitat in an urban environment (i.e. the San Gabriel River) compared to a more “natural” environment (i.e. SBNWR). Despite insignificant differences in the distance traveled, ROM, and core area size between sites, all metrics were all higher in the river. Additionally, there still was a significantly larger daily area use in the river, which suggests that the prey abundance within the river may be patchier and less abundant, while prey abundance (i.e. eelgrass) in the 7<sup>th</sup> St. Basin may be higher and more concentrated. The presence of eelgrass, which typically offer high primary and secondary productivity and supports an abundance and diversity of invertebrates (Beck et al. 2001) is found among restored estuaries along southern California (i.e. SBNWR and Bolsa Chica Ecological Reserve); however, due to the major anthropogenically-induced shifts in habitat structure in the San Gabriel River, eelgrass is not present. The lack of eelgrass may require turtles to search more area for sufficient nutritional prey items like mobile invertebrates (Lemons et al. 2011) leading to less tortuous movements (Papastamatiou et al. 2011, Ahr et al. 2015) and larger daily area use in the river (Makowski et al. 2006, Seminoff and Jones 2006). It has been shown that in response to habitat features, green turtles have an opportunistic feeding strategy where they have a combined diet (Amarocho and Reina 2008). Although the contribution of river flow to the net flow downriver is often low (with the exception of during rain events), tidal fluxes and power plant discharge can lead to variation in net flow downriver. Therefore, river velocity may also influence turtle movements (i.e. higher flow rate may result in less tortuous movements; Brooks et al. 2009). Lastly, the shape difference between the two sites should not affect tortuous movements because the widths were similar between the river and the basin (Fig. 1).

Despite the lack of eelgrass in the river, the higher number of green turtles occupying the river year round compared to the 7<sup>th</sup> St. Basin (Crear et al. 2016) suggests that they are able to exploit other resources (i.e. invertebrates and algae) in the river. In fact, a higher abundance of individuals may lead to an increase in search area, which is also supported by a larger daily area use and the lack of overlap of core areas among different individuals and between tracks of the same individual in the river. If resources are being used in a specific area (a different turtle’s core area), then a turtle may need to expand its search area (daily area) and find a different

location (core area) that has resources it can exploit. The lack of overlap among individuals' core and daily areas may also be driven by seasonal temperature differences in the river, which is a major factor that influences the long term movements of green turtles in the San Gabriel River (Crear et al. 2016). For example, Crear et al. (2016) found that green turtles in the San Gabriel River used more of the river during the spring and fall months compared to during the winter and summer months. During the more extreme temperature seasons (i.e. winter and summer), temperature may constrain the area use of many turtles to certain parts of the river, which would lead to area use overlap among individuals. Further, seasonality influences prey density, which may impact green turtle area use. For example, it was clear that algae concentration was more dense during the warmer months in both locations.

Resting behavior occurred primarily at night at both sites, a pattern observed in green turtles in other studies (Mendonca 1983, Taquet et al. 2006, Hazel et al. 2009) and suggests that the urbanized environment within the San Gabriel River may not alter the natural resting behavior of green turtles. Typically if individuals feed during the day, they might use periods at night to digest food and rest. Turtles that exhibited periods of resting during the day may have had two feeding bouts during the day, one in the morning and one in the afternoon, with a digestive resting period midday, which is a behavior previously observed in green turtles in the U.S. Virgin Islands (Ogden et al. 1983). Despite, the slight differences in resting behavior among individuals and low sample size, this study found similar results as previous literature suggests. Individuals that did not undergo resting over a 24-h period may have been foraging or searching for prey. Where we could correlate horizontal with acceleration data to predict periods of resting (Hart et al. 2016), we were unable to use this method to identify periods of foraging as turtle foraging behavior consists of more precise movements that cannot be identified through acoustic telemetry.

Green turtles were able to exploit some of the urbanized features within the San Gabriel River (bridge pilings and discharge outflows) as seen by a high affinity to these types of structured habitats while resting, compared to low relief substrates. Similar to other reef ledges, engineered structures offer ledges and outcroppings that can provide suitable resting sites for green turtles that block the net flow downriver (Shaver 1994, Brill et al. 1995, Makowski et al. 2006, Hazel et al. 2013). Turtles were also selecting for this habitat type during the day. Hard structures offer areas where a high abundance of invertebrates and algae can attach; therefore, turtles may be exploiting engineered structures along the side of the river to feed during the day. Similarly, Renaud et al. (1995) found green turtles feeding on algae along jetties. Further, turtles have also been observed using vertical features to self or symbiotically clean (Thomson et al. 2015), another behavior these individuals may undergo along engineered structures.

Despite the more "natural" environment within the SBNWR, green turtles showed a high affinity to the culvert within the 7<sup>th</sup> St. Basin. Similar to engineered structures in the San Gabriel River, the culvert offers attachment sites for invertebrates and algae. Further, the incoming tide and warm temperature may bring small fish and invertebrates into the 7<sup>th</sup> St. Basin. This potential food source may have drawn green turtles to the culvert opening during the day. In addition, the incoming and outgoing tide through the culvert scours out the bottom (Jirik and Lowe 2012), creating a slightly deeper habitat at the basin's entrance. While resting, green turtles selected areas adjacent to the culvert, which provides deeper habitat and may result in an increase in the duration of resting dives (Hart et al. 2016). This behavior occurs because at deeper depths, turtles need to take a big breath in order to obtain neutral buoyancy at the bottom. This allows for a longer resting time because there is more available oxygen for physiological processes, which minimizes expected energy expenditure (Minamikawa et al. 1997, Hays et al. 2004). This has been observed in green and loggerhead turtles, *Caretta caretta*, where that as dive depth

increased, dive duration increased as well in suspected resting dives (Minamikawa et al. 1997, Hart et al. 2016). Seeking out the deepest depth allows them to attain neutral buoyancy on the bottom, while maximizing the oxygen stored in their lungs (Minamikawa et al. 1997, Hays et al. 2004).

### Conclusions

The urbanized San Gabriel River that has rocky edges and no eelgrass offers a very different habitat for green turtles than the more “natural” restored 7<sup>th</sup> St. Basin that has a single culvert and an abundance of eelgrass. Despite the differences in habitat, green turtles seem to exploit the available resources, particularly those associated with manmade structures, at each site. Although periods of foraging could not be identified using our methods, the use of both sites for multiple 24-h periods by all actively tracked turtles suggests that they offer important foraging habitats that support green turtles. The ability for green turtles to undergo typical behavior for multiple 24-h periods in the absence of eelgrass and the presence of manmade structures within the San Gabriel River, suggests that green turtles may be able to adapt and use habitats in certain urbanized environments. Despite the low sample size, we can still provide managers with what may be expected in the future as more individuals move into these types of environments. As green turtle populations continue to increase and the ocean temperatures warm, we may see an increase in the abundance of individuals at their northern range, leading to range expansion and an increase in individuals settling in these highly developed regions. Therefore, as mitigation projects continue along the coastline, it may be beneficial for managers to consider species that may be able to utilize areas that humans have altered (Seney and Landry Jr 2008). Despite restoration efforts, humans are still heavily influencing coastal habitats; therefore, understanding how a recovering threatened species behaves in these altered and restored environments will help ensure populations continue to increase.

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## Range Expansion of the Eastern Fox Squirrel within the Greater Los Angeles Metropolitan Area (2005 – 2014) and Projections for Continued Range Expansion

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**Abstract.**—Monitoring the spread and distribution of introduced species in an area can be challenging due to a variety of issues. Range expansion may exceed expected rates if the area of introduction is more suitable than expected, and may be slowed by an area in which it is difficult to establish a population. The species of interest in this study is the Eastern Fox Squirrel (*Sciurus niger rufiventer*) and the focus of the study is the spread of the species in Southern California. Previous studies have shown a steady and continuous spread from main points of introduction in Southern California and the species is now considered well established in the region. In this study, we collected and mapped new location data within Southern California. We discuss the spread of the Eastern Fox Squirrel in this area from 2005 through 2014 and include habitat suitability models to project the potential future distribution of the species. Results show that the Eastern Fox Squirrel has spread east into Rancho Cucamonga, into southern portions of Irvine, and has maintained isolated populations in places such as San Diego and Riverside. Our models suggest potential future paths of movement for contiguous range expansion.

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The goals of this study were to (1) document range expansion of the Eastern Fox Squirrel (*Sciurus niger* – hereafter EFS) within the greater Los Angeles metropolitan area over the time period of 2005 – 2014, and (2) use an ecological niche model to project potential future range expansion of the species in Southern California. King et al. (2010) described the range of the EFS in Southern California as of 2004 with general information on range expansion from the time of introduction to Los Angeles in 1904 through 2004. Range expansion of the EFS over the 100-year period occurred through natural dispersal of animals and through human activity. Natural dispersal of animals would elicit a contiguous mode of range expansion that depended mostly on the rate of dispersal and the presence of available habitat. Range expansion due to human activity could produce a noncontiguous type of range expansion through live trapping and relocation some distance away from the leading edge of natural range expansion. King et al. (2010) found that through human activity, isolated pockets of animals appear where the species did not previously occur. These isolated pockets of animals would be absorbed into the metapopulation as years pass and range expansion through natural dispersal meets the isolated pockets of animals.

Mammals that are introduced to a particular location may, over time, spread out from the original place of introduction. Range expansion may continue as long as there is suitable available contiguous habitat, biotic factors such as competition with native species are not a limiting factor, and physical factors such as temperature or elevation do not make an area unsuitable for habitation, as found by Geluso (2004) and Goheen et al. (2003) for tree squirrels.

An invasive species such as the EFS provides a good model for looking at factors that influence range expansion of small mammals in a large metropolitan area, and at the rate of range expansion. King et al. (2010) and Koprowski (1994) found that the EFS has been introduced to many areas outside of its natural range, and within California it is strongly, though not exclusively, associated with human habitation and development – thereby providing copious data for analysis.

Another example of range expansion showing both contiguous and noncontiguous modes has been provided for the Eastern Gray Squirrel (*Sciurus carolinensis*, hereafter known as EGS) in the United Kingdom (Bertolino et al. 2008). The EGS was first introduced to the United Kingdom in the 1870's and soon after spread to parts of England, Wales and Scotland (Parsons 1937). While contiguous range expansion through natural dispersal was first evident in southern England, non-contiguous range expansion through human activity likely produced isolated pockets of animals in the middle and northern section of the United Kingdom as well as in Ireland (Teanga 2000).

While it is possible to describe range expansion of the EFS within the greater Los Angeles metropolitan area in fairly accurate detail, it is also possible to utilize ecological niche modeling software such as Maxent (Phillips et al. 2004, 2006) to make projections related to potential future range expansion of the EFS in Southern California. Cooper and Muchlinski (2015) suggested that lowland populations of the Western Gray Squirrel (WGS) occupy fragments of habitat which the EFS may occupy as range expansion continues. These lowland populations were at altitudes up to ~450 m elevation. Muchlinski et al. (2009) and Cooper and Muchlinski (2015) suggested that since the EFS has been documented to replace the WGS in some habitats where the two coexist, it is expected that additional lowland populations of the WGS residing in the greater Los Angeles metropolitan area and Southern California will be extirpated over time. At this point in time it is not possible to know if or how the EFS will impact populations of the WGS if the range of the EFS expands to habitats at higher elevations.

Range expansion of the EFS in the Los Angeles metropolitan area over the 10-year period between 2005 and 2014 occurred mainly on the eastern and southeastern fronts of range expansion. Therefore, these two fronts of range expansion, as well as projections for potential future range expansion, are the focus of this study.

## Materials and Methods

The baseline data set used in this study for monitoring range expansion (995 location points) was published by King (2004) and later by King et al. (2010). King (2004) utilized a citizen science approach along with information from several wildlife care centers to collect data on present (2003 – 2004) and historical sightings of the EFS. For the current study, location data from throughout California were gathered over the time frame of January 2005 through December 2014. Of the 1376 location points obtained for the area from Santa Barbara south to San Diego between 2005 and 2014, 48.3% of the location points came from wildlife rehabilitation centers, 24.7% came from online geodatabases such as the Global Biodiversity Information Facility (GBIF) and 26.8% came from AEM and several former graduate students trained in the identification of the EFS. Data obtained through the GBIF included research-grade observations submitted through various iNaturalist pages. Sources of all observations are shown in Table 1. Since the EGS is not present within Southern California, confusion of the EFS with the EGS was not an issue in species identification for this paper. Calculation of the rate of range expansion over the time period of 2005-2014 followed previously established methods from King et al (2010).

Table 1. Location sources for observations of the Eastern Fox Squirrel, *Sciurus niger* within Southern California from 2005 through 2014.

Data Source	Number of Location Points
California Wildlife Center	136
California Tree Squirrels	137
Alan Muchlinski and Students	233
Global Biodiversity Information Facility	341
Orange County Vector Control	45
Squirrelmender Wildlife Rehabilitation	34
Wetlands & Wildlife Care Center	171
California Department of Public Health	279
Total	1376

An ecological niche model for the EFS in Southern California area was created using the Maxent software program, a maximum entropy approach for modeling species habitat as described by Phillips et al. (2004, 2006) and Elith (2014). Merow et al. (2013) suggest that Maxent is the most widely used species distribution/environmental niche modeling software because it typically outperforms other programs based on the accuracy of the predictions from the model. Also, machine learning models such as Maxent, when used in the default mode, are less affected by highly correlated variables than traditional statistical models (Phillips et al. 2006; Elith et al. 2011). A process called regularization helps prevent overfitting of the model (Merow et al. 2013). The Maxent program has been used in ecological niche modeling for a large number of species, as seen in Phillips and Dudik (2008) and Kebede et al. (2014).

The Maxent program takes presence-only data, fits those data to a set of selected abiotic and biotic environmental predictors, and projects to other locations where the selected set of environmental predictors match in varying degrees the predictors where the species does exist. General biotic and abiotic factors used in our model are outlined in Table 2. Variables used from BIOCLIM<sup>1</sup> included bio 1 through bio 19, which represent annual trends for certain environmental variables, monthly trends on temperature and precipitation, as well as altitude. The remaining variables related to land development, land cover type, and tree canopy cover (Table 2) were obtained from the United States Geological Survey (USGS).

Location addresses for observations were converted to geographic coordinates by finding the latitude and longitude coordinates of each individual sighting through Google Maps. The coordinates were saved as a text file along with corresponding information related to species type, year, specific date seen if given, and additional information if given. The accuracy of location data varied by source, being between 3 to 10 m for data obtained using GPS location applications and between 15 to 30 m using street address locations on Google Maps. The accuracy of the location data is within the accuracy level of the environmental variables from BIOCLIM, which is 1 km<sup>2</sup>.

The machine learning methodology of Maxent makes the algorithm highly accurate in a predictive manner but more difficult to interpret in terms of highly rated variables than traditional methods because the method creates non-linear functions (Elith 2014). Maximum entropy models such as Maxent initially assume a uniform distribution for the species, then apply iteratively adjusted constraints to estimate the actual species distribution (Elith et al. 2011;

<sup>1</sup> <http://www.worldclim.org>

Table 2. Biotic and abiotic variables used in the Maxent model for future range expansion by the Eastern Fox Squirrel, *Sciurus niger*, in Southern California.

Variable	Description	Unit	Source
Climate	Variables bio 1 through bio 19; Annual trends, seasonality and extreme or limiting environmental factors	Varies	BIOCLIM
Temperature	Average monthly mean, minimum and maximum temperatures	(°C)	BIOCLIM
Precipitation	Average Monthly Precipitation	millimeters	BIOCLIM
Altitude	Elevation above sea level	meters	BIOCLIM
Impervious Surfaces	Percent of developed impervious land (paved surfaces)	Percent	USGS
Landcover Type	Categorical Description of Landcover	Categorical	USGS
Tree Canopy	Area or proportion of cell covered by tree canopy	Percent	USGS

Phillips et al. 2006). The output of Maxent is a relative probability distribution that sums to one. It provides the relative probability of each cell containing suitable habitat, in comparison to the other cells in the raster (Merow et al. 2013). The constraints are set up across environmental covariates, instead of across geographic space, then applied to the geographic space. Maxent applies the constraints, but maintains the most uniform distribution possible. Maxent randomly changes the coefficients for each predictor, or environmental variable, and accepts the variable if it increases the gain, or the deviance from the original maximum entropy model.

The pre-established environmental variables from BIOCLIM and the USGS (Table 2) were added for the analysis. These variables correspond with biotic and abiotic factors that would most likely represent where a species would be found. Fifteen replicates were done with data divided 75% for training the model and 25% for testing the model within each replicate. The maximum number of iterations within a replicate run was set at 5000 to allow enough iterations for convergence of a model.

The Random Seeding Option was utilized so that the first iteration within a replicate run would begin at a random data point within the training data set. Replicate Run Type was set to subsample so that data points were randomly split into 75% training and 25% testing subsets for each replicate. Subsampling is one form of cross-validation available within Maxent. Receiver Operating Characteristic (ROC) plots with average Area under the Curve (AUC) values were generated across the 15 replicate models. The summary response curve includes the mean AUC value  $\pm$  one standard deviation error bars (Phillips et al. 2006; Phillips and Dudik 2008).

The resulting average model from all trials was creating as a logistic output and imported into ArcMap for reclassification. The suitability classifications were made with Jenks Natural Breaks (Jenks 1967) which determines the best arrangement of values into classes. Habitat classifications used were Not Suitable, Low Suitability, Medium Suitability, High Suitability and Very High Suitability, which are relative and not absolute. In a binary output, all locations that are not classified as Not Suitable Habitat are considered to represent Suitable Habitat. Jenks Natural Breaks provides a division of habitat suitability according to natural grouping of values from the logistic output of the model, which although not absolute, does provide additional information about the habitats classified as suitable. Location sightings of the squirrels were added to the resulting maps.

The two maps showing the habitat suitability models represent what we refer to as minimum and maximum potential suitable habitat for the EFS in Southern California. The minimum

model was generated by using 1390 location points of the EFS from within Southern California (Santa Barbara to San Diego) over the time period of 2004 – 2015. The maximum model was generated by using a total of 5699 location points: 5475 from within the entire State of California + 224 from the native range of *S. niger rufiventer* over the same time period. We used location data for *S. niger rufiventer* from states where *rufiventer* is the only subspecies present within the state (Koprowski 1994). Lance et al. (2003) and Claytor et al. (2015) suggested that the subspecies *S. niger rufiventer* is the main subspecies present within California, and information on habitat suitability from the native range could be important in projecting potential future range expansion within California. The data from other states include the broader environmental conditions that the EFS tolerates rather than the more limited conditions currently encountered solely within Southern California. The maximum model could be more representative of the species' actual tolerance ranges, and therefore may better represent areas the species could colonize within Southern California. However, the exact accuracy of the models can only be determined by future studies that assess the presence of the EFS within various areas in the future. Since the dataset used for this study is available via a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License, we encourage researchers who are conversant with other ecological niche modeling programs to further investigate these data. Those individuals who submitted observations to iNaturalist are recognized in the data set.

A Maxent model can be evaluated by looking at how well it explains training data and how it predicts data from another data set. It is a common practice to randomly set aside a portion of the original data set for testing the model once it has been trained (Baldwin 2009). However, in presence only modeling test data are likely to have the same biases in geographic and environmental space as the training data. Therefore, test data may not provide a perfect test of accuracy in predicting species distributions.

To determine goodness of fit for the two models with test data we examined the model's discriminatory ability by measuring the AUC of the ROC plot (Baldwin 2009). The greater the area under the curve, the higher the predictive ability of the model, and the better fit it is to the data used to build the model. AUC values for the ROC plot can range from 0.5 to 1.0. A value of 0.5 indicates a fit of observation data (true positives plotted against false positives) no better than random, and a value of 1.0 indicates a perfect fit of observation data to the model (Baldwin 2009). The AUC is not a perfect objective measure of the predictive power of the model but few alternatives are available for presence only data since absences have not been tested (Merow et al. 2013). AUC is rank-based so models can only be compared using the AUC if they were built for the same landscape, used the same background sample, and tested the same species with the same test data (Elith et al. 2011).

## Results

The overall distribution of the EFS within the Los Angeles metropolitan area as of the end of 2014 is shown in Fig. 1. Shown in Fig. 2 are the range expansion fronts from 2004 and 2014 in the eastern and southeastern portions of the Los Angeles metropolitan area. The EFS now occupies areas to the east and south of the eastern front of range expansion in 2004, which was located at the western edge of the City of Claremont, including the Cities of Pomona, Claremont, Montclair, Upland, Ontario, and Rancho Cucamonga. Current borders of contiguous range expansion as of 2014 (Fig. 2) appear to be near Interstate Highway 15 which runs along the eastern edge of the Cities of Rancho Cucamonga and Ontario, and near California Highway 60 which runs along the southern edge of the Cities of Pomona, Montclair, and Ontario (Fig. 2).

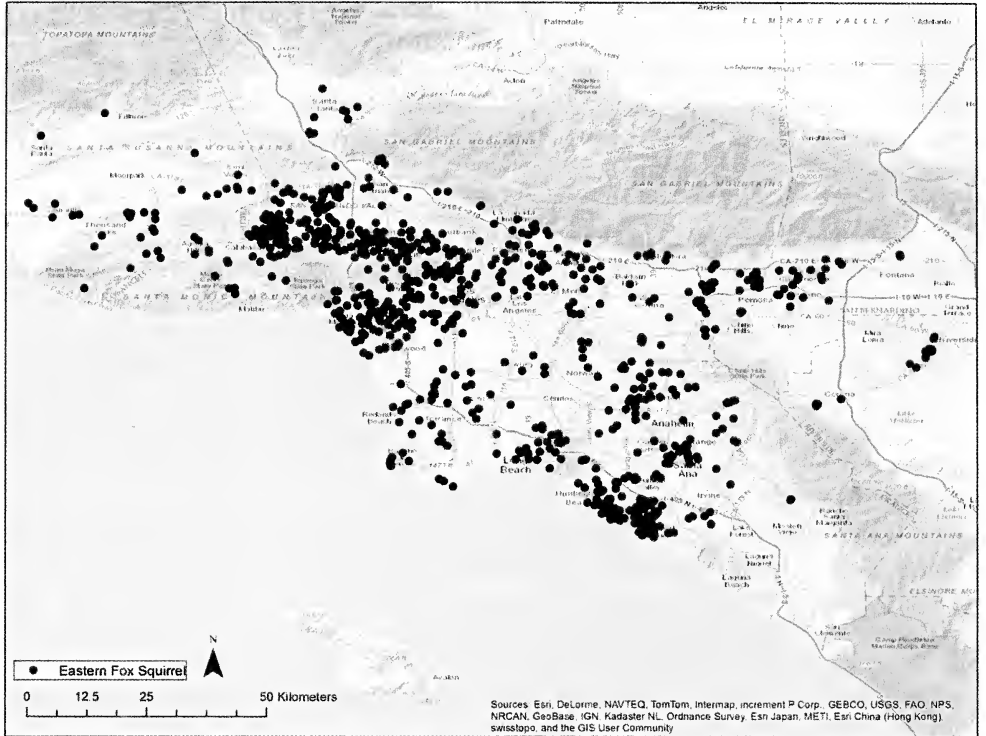


Fig. 1. Distribution of the Eastern Fox Squirrel (*Sciurus niger*) in the greater Los Angeles metropolitan area as of 2014.

The current boundaries on the expanding eastern front are the foothills of the San Gabriel Mountains to the north, Interstate Highway 15 to the east, and California Highway 60 to the south. Although animals have been sighted by AEM on property of Sierra Lakes Golf Club in the City of Fontana, it is very likely the presence of animals on the golf course is the result of human activity as the golf course is  $\sim 3.5$  km east of Interstate Highway 15 and  $\sim 10$  km east of the front of contiguous expansion range. The total linear distance of contiguous range expansion from the eastern most location observed in 2004 to the eastern-most location observed in 2014 (10 yrs.) was 15 km, giving a contiguous range expansion rate of 1.50 km/year.

We do not have reports of the EFS in the Chino Valley south of California Highway 60, east of Highway 71, and west of Interstate Highway 15. Therefore, the EFS appears to be absent, as of 2014, from the Cities of Chino and Chino Hills, including the heavily wooded flood plain behind Prado Dam at the junction of Highway 71 and Interstate Highway 91.

The current distribution of the EFS in the southeast Los Angeles metropolitan area runs through the Cities of Diamond Bar, Brea, Yorba Linda, Anaheim, Orange, Tustin, Santa Ana, Garden Grove, Westminster, Fountain Valley, Huntington Beach, Costa Mesa, and Irvine. The front of contiguous range expansion in the southeastern direction appears to be along the southeastern boarder of the City of Irvine (Fig. 2), where additional residential development is occurring at this time. Contiguous range expansion to the east of the City of Diamond Bar appears to have been halted by an area of open, mostly tree-less land that runs from Highway 60 in the north to the San Juan Hills in the south. This area of open space currently separates





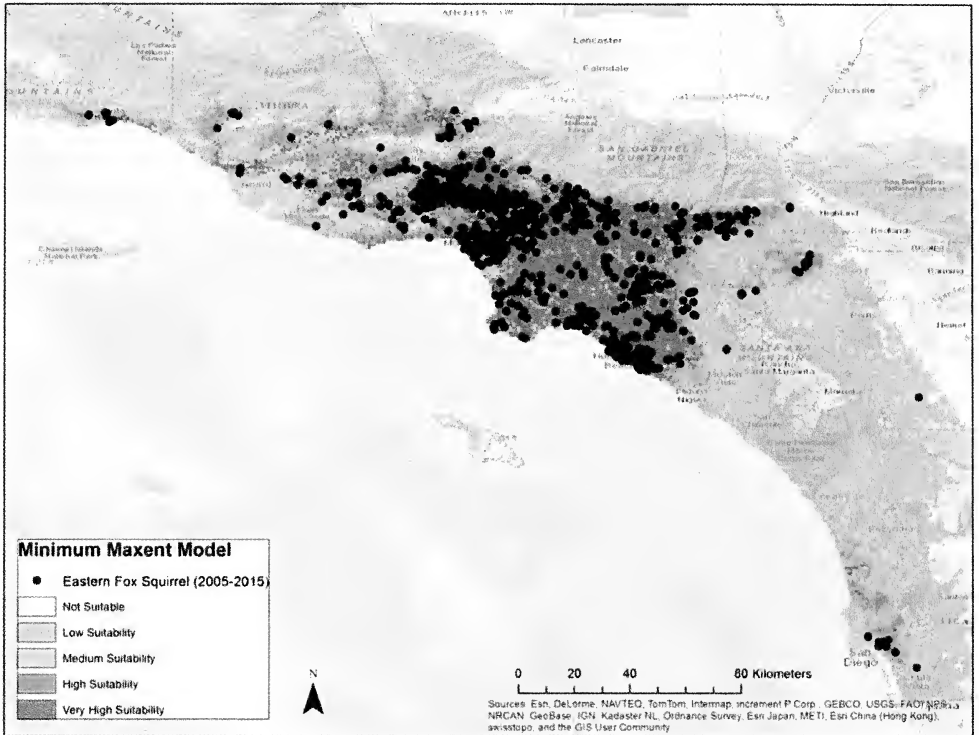


Fig. 3. A minimum habitat suitability map developed for the Eastern Fox Squirrel (*Sciurus niger*) using the Maxent software program. Location data along with abiotic and biotic variables for this model included data only from Southern California over the time period of 2004 through 2015.

Riverside. Arrival of the EFS in the City of Corona has occurred within our 10-year study period but the population in Riverside has been present in the Wood Streets Area of Riverside for at least 40 to 50 years (Gilbert Garcia, former Wood Streets Resident, Personal Communication) (Fig. 2). The presence of the isolated population in Riverside was not captured in the study conducted in 2004 and expansion of this population in terms of geographic area seems to have been limited.

The minimum projection for potential range expansion by the EFS within Southern California is shown in Fig. 3. Since the Maxent model is based upon presence only data, with extrapolation to habitats that share to varying degrees the abiotic and biotic characteristics similar to habitats where the species has been observed within California, areas where the EFS has been observed are shown in bright red. Areas in white would be considered unsuitable habitat based upon the variables used in the model. Moving from a brighter to a cooler shade of color would indicate a reduction in the potential of the habitat being suitable for the EFS, based upon location and environmental data only from within Southern California.

Based upon the minimum model, most of the area between the leading edge of contiguous range expansion from 2014 to the isolated populations in Fontana, Riverside, Corona, and Foothill Ranch appears to be suitable habitat for the EFS. Therefore, over time, we would expect developed areas south of Interstate Highways 210, 10, and 60, and north of Interstate Highway 91 to be populated with EFSs. We would also expect range expansion southeast of the City of Irvine along the Interstate Highway 5 corridor to the City of San Clemente.

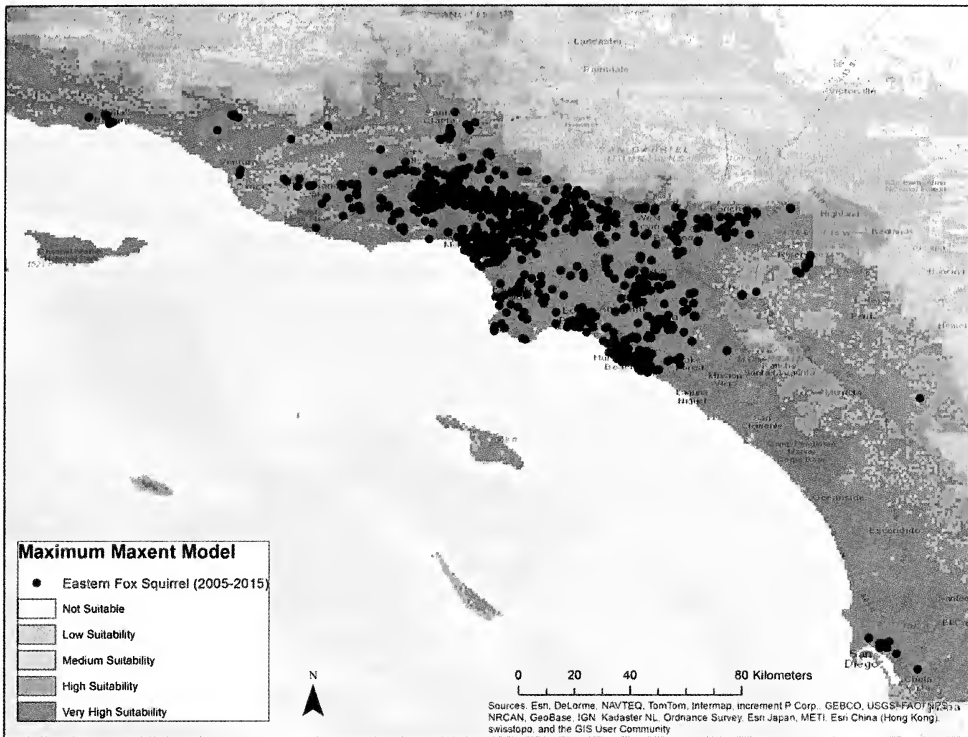


Fig. 4. A maximum habitat suitability map developed for the Eastern Fox Squirrel (*Sciurus niger*) using the Maxent software program. Location data along with abiotic and biotic variables for this model included data from within the entire State of California along with data from others states over the time period of 2004 through 2015 where the subspecies *Sciurus niger rufiventer* is the only subspecies found in that state.

According to the minimum model the Camp Pendleton Marine Base may serve as a low suitability habitat providing a break between suitable habitat around San Clemente and suitable habitat to the south beginning near Carlsbad. A large amount of suitable but currently unoccupied habitat exists within San Diego County between and along the Interstate 5 and Interstate 15 corridors.

The maximum projection for potential range expansion by the EFS within Southern California is shown in Fig. 4. Regions where the maximum model projects an increase in very high suitability to high suitability habitat include (1) the area from the current front of range expansion in Orange and San Bernardino Counties a little further to the east and then southeast to San Diego, including the coastal Interstate 5 and inland Interstate 15 corridors, along with the coastal mountains between the two corridors, and the Santa Ana Mountain Range; (2) the Santa Monica Mountains and areas to the north and northwest of the this mountain range; and (3) the Santa Ynez Mountains north of Santa Barbara. The vast majority of habitat in these areas is at an elevation below 1000 m with some habitat in the Santa Ynez Mountains extending up to 1400 m. An increase in medium to low suitability habitat is observed in the Tehachapi Mountains, in the high desert areas around Palmdale, Lancaster and Littlerock eastward to developed areas around Victorville, Hesperia, and Apple Valley, which are at elevations near or below 1000 m.

Range expansion by the EFS into urbanized areas within deserts is certainly possible based upon the presence of the EFS within residential areas of Yuma, Arizona, along with their presence

in some agricultural areas across the Colorado River inside of California (Jack Crayon, California Department of Fish and Wildlife, Personal Communication). Potential range expansion of the EFS into desert regions that are associated with human habitation seems to mark a significant departure from the native habitat of the species.

The goodness of fit of test data for our maximum Maxent model is indicated by an AUC value of 0.918  $\pm$  0.002SD for the Maxent ROC plot. The AUC value of the model using test data only from Southern California is 0.966  $\pm$  0.003SD. Since the two models were generated from different data sets we cannot say that the model with the higher AUC value represents a better model than the model with the lower AUC value. However, the high AUC values for both models indicate a very good fit of the data used to generate each model. The low values of the standard deviations also indicate a tight fit of the data to each model.

### Discussion and Conclusions

The introduction and spread of non-native invasive species through a previously uninhabited area tends to follow a general process. The initial arrival, which can be by human introduction, introduces the species to the general area. Afterwards, the species establishes its place in the local niche. This is the ideal time to control and eradicate the species before it becomes impractical to contain. If the species is not contained by this time, then the invasive species will begin to displace native species, and the focus shifts from eradication of the invasive to mitigating damage caused to the native species. If nothing can be done to contain the invasive species at this time, then the invasive species dominates the ecosystem, and land managers can only try to maintain the current state of invasive and native species at that point (CDFW 2015).

Geography is also an important contributor to the current spread and range of the invasive species. For the EFS, knowing the geography of the area that the species is currently present in and has been present in can be extremely important for population control. The EFS has expanded its geographic range within the greater Los Angeles metropolitan area over the 10 yrs. of this study and continued range expansion in the northwest, east, and southeast directions is highly probable. King et al. (2010) estimated range expansion rates from 0.44 to 3.44 km/yr. based upon historical records. Our study provided contiguous range expansion rate estimates of 1.50 to 3.00 km/yr. and are probably a more realistic estimate of the contiguous range expansion rate through highly suitable suburban habitat.

Not all areas of suitable habitat behind the front of contiguous range expansion are occupied immediately by the EFS. Abiotic factors such as the presence of freeways or the presence of large industrial areas, and biotic factors such as the absence of adequate tree coverage can leave pockets of habitat which are not immediately occupied by the EFS. Frank G. Bonelli Regional Park in the City of San Dimas is an example where the presence of a freeway may have locally stopped animals from continued eastward dispersal. While the EFS was present in surrounding cities such as LaVerne, Claremont, and Montclair by 2004, the species did not enter the northern section of Bonelli Park until 2010 and the southern section of the park until 2012 (AEM). The first animals observed in the southern section of the park were most likely relocated by humans from the western, residential side to the eastern, park side of Interstate Highway 57. Animals could have entered the northern section of the park by dispersing south from previously occupied areas.

In many regions of Southern California, the higher elevation oak/conifer forests are separated from areas where EFSs currently reside by a zone of chaparral vegetation which is not suitable for habitation by tree squirrels. The zone of chaparral vegetation may act as a barrier to direct dispersal of the EFS to the oak/conifer forests above 1000 m elevation. Therefore, appearance

of the EFS in high elevation oak/conifer forests in southern California would most likely be a sign of human-assisted dispersal to those areas.

A major issue to address is what may happen if the EFS is introduced to higher elevations of the local mountain ranges. By adding environmental data to the ecological niche model from observations of the subspecies *Sciurus niger rufiventer* found within the native range, there appears to be a slight increase in suitable habitat within the higher elevation mountain ranges. However, elevations above 1000 m do not generally appear as suitable habitat with the maximum model. The highest elevation within the Santa Monica Mountains is approximately 1000 m and the maximum model describes this area as highly suitable habitat for the EFS. Several peaks within the Santa Ana Mountain Range are above 1000 m elevation but many areas are below the 1000 m level. Habitat within certain higher elevation areas of the San Bernardino Mountains, especially around the cities of Big Bear, Forest Falls, Lake Arrowhead, and Lake Gregory is highly fragmented due to human habitation. Also, ground cover within the coniferous forest around these areas of human habitation is minimal, a situation which is very conducive to the EFS (Gatza 2011). Even though the maximum model does not describe the higher elevations of the San Bernardino Mountain Range as suitable habitat, vigilance for human initiated introductions should be maintained.

The Santa Monica Mountains have an abundance of oak trees which have supported significant populations of the WGS. As pointed out by Erkebaeva (2013), replacement of the WGS by the EFS occurs faster in oak woodlands than in mixed oak/conifer woodlands below 1000 m. Significant residential development with associated habitat fragmentation is also found within the Santa Monica Mountains. Habitat suitability models have shown that the species of trees in an area, particularly a low to medium percentage of oak trees and medium to high percentage of conifers, have a positive relationship with the relative abundance of the WGS (Erkebaeva 2013).

In terms of preserving the WGS in Southern California, a focus could be placed on the conservation of natural areas and limitation of habitat fragmentation. Proper control methods can help reduce the rate at which invasive species such as the EFS can expand. A related issue is potential relocation through human activity of the EFS to areas in the San Gabriel and San Bernardino Mountain Ranges. These areas can be kept as exclusive WGS habitat if the presence of the EFS is caught early after an initial introduction and mitigation measures are activated. However, it is often difficult to track releases and determine the extent of a new population until it is already firmly established.

Maintaining local native vegetation and controlling invasive populations is important in controlling the rate at which the EFS can establish itself in an environment. With continued decadal surveys, trends can be found over time to determine if there are more specific patterns that can affect the distribution of both the EFS and the WGS. For now, a watchful eye on both species and proper management will help to keep the EFS in controlled populations and the WGS in viable populations.

#### Acknowledgements

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Rehabilitation Center, Suisun Wildlife Rescue Center, Sulphur Creek Nature Center, Wetlands and Wildlife Care Center, WildCare, and Wildlife Center Silicon Valley. We also thank the many individuals who utilized iNaturalist or other sources to submit observations of the EFS within California and other states. Recognition of individuals is available through the GBIF ID Number for each observation contained within the dataset. We thank the three anonymous reviewers who provided constructive comments to improve this manuscript. Maps were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. The DOI's for the data used to generate the Minimum Maxent Model and Maximum Maxent Model are 10.13140/RG.2.2.13672.06407 and 10.13140/RG.2.2.20382.95043, respectively.

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## First Reported Occurrence of the Southern Sea Otter *Enhydra lutris lutris* at California's Santa Barbara Island Since 1940

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Sea otters once ranged along the North Pacific rim from the northern Japanese islands to mid-Baja California, Mexico. There are three recognized subspecies of sea otters: the Russian or Asian sea otter (*Enhydra lutris lutris*); the Alaskan or northern sea otter (*E. I. kenyoni*); and the California or southern sea otter (*E. I. nereis*) (Wilson et al. 1991). The southern sea otter occupies the most southerly range, with populations in only two areas of California: the mainland coastline from San Mateo County to Santa Barbara County and San Nicolas Island, Ventura County.<sup>1</sup> Historically, 16,000–20,000 sea otters are believed to have resided in the area that is now California.<sup>2</sup> The southern sea otter was afforded protection in California by the California Department of Fish and Game in 1913.<sup>3</sup>

In the 1970s, the California population of sea otters was restricted to the Central California coast.<sup>4</sup> Primarily due to concerns about the vulnerability of this population to oil spills, the southern sea otter was listed as threatened by the United States Fish and Wildlife Service (the Service) under the Endangered Species Act in 1977.<sup>5</sup> The Service approved the first recovery plan for the southern sea otter in 1982<sup>6</sup> and released a final environmental impact statement in 1987. This EIS evaluated several options including translocating southern sea otters from California's central coast in an attempt to form a discrete colony of animals at San Nicolas Island, located 111 km (60 nm) off the Southern California coastline.<sup>7,8</sup>

Through translocation, the Service hoped to establish a self-sustaining southern sea otter population at a location within their historic range, but well away from the central coast population to lessen the risk to the species should a natural or man-made catastrophe decimate the central coast population. To achieve project goals, the San Nicolas Island colony would

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<sup>1</sup> Tinker, M. T., and Hatfield, B. B. 2016. California sea otter (*Enhydra lutris nereis*) census results, spring 2016: U.S. Geol. Survey Data Series 1018, 10 p., <http://dx.doi.org/10.3133/ds1018>.

<sup>2</sup> California Department of Fish and Game. 1976. A proposal for sea otter protection and research, and request for the return of management to the state of California. Sacramento, California. 270 pp.

<sup>3</sup> Wild, P. W., Ames, J. A., 1974. A report on the sea otter, *Enhydra lutris* L., in California. Calif. Dep. Fish Game Marine Resources Tech. Rep. 20:1-93.

<sup>4</sup> Riedman, M. L., and J. A. Estes. 1990. The sea otter *Enhydra lutris*: behavior, ecology, and natural history. United States Fish and Wildlife Service, Biolog. Report 90(14), Washington, D.C.

<sup>5</sup> United States Department of the Interior, Fish and Wildlife Service. 1977. Determination that the southern sea otter is an endangered species: Fed. Reg. V. 42, No. 10, Jan. 14, 1977. Pp 2965-2968.

<sup>6</sup> United States Department of the Interior, Fish and Wildlife Service. 1982. Southern sea otter recovery plan. United States Fish and Wildlife Service, Portland, Oregon.

<sup>7</sup> United States Department of the Interior, Fish and Wildlife Service. 2012a. Final supplemental environmental impact statement on the translocation of southern sea otters. Ventura Fish and Wildlife Office, Ventura, California. 348 pp. + front matter and appendices.

<sup>8</sup> United States Department of the Interior, Fish and Wildlife Service. 2012b. Endangered and threatened wildlife and plants; termination of the southern sea otter translocation program. Federal Register, December 19, 2012, 77(244).



have to grow to a self-sustainable size, and furnish up to 25 otters per year to repopulate any areas affected by a catastrophe along the central coast.<sup>8</sup> The translocation program established two geographic areas, a translocation zone surrounding San Nicolas Island and an “otter free” management zone that included all other Southern California waters from Point Conception to the Mexican Border. The otter free zone was created as an attempt to exclude translocated otters from other nearby islands and coastal shorelines where potential conflicts between otters and the lobster and shellfish fisheries might occur. It was also created to address the concerns of oil and gas producers that the presence of sea otters could lead to restrictions on oil and gas development (Carswell et al. 2015; Larson et al. 2015). Any otter found within the otter free zone was to be captured and released into habitat occupied by the central coast or San Nicolas Island populations.<sup>8</sup> In practice, captured sea otters were only released along coastal kelp beds, and not at San Nicolas Island.

Between August 1987 and March 1990, the Service released 140 otters at San Nicolas Island (Rathbun et al. 2000). Some otters died as a result of translocation, many swam back to the central coast, and some moved into the otter free zone.<sup>8</sup> Beginning with the first translocation, the Service, in coordination with the California Department of Fish and Game, captured and removed otters found within the otter free zone until 1993, when captures were suspended out of concern that sea otters were dying as a result. In January of 2001, the Service issued a statement that they would no longer remove otters from the otter free zone.<sup>7</sup> A revised recovery plan was issued that detailed why the attempt to create a managed population of otters at San Nicolas Island was not meeting expectations, and that the Endangered Species Act’s goals would be best pursued by allowing otters to expand their range naturally.<sup>9</sup> The Service dissolved the San Nicolas Island translocation and otter-free zones, ending the requirement to capture otters found away from San Nicolas Island.<sup>10 11</sup> In 2016, the annual California Sea Otter Census detected 92 juvenile and older otters and 12 pups at San Nicolas Island, and 3,078 juvenile and older otters and 433 pups within the mainland population.<sup>12</sup>

Since the translocations to San Nicolas Island began, otters have been reported from several Southern California islands and coastal areas<sup>13</sup> as well as several islands and coastal areas of Baja California (Schramm et al. 2014). However, despite Santa Barbara Island being the closest otter-populated land mass to San Nicolas Island, no otter had been reported from Santa Barbara Island since 1940.<sup>14</sup>

Ogden (1941) reviewed the sea otter trade from 1741 to 1848; no mention was made of pelts taken from, or hunting trips made to, Santa Barbara Island. Leatherwood et al. (1978)

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<sup>9</sup> United States Department of the Interior, Fish and Wildlife Service. 2003. Final revised recovery plan for the southern sea otter *Enhydra lutris nereis*. United States Fish and Wildlife Service, Portland, Oregon.

<sup>10</sup> United States Department of the Interior, Fish and Wildlife Service. 2012a. Final supplemental environmental impact statement on the translocation of southern sea otters. Ventura Fish and Wildlife Office, Ventura, California. 348 pp. + front matter and appendices.

<sup>11</sup> United States Department of the Interior, Fish and Wildlife Service. 2012b. Endangered and threatened wildlife and plants; termination of the southern sea otter translocation program. Federal Register, December 19, 2012, Vol. 77(244).

<sup>12</sup> Tinker, M. T., and Hatfield, B. B. 2016. California sea otter (*Enhydra lutris nereis*) census results, spring 2016: U. S. Geological Survey Data Series 1018, 10 p., <http://dx.doi.org/10.3133/ds1018>.

<sup>13</sup> United States Department of the Interior, Fish and Wildlife Service. 2015. Southern sea otter *Enhydra lutris nereis* 5-year review: summary and evaluation. U.S. Fish and Wildlife Service, Ventura Fish and Wildlife Office, Ventura California.

<sup>14</sup> Hatfield, B. July 5, 2016. Personal communication regarding observations of southern sea otters at Santa Barbara Island. Santa Cruz Field Station, Piedras Blancas Office.



Fig. 1. Southern sea otter in kelp at Santa Barbara Island on 2 July 2016 (Photo M. Couffer)

summarized observations of sea otters along the California coast between the 1900s and 1970s. They reported that from the beginning of the 1900s to the date of their publication, only two observations of sea otters at Santa Barbara Island were made, both during March of 1940, before any translocations were made to San Nicolas Island. These observations are often assumed to have been made of two separate animals, however, it is possible that the two observations were of the same animal. A search by individuals at several agencies and institutions failed to produce the original references for comparison.

The first observation at Santa Barbara Island, reported in Kenyon (1969), was a 28 May 1940 letter by J. C. von Bloeker and R. M. Bond that stated “Kenneth E. Stager saw a sea otter asleep in the rocks on the northwest side of Santa Barbara (Island) on March 17<sup>th</sup> [1940]. He approached to within 30 feet of it before it awakened and took to the water. He is familiar with these animals off the Monterey County coast (as I am also) and I see no reason to doubt his record.” Jack von Bloeker (1965) reported a second observation of “...one in the kelp off Santa Barbara Island in March of 1940 by Lloyd Martin, John R. Pemberton, and Kenneth E. Stager”.

On 2 July 2016, the author was in the wheelhouse of the dive charter vessel *Horizon* off the southeastern tip of Santa Barbara Island when he detected a southern sea otter near the outer edge of a bed of giant kelp (*Macrocystis pyrifera*) off the southeastern tip of the Island (Fig. 1). The specific location was 0.83 km (0.45 nm) southeast of the tip of Santa Barbara Island, along the 20 m (66 foot) depth curve at 33° 27.567' N by 119° 01.759' W. The otter was located within the Channel Islands National Marine Sanctuary, as well as within the Santa Barbara Island State Marine Reserve, a Marine Protected Area, where commercial and recreational take of all marine resources is prohibited.

The otter was first sighted at 0700 hours, and the captains, divers and crew were alerted. As the boat moved between dive sites throughout the day, an otter was seen and photographed again at 1540 hours and at 1800 hours floating on the surface amongst kelp within the same general

area of the kelp bed where it was first detected. The otter bore no flipper tags, but both sightings are presumed to be of the same otter. A complete survey of all kelp beds surrounding the island was not conducted, so it is unknown whether or not other portions of the island's perimeter were occupied by otters. No dives were made near the otter.

The otter was not identified to sex. During the periods when the otter was at the surface, its lower abdominal area where one might have detected a bulging baculum to identify a male was below the water's surface or covered by kelp. None of the photos taken of the otter were helpful in sexing the animal. Water temperatures were recorded every few seconds on the author's dive computer during four recreational scuba dives around the southern end of Santa Barbara Island; they varied from 10° C (50° F) at 26 meters (86 feet) to 17° C (63° F) at the surface. Kelp beds in the area on the date of the sighting were expansive, and kelp was visible at the surface during all tides. The Horizon returned to Santa Barbara Island on two subsequent voyages; captain Cary Humphries reported to the author that on 12 July 2016 and 16 July 2016, one sea otter was observed in the same kelp bed where the author had first located an otter on 2 July 2016.

Most extralimital otters sighted outside of their established populations have been found to be males that can make occasional long-distance movements for periods of days or weeks, but then return to the established populations.<sup>15</sup> Santa Barbara Island is approximately 45 km (25 nm) east northeast of San Nicolas Island, and 60 km (33 nm) from the closest mainland point. Another possible source population for this otter occupies the Santa Barbara County coastline, approximately 160 km (86 nm) from Santa Barbara Island. The Northern Channel Islands could have been used to island-hop from the Santa Barbara coastline to Santa Barbara Island. Approximate distances from the closest points on the Northern Channel Islands to Santa Barbara Island are 65 km (35 nm) for Anacapa Island, 76 km (41 nm) for Santa Cruz Island, and 101 km (55 nm) for Santa Rosa Island. As the otter was not tagged and had no identifying marks, it is impossible to determine its source population. Santa Barbara Island is surrounded by islands with the mainland to the east, so the otter could have arrived at Santa Barbara Island from any direction while leaving from or returning to a source population.

These observations show that, in the short term, dispersing sea otters can use the Santa Barbara Island kelp beds to rest and forage while transiting between other islands or the mainland. The otter's presence within a marine protected area for a minimum of two weeks may also speak to the benefits of the establishment and maintenance of marine protected areas. In the long term, Santa Barbara Island could become more than just a stop on an island-hopping transit, and eventually support a resident southern sea otter colony.

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## Development of Oral Structure in *Salmonema ephemeridarum* (Nematoda: Spirurida: Cystidicolidae)

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The morphology of the oral region is important in the identification of adult and larval parasitic nematodes. This is nowhere more true than in the assignment of cystidicolid nematodes of fishes to one of approximately 23 genera. However, the small size of the anterior end of these worms has complicated identification of worms (Moravec 2007) and resulted in a poor understanding of the morphology of oral structures, including the oral structure of infective/third stage larvae/juveniles, which are found in crustacean and insects. The purpose of this study is to utilize Scanning Electron Microscopy (SEM) to document the morphogenesis of oral structures of the cystidicolid nematode *Salmonema ephemeridarum* (Linstow 1872) and to provide information on the certainty of the identification of third stage larva to genus and species.

Adult female worms were collected from brook trout, *Salvelinus fontinalis* (Mitchell 1814), captured in Rocky Saugeen River, Ontario, Canada in June 1987. Larvated eggs were fed to larval mayflies (Ephemeroptera) collected from the Eramosa River where it passes under Stone Road, Guelph Ontario (43.547363, -80.1997499). Mayflies successfully infected included *Stenonema ithaca*, *Stenonema* sp. and *Isonychia* sp. No nematode larvae were found in 60 mayflies collected at this locality, and no salmonids are present in this portion of the Eramosa River (Osmond 1971). Mayflies were held in an aquarium at 21°C and examined for parasite larvae at intervals for 62 days. Adult worms used for SEM were from natural infection of the brook trout. Worms processed for SEM were cleaned in saline preserved in 1.25% gluteraldehyde, post-fixed in 1% osmium tetroxide, dehydrated in an ethanol series, critical point dried using CO<sub>2</sub>, mounted on stubs, coated with gold palladium alloy and viewed with a Jeol (Model JSM 35-C) scanning electron microscope. General terminology follows Anderson et al. (2009) and terminology of the oral morphology of third-stage and adult worms follows Appy (1981).

First stage larvae, present one to five days post infection (dpi), possessed an oral opening, a pore, and a hooked tooth (Fig. 1A). Second stage larvae (11 to 17 dpi) possessed a smooth circular oral opening, with presumptive lateral amphids (Fig. 1B). Oral structures of the third stage larva (> 17 dpi) are visible inside the oral opening of some molting second stage larvae. The oral structure of third stage larvae consisted of a dorsoventrally elongate oral opening with broad, relatively flat pseudolabia emanating from the cuticular lining of the buccal cavity (stoma) (Fig. 1C). The sublabia appear contiguous ventrally and dorsally and their apical surface appears smooth. Four cephalic papillae and amphidial openings are visible. The oral morphology of adult worms is similar to third stage larvae except that in adults the sublabia appear disconnected ventrally and dorsally and have an indentation forming two lobes (Fig. 1D).

While SEM has become more common in the descriptions of adult cystidicolids (Appy 1981; Ko 1986; Moravec 2007) there are only a few cases where SEM has been used to describe third stage larva (Appy and Dadswell 1983; Moravec et al. 2003) and no studies have depicted first- and second-stage larvae. The boring tooth in first-stage larva was previously identified in light microscopic studies as a refractile body (Moravec 1967; Appy and Dadswell 1983) and is presumably used to penetrate the gut wall and gain access to the body cavity and migrate into the

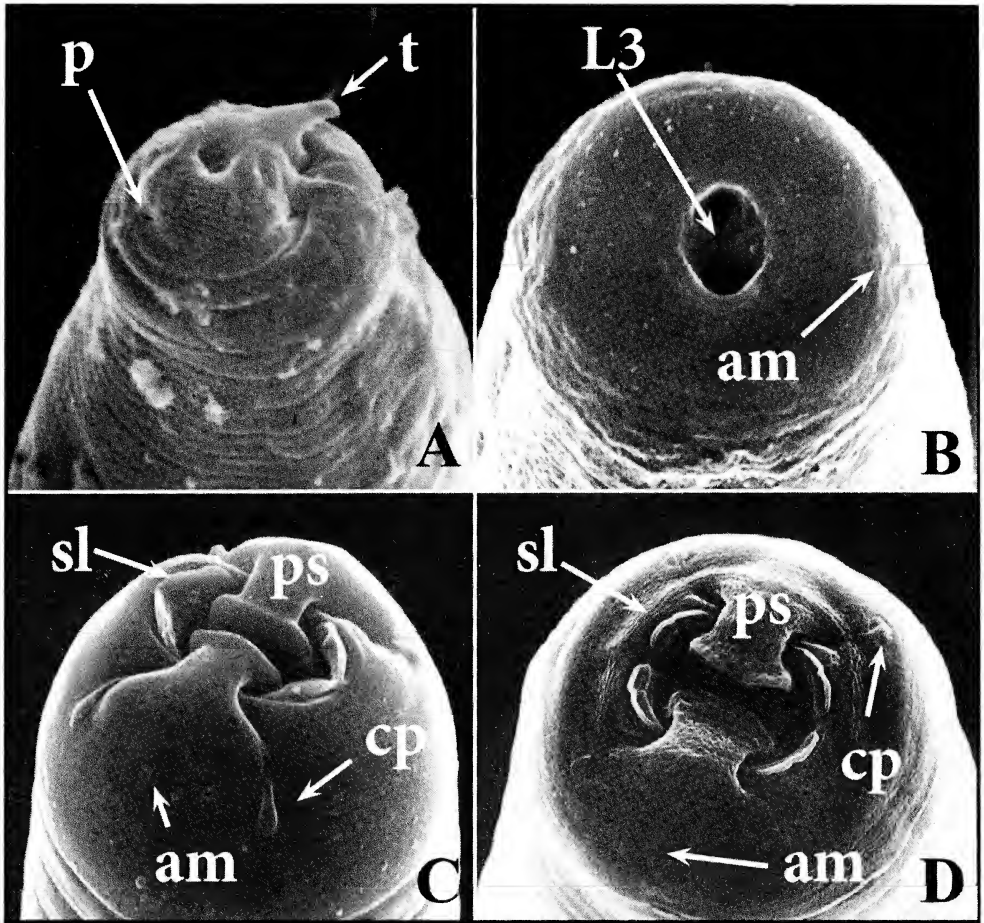


Figure 1. Scanning electron micrographs of the oral end of *Salmonema ephemeridiarum*: first stage larva (A), second stage larva (B), third stage larva (C) and adult (D). am = amphid, cp = cephalic papilla, L3 = third-stage larva, p = pore, ps = pseudolabium, sl = sublabia, t = tooth.

muscle tissue of the mayfly. The pore adjacent to the oral opening most likely provides a means for the larvae to release chemicals from glandular cells located adjacent to the oral opening; such cells have been previously identified in spirurid nematodes (Quentin and Poinar 1973). The second stage larvae, which are short-lived in the intermediate host, have simpler oral regions.

The oral morphology of third stage larvae are very similar to adult worms although the sublabia of adult worms appear to be more clearly separated and have a more defined notch in the anterior margin. SEM studies on larval stages of the allied genera *Capillospirura* and *Ascarophis* (Appy and Dadswell 1987; Appy and Butterworth 2011, respectively) also show the oral morphology of third stage larvae to be similar if not identical to the adult stage. As a result it is anticipated that third stage larvae of other cystidicolids found in invertebrates can be assigned to a genus and possibly to species in localities where the morphology of adult worms is well understood.

Cystidicolid nematodes are frequently associated with precocious development, including continued growth of infective larvae to a relatively large size and advanced development of reproductive structures in the intermediate host (Smith and Lankester 1979; Anderson and

Bartlett 1993; Anderson 2000). At least one species of *Ascarophis* has been experimentally shown to develop to the adult stage in the invertebrate host (Fagerholm and Butterworth 1988; Appy and Butterworth 2011). It is apparent that this precocious development of reproductive structures, which is thought to enhance transmission (Anderson and Bartlett 1993), also applies to somatic development of the worm including feeding structures, which are complete or nearly complete at the third stage in the intermediate host.

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## Abnormal Coloration in Bighorn Sheep (*Ovis canadensis*)

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Reports of abnormal coloration in wild vertebrates are encountered frequently in the literature. Abnormal white coloration manifests itself as albinism or leucism, and those terms are often used interchangeably, albeit erroneously (Curatolo 1979; McCardle 2012). Albinistic individuals are characterized by a complete lack of pigmentation in the skin and hair and have pink eyes; leucistic individuals (Fig. 1), however, are deficient in pigmentation and are white in color, but exhibit pigmented skin and eyes that are normally colored or blue (Abreu et al. 2013 for review). Leucism is a double-recessive trait (Cruikshank and Robinson 1997); hence, normally colored parents have the potential to produce leucistic offspring, but the genetics of albinism should not be confused with the genetics of leucism (Searle 1968).

Piebaldism involves a lack of pigmentation (Abreu et al. 2013) in some parts of the body, and piebald individuals are characterized by normally colored eyes (Fertl and Rosel 2002; Acevedo and Aguayo 2008). Miller (2005) noted that piebaldism has been referred to as partial albinism by some investigators, whereas others have not considered the differences between piebaldism and leucism; thus, the terminology associated with reports of abnormally pigmented animals frequently is confounded (Abreu et al. 2013). Melanistic individuals exhibit dark or even black pelage or appendages resulting from the excessive deposition of melanin, and this condition occurs less frequently than does albinism (Sage 1963).

Shackleton (1985) had reported an absence of records of abnormal coloration in bighorn sheep (*Ovis canadensis*) despite published reports of white-colored individuals (Jones 1958; Hansen 1965a; Cooper 1974; O'Connor 1974; Wilson et al. 1975; McQuivey 1975, 1978; Jones 1980). Individuals exhibiting piebaldism also had been previously described (Hansen 1965a, 1965b), as had melanistic bighorn sheep (O'Connor 1974) and others whose coloration was described by Bunch and Nguyen (1982) as “melanistic black”. Similar to Shackleton’s (1985) report, McCardle (2012) did not include any records of white, albinistic, or leucistic bighorn sheep in a much more recent review.

My interest in this subject dates to 1976—when I learned that  $\geq 2$  white-colored individuals had been seen in the Clark Mountain Range, San Bernardino County, California—and I have since then recorded all records of abnormally colored bighorn sheep that I became aware of. I also used several web-based bibliographic databases (EBSCOhost, JSTOR, Google Scholar, Harzing’s Publish or Perish) and a web-based search engine (Google) to search for words or phrases (albinistic, leucistic, piebald, melanistic, pelage color, etc.) specific to abnormal coloration in bighorn sheep and reviewed results of those searches for references to abnormal coloration in that species. Additionally, I contacted numerous bighorn sheep biologists and other colleagues in the United States and Canada, as well as guides, outfitters, and hunters that had accumulated extended periods of time in the field, and queried each regarding observations of abnormally colored bighorn sheep. Finally, a simple questionnaire was distributed via e-mail to members and affiliates of the Northern Wild Sheep and Goat Council or the Desert Bighorn Council.





Fig. 1. Leucistic female and normal female bighorn sheep and leucistic male and normal male bighorn sheep in the Clark Mountain Range, San Bernardino County, California, 25 September 1998. Photograph by George C. Kerr, Society for the Conservation of Bighorn Sheep, used with permission.

In western North America, bighorn sheep occupy suitable habitat in two Canadian provinces, 5 states in Mexico, and 15 of the contiguous United States. I carefully reviewed information from throughout the range of that species, including descriptions obtained from the literature or from electronic references, and the photographs, electronic images, or detailed descriptions provided by respondents. When information or the quality of an image was sufficiently detailed, I determined if individuals described either as ‘white’ or ‘albino’ were leucistic or albinistic. In addition, I reviewed the results of waterhole counts, aerial surveys, and other aerial events conducted from 1976 to 2009 by personnel from the California Department of Fish and Game (CDFG) or Bureau of Land Management (BLM) in the Nopah Range, Inyo County, California and the Kingston, Mesquite, and Clark Mountain ranges, San Bernardino County, California—areas from which leucistic bighorn sheep previously had been reported. I also reviewed results of aerial surveys of the Avawatz Mountains, San Bernardino County, an area of interest because the Southern Piute word *avawatz* implies “white sheep” (Werner 1951).

Contrary to information provided by Shackleton (1985) and McCardle (2012), observations of leucistic, melanistic, or piebald bighorn sheep have, for many years, been reported from throughout the range of the species (Table 1). In addition to the reports published prior to the reviews of Shackleton (1985) and McCardle (2012), abnormally colored bighorn sheep have now been described from  $\geq 30$  geographic areas from British Columbia southward to Baja California Sur, and as far east as North Dakota. Further, white coloration has been reported among four

Table 1. Locations of reported observations of unique color morphs of bighorn sheep (*Ovis canadensis*) in North America. This compilation almost certainly does not include every geographic area from which color morphs have been reported, but it does establish the widespread distribution of leucistic (L) or piebald (P) bighorn sheep, and those described as 'albino' ('A') or simply as 'white' ('W') by the reporting party. The sex(es) of the bighorn sheep seen appear parenthetically; if not indicated, sex was not determined or otherwise was not available.

Location	Trait <sup>1</sup> (Sex)	Source
Clark Mountain Range, CA	'W'	R. Campbell, Society for the Conservation of Bighorn Sheep
	'L' (♂, ♀)	V. Bleich, R. Weaver; California Department of Fish and Game (CDFG; multiple observations)
	L	McQuivey (1978; leucism determined from McQuivey's [1975, 1978] published descriptions)
Kingston Range, CA	'W' (♀)	J. Jaeger (University of Nevada, Las Vegas; in litt.)
Nopah Range, CA	L (♂)	Yearling captured on 13 November 1989 by R. Clark (CDFG) and W. Boyce (UC Davis)
Stateline Hills, CA and NV	'L' (♂)	McQuivey (1978); J. Jaeger (in litt.) A. Pauli (CDFG; in litt.)
Cottonwood Mountains, CA <sup>2</sup>	'W'	J. Wehausen, White Mountain Research Station (personal communication)
Spring Mountains, NV	'W' (♂, ♀)	Hansen (1980); J. Rozich, U.S. Forest Service (USFS); C. Stevenson, Nevada Division of Wildlife (NDOW); P. Cummings, NDOW; B. Jefferson, Fraternity of the Desert Bighorn; J. Zenz, bighorn sheep outfitter (each via personal communication); NWRBC (1995)
	'A' (♀)	Cooper (1974)
	'A', 'W'	McQuivey (1975)
	'L' (♂, ♀)	McQuivey (1978) (leucism determined from McQuivey's published descriptions)
	'L' (♂),	V. Clark (personal communication; leucism determined from photograph)
	L (♂, ♀)	<a href="http://www.birdandhike.com/Wildlife/Mamm/08Art/05_Bov/Ovis_can/RedRocks/WhiteSheep/_Ovi_can_white.htm">http://www.birdandhike.com/Wildlife/Mamm/08Art/05_Bov/Ovis_can/RedRocks/WhiteSheep/_Ovi_can_white.htm</a> (leucism determined from photograph)
	L (♂)	<a href="http://www.fineartamerica.com/featured/desert-bighorn-sheep-white-phase-donnie-barnett.html">www.fineartamerica.com/featured/desert-bighorn-sheep-white-phase-donnie-barnett.html</a> (leucism determined from photograph)
	L (♂)	<a href="http://www.summitpost.org/white-lamb-with-normal-bighorns/355935">www.summitpost.org/white-lamb-with-normal-bighorns/355935</a> (leucism determined from photograph)
	L (♂)	<a href="http://www.aroundthebendfriends2.blogspot.com/2012/03/white-bighorn-32412.html">www.aroundthebendfriends2.blogspot.com/2012/03/white-bighorn-32412.html</a> (leucism determined from photograph)
	Near Las Vegas, NV	'A' (♂)
Muddy Mountains, NV	'W'	McQuivey (1978)
El Dorado Mountains, NV	'W'	McQuivey (1978)
Pintwater Range, NV	'P', 'W' (♂, ♀)	Hansen (1965a)
	'W'	E. Pribyl, Fraternity of the Desert Bighorn (personal communication)
Highland Range, NV	'W'	E. Pribyl (personal communication)
Hiko Range, NV	'W' (♂)	J. Zenz; C. Stevenson; P. Cummings; E. Pribyl (each via personal communication)

Table 1. (Continued).

Location	Trait <sup>1</sup> (Sex)	Source
Ruby Mountains, NV	L (♂)	L. Spradlin (personal communication; leucism determined from photograph)
Sierra Ancha, AZ	'L' (♂, ♀)	D. Darveau, Arizona Game and Fish Department (AZGFD; personal communication)
Near Roosevelt Lake, AZ	L (♂, ♀)	<a href="http://www.coueswhitetail.com/forums/topic/18168-some-white-bighorn-sheep/">www.coueswhitetail.com/forums/topic/18168-some-white-bighorn-sheep/</a> (probably leucistic as determined from photographs)
Silver Bell Mountains, AZ	'P' (♂)	D. Aubuchon, AZGFD; B. Brochu, AZGFD (each via personal communication)
Little Harquahala Mtns, AZ	'L' (♀)	M. Brown (AZGFD, personal communication; leucism determined from description)
Grand Canyon, AZ	L (♀)	<a href="http://archive.library.nau.edu/cdm/singleitem/collection/cpa/id/3686/rec/11">archive.library.nau.edu/cdm/singleitem/collection/cpa/id/3686/rec/11</a> (leucism determined from photograph)
	'W' (♀)	M. Jorgensen, California Department of Parks and Recreation (personal communication)
	L (♂)	M. Jorgensen (personal communication; leucism determined from description of image)
Wind River Range, WY	L (♂)	Ferris (2013; leucism determined from photograph)
	'W' (♂)	K. Hurley, Wyoming Game and Fish Department (personal communication)
Thoroughfare Canyon, WY	'W'	J. Stradley and K. Alt, Montana Department of Fish, Wildlife and Parks (personal communication)
Skaha Lake, BC, Canada	L (♀)	A. Reid, British Columbia Ministry of Forests, Lands and Natural Resource Operations (personal communication; leucism determined from photograph)
	L (♀)	<a href="http://oliverdailynews.com/steep-feeding/">http://oliverdailynews.com/steep-feeding/</a> (leucism determined from photograph)
Badlands, ND	'W'	Morsette (1996)
T. Roosevelt National Park, ND	'L'	B. Wiedmann, North Dakota Game and Fish Department (personal communication)
	'W'	<a href="http://www.minotdailynews.com/page/content.detail/id/571621/Of-black-squirrels-and-white-bighorns.html?nav=5012">www.minotdailynews.com/page/content.detail/id/571621/Of-black-squirrels-and-white-bighorns.html?nav=5012</a>
Not disclosed	'W'	Jones (1980)
Bitterroot Range (Unit 20A), ID	L (♀)	K. Hurley (personal communication; leucism determined from photograph)
Sheep Mountain (Unit 36A), ID	'W' (♂)	K. Hurley (personal communication)
	'W' (♀)	J. Walters and M. Johnson, USFS (personal communication)
Lemhi Range, ID	'L'	J. Walters and M. Johnson, USFS (personal communication)
West of Abajo Mountains, UT	'L' (♀)	B. Crompton, Utah Division of Wildlife Resources (UDWR; personal communication)
Bookcliff Mountains, UT	'P' (♂)	R. Thacker, UDWR (personal communication)
San Juan River Canyon, UT	'P' (♂)	G. Wallace, UDWR (personal communication)

Table 1. (Continued).

Location	Trait <sup>1</sup> (Sex)	Source
Antelope Island, UT <sup>3</sup>	'L' (♂) L (♂)	R. Robinson, UDWR (personal communication) <a href="https://www.facebook.com/wildlifecaptureequipment/photos/a.1914961962062962.1073741852.1473946379497858/1914962002062958/?type=3&amp;theater">https://www.facebook.com/wildlifecaptureequipment/photos/a.1914961962062962.1073741852.1473946379497858/1914962002062958/?type=3&amp;theater</a> (leucism determined from photograph)
Sierra de San Pedro Martir, Baja California, Mexico	'W'	Wilson et al. (1975)

<sup>1</sup>Single quotation mark around a trait indicates it was described by the original observer(s); an absence of quotes indicates the designated trait was assigned by V. Bleich from information available from, or provided by, the source.

<sup>2</sup>Riverside County.

<sup>3</sup>UDWR personnel translocated this individual, a male lamb, from Antelope Island to the Canyon Mountains, Utah, in January of 2016.

of the five clades (*O. c. canadensis*, *O. c. cremnobates*, *O. c. nelsoni*, and *O. c. mexicana*) of bighorn sheep recognized by Buchalski et al. (2016). Reports of piebald or melanistic individuals were, however, much less common than reports of white-colored animals (Table 1). Although there likely are additional records of abnormal coloration in bighorn sheep not reported herein, this paper corrects the omissions of Shackleton (1985) and McCardle (2012) and, hopefully, will stimulate others to record additional observations of anomalous coloration in that iconic species.

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## CONTENTS

A New Species of <i>Lepeophtheirus</i> (Copepoda; Caligidae) Parasitic on Three Kelpfish Species (Clinidae) from the Southern California Coast. Julianne Kalman Passarelli and Danny Tang.....	1
Habitat Use and Behavior of the East Pacific Green Turtle, <i>Chelonia mydas</i> , in an Urbanized System. Daniel P. Crear, Daniel D. Lawson, Jeffery A. Seminoff, Tomoharu Eguchi, Robin A. LeRoux, and Christopher G. Lowe.....	17
Range Expansion of the Eastern Fox Squirrel within the Greater Los Angeles Metropolitan Area (2005 – 2014) and Projections for Continued Range Expansion. Rosemary B. Garcia and Alan E. Muchlinski.....	33
First Reported Occurrence of the Southern Sea Otter <i>Enhydra lutris lutris</i> at California's Santa Barbara Island Since 1940. Michael C. Couffer.....	46
Development of Oral Structure in <i>Salmonema ephemeridarum</i> (Nematoda: Spirurida: Cystidicolidae). Ralph G. Appy.....	51
Abnormal Coloration in Bighorn Sheep ( <i>Ovis Canadensis</i> ). Vernon C. Bleich.....	54

Cover: Leucistic female and normal female bighorn sheep and leucistic male and normal male bighorn sheep in the Clark Mountain Range, San Bernardino County, California, 25 September 1998. Photograph by George C. Kerr, Society for the Conservation of Bighorn Sheep, used with permission.