

Regional extinction of a conspicuous dorid nudibranch (Mollusca: Gastropoda) in California

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Abstract *Felimare californiensis* (= *Hypselodoris californiensis*) was once common throughout the Southern California Bight (SCB) and California Channel Islands. This well-known shallow-water nudibranch, which specializes on dysideid sponges, has persisted for decades in Mexico, but in California disappeared from its entire range by 1984. Since reappearing in 2003, it has been found only at Santa Catalina Island, plus sightings of single individuals in 2011 at Santa Cruz Island and San Diego. The decline of *F. californiensis* in California was documented using published historical records, museum collections, unpublished field accounts, and images posted online. The loss of this emblematic species is unique among Californian nudibranchs, including (1) its congener *Felimare porterae* (= *Mexichromis porterae*), with which it appears to overlap in diet, and (2) opisthobranch species with similar historical

geographic ranges and mode of development. The decline in *F. californiensis* is not predicted by warming trends and climate variation over the past 40 years, including the strong El Niño events of 1983 and 1998. Coastal pollution from the large human population in southern California may have impacted *Dysidea ambliia*, the primary reported prey of *F. californiensis*. Historical overcollecting of the nudibranch and habitat loss through the development of major ports likely also contributed to its decline. Sightings since 2003 are consistent with a nascent recovery, as elements of water quality have improved in the SCB in recent decades.

Introduction

Humans have heavily impacted marine biota and ecosystems in the Southern California Bight (Dayton et al. 1998; Tegner and Dayton 2000; Sagarin et al. 2007; Halpern et al. 2008; Puritz and Toonen 2011). However, despite our large population and pervasive reach, only a handful of historical extinctions of marine species have been documented in the region (Carlton et al. 1999; Dulvy et al. 2003; Régnier et al. 2009). Sea otters and white abalone are the most prominent examples, not just for the ecological cascades triggered by their removal, but also for the stark realization that we could so quickly extinguish their populations (Jackson et al. 2001; Roberts 2007). In contrast, two obscure species, the marsh horn snail *Cerithidea fuscata* and the mid-intertidal limpet *Lottia edmitchelli* (= *Collisella edmitchelli*), had such limited distributions that their passings were nearly missed (Carlton 1993).

Here, we document the regional extinction of *Felimare californiensis* (Bergh 1879), an emblematic nudibranch gastropod once widespread and common in shallow-water, hard bottom habitats on the mainland coast of southern

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California. We also summarize knowledge of its biology and evaluate hypotheses for its decline. Unlike otters and abalone, *F. californiensis* had no direct commercial importance to humans. However, simply finding one “on a foggy morning between Pacific tides” (Ricketts et al. 1985) once inspired exhilaration, even pride, for its size, graceful form, and especially its stunning colors.

Dark blue with gold spots and up to 80 mm long, *F. californiensis* (Fig. 1) is one of the most distinctive dorid nudibranchs in the northeast Pacific Ocean. This species was well known to zoology students and professors working out of the marine laboratories from San Diego to Monterey in the early twentieth century and was included in most of the guidebooks to the common seashore fauna of the region (see Johnson and Snook 1927; Ricketts and Calvin 1939; Hedgpeth and Hinton 1961; Hinton 1969; Morris et al. 1980). Johnson and Snook (1927) described it as “fairly abundant in the tide pools from Monterey to San Diego,” while Hinton (1969) described it as “moderately common at lowest tides.” In the past decade, however, *F. californiensis* has been regularly found only at Santa Catalina Island (M. Miller in Geitler 2009; Bushing 2011), and as first noted by Michael Miller in Behrens (2001), it

does not appear to have been found on the mainland of California in decades.

Bergh (1879) originally described *F. californiensis* as *Chromodoris californiensis*, based on a specimen collected intertidally on Santa Catalina Island by William Healey Dall in 1874. Twenty-two years later, while working out of the University of California (UC) Marine Laboratory in San Pedro (which moved 2 years later to La Jolla and evolved into the Scripps Institution of Oceanography), biologists Theodore D. A. and Wilmette Cockerell found this species in the local tide pools. Apparently unaware of Bergh’s earlier description, Cockerell (1902) named the species *Chromodoris universitas*, for its “colors... of the University of California” and also because it was “collected at San Pedro by the naturalists of the University of California Marine Laboratory.” After realizing that the two descriptions represented the same species, Cockerell and Eliot (1905) synonymized *C. universitas* with *C. californiensis*. Despite the synonymy, Bergh’s older epithet (no doubt named for the State) is consistent with Cockerell’s honorary one. *F. californiensis* is commonly referred to as the California chromodorid, or California blue dorid, and is also known to some as the “Cub Scout nudibranch” owing

Fig. 1 *Felimare californiensis* from Catalina Island. **a** 70 mm long, August 2006. Image by Kenneth Kopp. **b** Feeding on dysideid sponge, July 2008. Note extended buccal mass and feeding scars on sponge surface. Image by Kenneth Kopp. **c** Laying an egg ribbon in laboratory aquarium at USC Wrigley Marine Laboratory, September 1972. Image by Jack Engle



to its similarity in color to the uniforms of the (United States) Scouting group. *F. californiensis* was once placed in the genus *Glossodoris*, and more recently in *Hypselodoris* (see McDonald 1983, p. 191; Behrens and Hermsillo 2005). However, in their revision of the classification of the Chromodorididae, Johnson and Gosliner (2012) apply the name *Felimare* to a clade consisting of all eastern Pacific, Atlantic and Mediterranean species of *Hypselodoris* and two species of *Mexichromis*. We follow their classification here.

Methods

To obtain records of *F. californiensis*, we searched published literature, government agency reports, the museum collection databases of the California Academy of Sciences (CAS) and the Natural History Museum of Los Angeles County (LACM), and unpublished field accounts of California nudibranchs by James R. Lance, Richard A. Roller, and Gary R. McDonald. The field accounts of Lance and Roller are housed at CAS, and the data from the Lance accounts for outer coast sites in San Diego County are publicly accessible online (California Academy of Sciences and Goddard 2013). GR McDonald (pers comm, March 9, 2010) sent JG an Excel spreadsheet containing the data from his field accounts, which cover the years 1967–2010. We also searched the World Wide Web for images and records of *F. californiensis*; these were used when identification was unequivocal, and dates of observation and specific locality information provided. We requested records of the nudibranch from scientists involved in long-term monitoring of rocky intertidal and subtidal habitats in southern and central California, as well as amateur naturalists and divers with long-term interest and expertise in nudibranchs from California.

We also used personal observations of nudibranchs from intertidal sites formerly known to support *F. californiensis* (see Table S1). These were counts conducted sporadically since 1999 by JG as part of an ongoing survey of nudibranch biodiversity in southern California. At each site, counts focused on low intertidal pools and the under-rock habitats supporting the sessile prey of nudibranchs. Counts started approximately 1 h before low tide and lasted 2–3 h depending on the size of the site and number of observers and were not conducted during inclement conditions (e.g., high surf) that would have impeded views into pools and under-rock habitat.

We compiled records of occurrence in three supplementary Tables: (S1) positive records, (S2) negative records for intertidal sites with historical records of the species, and (S3) negative, multiyear subtidal records from the Monterey Peninsula and the Southern California Bight (SCB).

In Table S2, we generally did not include negative records obtained in long-term monitoring by the Multi-Agency Rocky Intertidal Network (MARINe) and the Coastal Biodiversity Survey at UC Santa Cruz. Although geographic coverage by these groups is extensive, and they sample at or near sites where *F. californiensis* has been found historically, their sampling is generally restricted to key sessile and sedentary species on exposed bedrock surfaces (Engle 2008; PISCO 2009; Coastal Biodiversity Survey 2010). They, therefore, rarely encounter nudibranchs, which prefer less easily sampled tide pools, boulder fields, and shaded under-rock habitats.

One of us (AV) dissected 21 museum specimens of *F. californiensis* to examine the alimentary canal (esophagus) for identifiable prey items.

Results

Habitat

Felimare californiensis has been reported historically from low intertidal pools on rocky shores (Lance 1953–2001), “shallow reefs” (McBeth 1970), and boulder reefs and surfgrass, *Phyllospadix* spp., beds (Kobayashi 1979). In 1959, it was observed at Redondo Beach on an artificial reef made of old streetcars (Carlisle et al. 1964), and in the early twentieth century, it was found on pilings in Newport Bay, presumably at low tide (MacFarland 1966). Recent subtidal sightings of *F. californiensis* at Santa Cruz and Santa Catalina Islands have been from undercut rock walls, high relief boulder fields, or rocky reefs (Hoover 2011, pers obs).

Diet, chemical defense, and mimicry

McBeth (1971) reported *F. californiensis* feeding in the San Diego area on the spiculate tetractinomorph and ceractinomorph sponges *Stelletta estrella* and *Haliclona* sp. However, subsequent reports, including from San Diego, have only included the non-spiculate, fibrous dictyoceratid sponge *Dysidea ambliia* (de Laubenfels, 1930) (see Hochlowski et al. 1982; McDonald and Nybakken 1997; also see Fig. 1b and records from Paradise Cove, Malibu listed in Table S1). Members of the genus *Hypselodoris* (and now *Felimare*) worldwide have since been shown to specialize on dictyoceratid sponges, especially species of Dysideidae, and utilize biologically active secondary metabolites (especially sesquiterpenes and furanosesquiterpenes) acquired from these sponges for defensive purposes (reviewed by Rudman and Bergquist 2007; Cimino and Ghiselin 2009). Additionally, species of *Hypselodoris* and *Felimare*, including *F. californiensis*, share a finely denticulate radular tooth morphology common to dorid

nudibranchs specialized for feeding on non-spiculate sponges (Goddard 1981; Rudman and Bergquist 2007). Some of these sponges, including species of *Dysidea*, incorporate sand, debris, and foreign sponge spicules into their spongin fiber skeleton (e.g., Carballo et al. 2006).

Our examination of gut contents of LACM specimens of *F. californiensis* revealed an abundance of spongin fibers and sand grains, and a few siliceous and calcareous sponge spicules and Foraminifera (Table 1), all consistent with feeding on dysideids (de Laubenfels 1932; Carballo et al. 2006). Moreover, specimens of *F. californiensis* collected in San Diego contained the metabolites furodysin and pallescensin A (Hochlowski et al. 1982), which are found in *Dysidea amblia* (Thompson et al. 1985), as well as euryfuran, which was isolated from *Euryspongia* sp., another dysideid sponge collected from San Diego (Hochlowski et al. 1982; Thompson et al. 1985). *Felimare californiensis* from the Gulf of California contained the metabolites dendrolasin and nakafuran 8, both of which have been isolated from other dysideids (Karuso and

Scheuer 2002; Carballo et al. 2006). Metabolites isolated (but not characterized) from the sponges reported by McBeth (1971) as prey of *F. californiensis* had different bioassay profiles compared to those isolated from *Dysidea amblia* and *Euryspongia* sp. (Thompson et al. 1985), suggesting different metabolites are present in those sponges. Therefore, *F. californiensis* appears to specialize on dysideids, including *Dysidea amblia* and *Euryspongia* sp. in California.

Metabolites extracted from *F. californiensis* by Hochlowski et al. (1982) have been shown to inhibit feeding by fish (Schulte et al. 1980; Thompson et al. 1985; Karuso and Scheuer 2002), and like other species of *Felimare* and *Hypselodoris*, *F. californiensis* is considered to be warning colored (see Cimino and Ghiselin 2009). Moreover, in the Gulf of California, *F. californiensis* appears to be part of a Müllerian mimicry complex involving *F. ghiselini*, *F. agassizi*, some color forms of *Polycera alabe* and *Navanax inermis*, as well as the turbellarian flatworm *Pseudoceros bajae* (Gosliner and Behrens 1990; Cimino and Ghiselin

Table 1 Gut contents of *Felimare californiensis* from Natural History Museum of Los Angeles County (LACM)

LACM voucher no.	Locality	Year of collection	Esophageal content
127287	Palos Verdes, California	1949	Empty
70-8	Santa Catalina Island, California	1970	–
68532	Santa Catalina Island, California	1970	Empty
68548	Santa Catalina Island, California	1971	Spongin fibers, sand grains, Foraminifera, few spicules
71-91	Isla San Gerónimo, Baja California	1971	Empty
68541	Baja California	1971	Spongin fibers, sand grains, Foraminifera, bryozoan fragments, few spicules
71-183	Bahía Magdalena, Baja California	1971	Empty
71-170	Outer coast, Baja California	1971	Empty
68536	San Clemente Island, California	1971	Spongin fibers, sand grains, few spicules
36574	Anacapa Island, California	1971	Empty
68535	San Clemente Island, California	1971	Empty
68537	Cortes Bank, California	1971	Spongin fibers, bryozoan fragments, few spicules
72-112	Isla San Martín, Baja California	1972	Spongin fibers, bryozoan fragments, few spicules
68533	Santa Catalina Island, California	1972	–
68539	Isla San Martín, Baja California	1973	Amorphous soft material
68538	Isla Coronado, Baja California	1973	Empty
68556	Isla San Martín, Baja California	1973	Empty
45058	San Diego, California	1974	–
68540	Bahía de Los Ángeles, Baja California	1975	–
68534	Santa Catalina Island, California	1975	–
62515	San Carlos, Sonora	1978	Empty

Dashes correspond to specimens with damaged, missing, or minute esophagus

2009), similar to a mimicry complex of warning colored and chemically defended species of *Felimare* known from the northeastern Atlantic (Haber et al. 2010).

Life history

Based on a photograph of an egg-laying individual (Fig. 1c) and egg mass dimensions reported by Ingram (1935), *F. californiensis* lays eggs approximately 100 µm in diameter and, therefore, has planktotrophic larval development (Goddard 2004; Goddard and Green 2013). Egg-laying has been observed from July to September (Ingram 1935; CH, pers obs; Fig. 1c), and based on in situ observations by one of us (CH) of three egg masses laid at Santa Catalina Island in September 2012, *F. californiensis* develop to hatching in >7, but <12 days at 17–19 °C, also consistent with the development of planktotrophic larvae. The adult lifespan of *F. californiensis* is unknown, but is probably a year or less, as in other dorids from temperate waters (Thompson 1964, 1976; Eyster and Stanczyk 1981; Todd 1981; Bertsch and Marlett 2011). Individuals <30 mm long have been recorded from June to October on the Pacific coast of Baja California Sur, but have rarely been observed in the SCB (Table S1). Large individuals (>65 mm long) have been recorded in all seasons in the SCB, but appear to be more prevalent from mid-spring to mid-fall, overlapping the spawning season (Table S1).

Predators, competitors, and parasites

Nothing is known about predation in the field on *F. californiensis*, but like other nudibranchs, it is likely attacked by fish, decapod crustaceans, and asteroids (Mauzey et al. 1968; Harris 1986; Gochfeld and Aeby 1997). In laboratory trials, the trail-following cephalaspidea opisthobranch *Navanax inermis* consumed *Felimare californiensis*, along with a wide variety of other soft-bodied nudibranchs (Paine 1963).

In California, *Felimare porterae* (Cockerell, 1901) has been reported feeding solely on *Dysidea amblia* (McDonald and Nybakken 1997) and, therefore, might compete directly with *F. californiensis* for prey. *Cadlina flavomaculata* MacFarland 1905, *C. limbaughorum* Lance 1962, and *C. luteomarginata* MacFarland, 1966 from California reportedly also consume *D. amblia*, but as part of broader diets (McDonald and Nybakken 1997; Goddard 1998; Penney 2002), and are, therefore, less likely to compete with *F. californiensis*.

Splanchnotrophic copepods endoparasitize a wide variety of shell-less opisthobranchs, including, at low prevalence, a few species of chromodoridids (Huys 2001; Uyeno and Nagasawa 2012). To our knowledge, these have not

been observed in *F. californiensis*, and other parasites of *F. californiensis* are unknown.

Historical range and current distribution

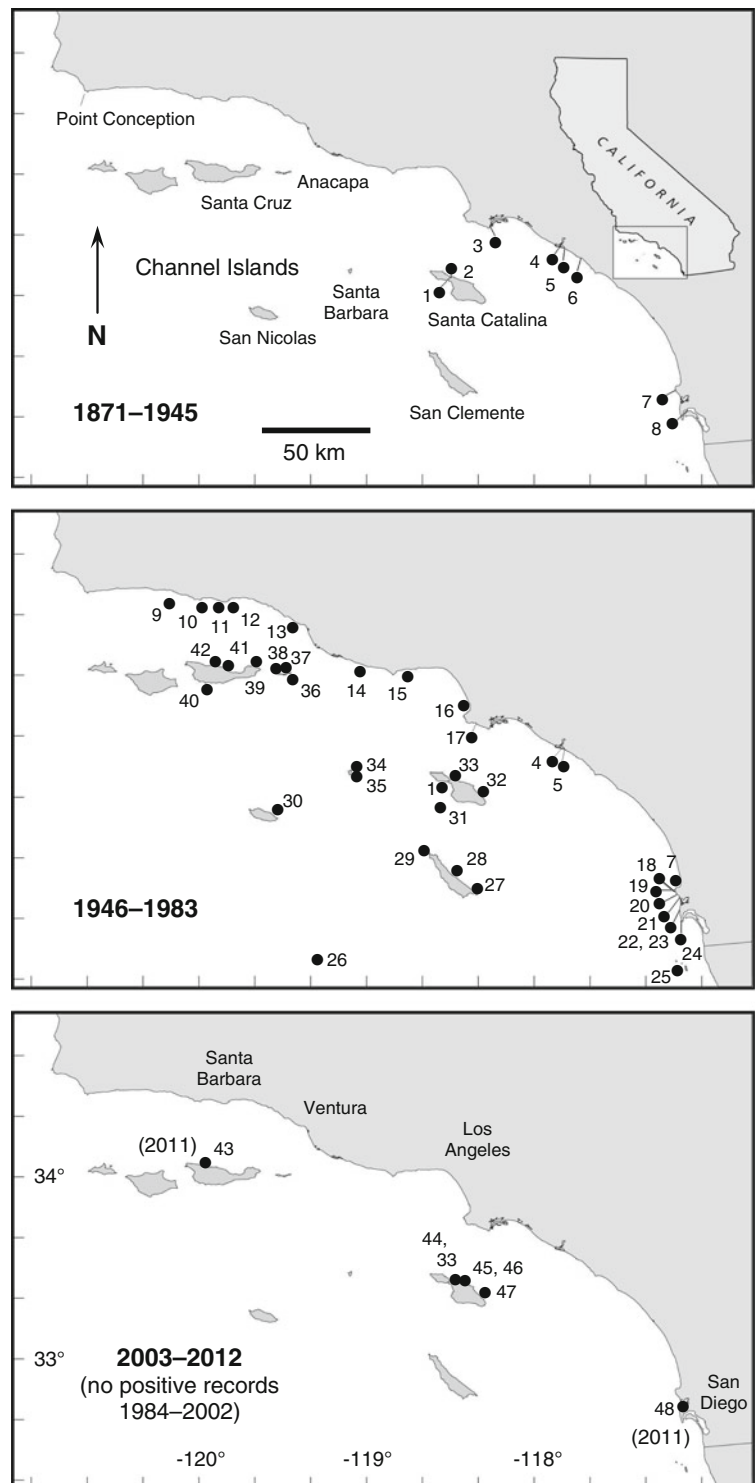
Felimare californiensis has been recorded from Monterey, the Southern California Bight south to Bahía Magdalena in Baja California Sur, and the Gulf of California from the La Paz region north to Bahía de los Ángeles, Baja California and Cabo Tepoca, Sonora (Bertsch 1978, 2008; Angulo-Campillo 2005; Behrens and Hermosillo 2005; Kerstitch and Bertsch 2007, and see Table S1). It has been found intertidally and subtidally to at least 33 m (Table S1). As discussed by Bertsch (1978), early records of *F. californiensis* from the Gulf of California are unreliable, owing to taxonomic confusion with the similarly colored congeners *F. agassizii* and *F. ghiselini*. It should be noted, however, that both of the latter species are unknown from California waters (Behrens and Hermosillo 2005).

W. H. Dall first observed *Felimare californiensis* on the Monterey Peninsula around 1871 (Bergh 1879; and see Woodring 1958). After that, no records, positive or negative, of the species exist until F. M. MacFarland arrived at the newly opened Hopkins Marine Station in 1892. Searching for opisthobranchs regularly in the Monterey area, MacFarland did not find *F. californiensis* from 1892 to 1907 (MacFarland 1905, p. 130, 1966). F. W. Weymouth, also working out of Hopkins Marine Station, found a specimen in 1908, and MacFarland found more in 1909 (MacFarland 1966, p. 162). No specimens of *F. californiensis* have been recorded from the Peninsula since then, intertidally or subtidally (Tables S2, S3, and see note for Monterey records in Table S1).

In contrast to the Monterey area, *Felimare californiensis* has been recorded from the SCB frequently for 140 years (Fig. 2, Table S1). In the late nineteenth century and first half of the twentieth century, it was known from the Palos Verdes Peninsula south (Fig. 2), largely reflecting the location of marine laboratories and zoologists in San Pedro (UC), Corona del Mar (California Institute of Technology), Laguna Beach (Pomona College), and La Jolla (UC).

As recently as the 1970s, *F. californiensis* was observed frequently throughout the SCB, both subtidally and intertidally, and on both the mainland and at all but the two westernmost Channel Islands (Fig. 2, Table S1). At La Jolla in the late 1960s, *F. californiensis* was common in the shallow subtidal (TM Gosliner, pers comm to JG, Sept 2011), and McBeth (1970, p. 21) stated “*Hypselodoris californiensis* usually was found in groups of 10–20 individuals living on shallow reefs.” On one dive in August 1968, McBeth observed >65 individuals under a ledge on a rocky reef at 6-m depth (Lance 1953–2001). Ten years later, the density of *F. californiensis* in surfgrass beds and

Fig. 2 Location of historical sightings of *Felimare californiensis* in Southern California Bight. Simple filled circles represent subtidal records of nudibranch; those connected by lines to shore represent intertidal records. Based on records documented in Table S1. Site key: 1 S Isthmus, 2 N Isthmus, 3 San Pedro, 4 Newport Bay, 5 Little Corona, 6 Laguna Beach, 7 La Jolla, 8 San Deigo and San Diego Bay, 9 Naples Reef, 10 Coal Oil Point, 11 Mohawk Reef, 12 Leadbetter, 13 Rincon Island, 14 Mugu Lagoon to Latigo Point, 15 Paradise Cove, 16 Redondo Beach, 17 Portuguese Bend, 18 South Casa Reef, 19 Windansea Reef, 20 Bird Rock, 21 False Point, 22 Hill Street, 23 Ladera Street, 24 Point Loma, 25 Coronados Islands, 26 Cortes Bank, 27 Pyramid Head, 28 San Clemente Island, 29 Castle Rock, 30 SN2, 31 Farnsworth Bank, 32 Santa Catalina Island, 33 Big Fisherman Cove, 34 Grave/Middle Canyon, 35 SE Sea Lion, 36 South side of East Island, 37 North side of Middle Island, 38 Anacapa Island, 39 Little Scorpion Anchorage, 40 Morse Point, 41 Fry's Harbor, 42 Diablo Rock, 43 Fern Grotto, 44 Isthmus Reef, 45 Sea Fan Grotto, 46 Yellowtail Point, 47 Casino Point, 48 Mission Bay



boulder reefs in La Jolla was estimated at 0.08–0.04 individuals m^{-2} , respectively (Kobayashi 1979).

After 1980 on the mainland, and after 1983 in the Channel Islands, *F. californiensis* disappeared from the SCB, with no new records of the species until 2003, when it was sighted at Casino Point on Santa Catalina Island (Fig. 2, Tables S1, S2, S3). Since then, *F. californiensis*

has been reported regularly, but in low numbers, from Santa Catalina Island, and single specimens were found in 2011 at Santa Cruz Island and in lower Mission Bay, San Diego (Fig. 2, Tables S1, S2, S3). Prior to the recent sighting in Mission Bay, the last records of *F. californiensis* on the mainland coast of California were from the rocky intertidal at Ladera Street, Sunset Cliffs in San Diego

in June 1977 (Table S1, California Academy of Sciences and Goddard 2013), and subtidally at Point Loma (15-m depth) in August 1980 (Hochlowski et al. 1982). In contrast, *F. californiensis* has persisted along both sides of the Baja California peninsula during the past three decades (Table S1).

The historical loss of *F. californiensis* from the mainland is especially well documented in San Diego County (Figs. 2, 3; Tables S1, S2). In 100 sampling trips to seven intertidal sites in San Diego County prior to the disappearance of *F. californiensis* from each site, James Lance found the dorid 36 times, including 6/10 and 11/14 trips to Ladera Street and Hill Street, respectively (California Academy of Sciences and Goddard 2013). He found seven individuals on June 13, 1968, at South Casa Reef (La Jolla), the highest number recorded on any sampling trip. He did not find another specimen of this species in 98 total sampling trips to these same seven sites from 1977 to 2001 (California Academy of Sciences and Goddard 2013), and *F. californiensis* has not been found in more recent sampling conducted at six of Lance's former sites (Figs. 2, 3, Table S2). Subtidally, *F. californiensis* has not been observed in thousands of hours of regular monitoring and observations by professional researchers and dedicated amateurs (Table S3). The paucity of recent observations of *F. californiensis* is, therefore, not due to lack of observation.

Discussion

Although *Felimare californiensis* has persisted in Mexican waters around Baja California, in California, it disappeared from its entire range in 1983 and since 2003 has been observed regularly, but in low numbers, only at Santa Catalina Island. This is despite (1) the strong El Niño events of 1983 and 1998, which transported southern

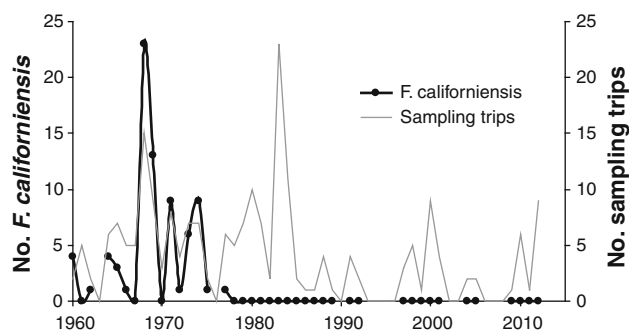


Fig. 3 Total number of *Felimare californiensis* found at 7 intertidal sites in San Diego, versus total number of sampling trips, 1960–2012. Based on data from California Academy of Sciences and Goddard (2013); JG (unpublished data); J Jacobs, J Albers-Mead, B Green (pers comms)

species from the Californian and Panamic Biogeographic Provinces far north of their usual ranges (Pearcy and Schoener 1987; Engle and Richards 2001; Lluch-Belda et al. 2005; Zeidberg and Robison 2007; Goddard in preparation), (2) the 1976 climate shift in the Northeast Pacific Ocean, which triggered northward range shifts of southern biota, including one nudibranch (Lluch-Belda et al. 2003; McGowan et al. 2003; Zacherl et al. 2003; Dawson et al. 2010; Goddard et al. 2011), and (3) range shifts and increases in the abundance of southern biota associated with longer-term warming in the northeastern Pacific Ocean (Barry et al. 1995; Sagarin et al. 1999; Lluch-Belda et al. 2003; Field et al. 2006a, b, 2007; Zeidberg and Robison 2007; Doney et al. 2012).

The brief presence of *F. californiensis* on the Monterey Peninsula in the Oregonian Biogeographic Province in 1908–1909 likely resulted from northward advection by the California Countercurrent of larvae originating from the SCB or northern Baja California. This countercurrent flows nearshore seasonally, sometimes commencing in late summer while *F. californiensis* is spawning in the SCB, but it also intensifies during El Niño events and on decadal time scales in conjunction with a relaxation of the southward flowing California Current (Strub and James 2000; Lluch-Belda et al. 2003; Thomson and Krassovski 2010). In contrast to its occurrence on the Monterey Peninsula, *F. californiensis* was clearly well established in the SCB, as indicated by 140 years of records and its historical abundance there.

The closest relatives of *F. californiensis* in California are the chromodoridids *Felimare porterae* and *Felimida macfarlandi* (see Johnson and Gosliner 2012). Both species range north to Monterey (Behrens and Hermosillo 2005), but, unlike *F. californiensis*, have persisted in southern California to the present, both intertidally and subtidally (e.g., National Park Service 1982–2006; Bartick 2007; Green 2009, 2010; Albers-Mead 2010a; Murvine 2012; California Academy of Sciences and Goddard 2013; JG, pers obs, 2000–12). Both can also still be found in the Monterey Bay area, both intertidally and subtidally (BAUE 2010; McDonald 2010). To our knowledge, *F. californiensis* is the only opisthobranch gastropod—conspicuous or not—to have completely disappeared from its mainland range in California. This includes other sponge-feeding species with geographic ranges similar to the historical range of *F. californiensis* (Table 2), as well as other nudibranchs known to undergo dramatic annual and interannual fluctuations in abundance (Nybakken 1974, 1978; Schultz et al. 2011; California Academy of Sciences and Goddard 2013; JG, pers obs).

The loss of *F. californiensis* from mainland waters is not an artifact of decreased search effort. During the past few decades, professional researchers and dedicated amateurs have conducted thousands of hours of observation, focused

Table 2 Selected recent sightings in California of sponge-feeding opisthobranchs with geographic ranges similar to historical range of *F. californiensis*

Species	Locality	Date	Reference ^a
<i>Tyrodina fungina</i>	Little Corona del Mar, Orange Co.	February 2012	JG
	Shaw's Cove, Laguna Beach (subtidal)	January 2005	Lee (2006)
	South Casa Reef, La Jolla	June 2012	JG
	Ladera St., San Diego	June 2012	JG
<i>Berthellina ilisima</i>	Anacapa Island (subtidal)	2004	NPS
	Santa Cruz Island (subtidal)	2001	NPS
	Santa Catalina Island (subtidal)	March 2011	Anonymous (2011)
<i>Conualevia alba</i>	Monterey (subtidal)	October 2006	AD
	Naples, Santa Barbara Co.	January 2008–Sept 2012	JG
	Bird Rock, La Jolla	April 2009	JG
<i>Doriopsilla albopunctata</i>	Asilomar, Monterey Co.	November 2007–October 2011	Schultz et al. (2011)
	Carmel Point, Monterey Co.	October 2012	JG
	Hazard Canyon, San Luis Obispo Co.	April 1999–July 2012	JG
	Tarpits Reef, Carpinteria	June 2012	JG
	Tarantula Reef, Santa Barbara Co.	May 2012	JG
	Bird Rock, La Jolla	June 2012	JJ
	Hill St., San Diego	June 2012	JG
<i>Doriopsilla gemela</i>	Naples, Santa Barbara Co.	November 2009	JG
	Bird Rock, La Jolla	January 2000, September 2010, July 2012	JG; JJ
	Ladera St., San Diego	June 2012	BG
<i>Doriopsilla nigromaculata</i>	South Casa Reef, La Jolla	2012	JJ
<i>Doriopsilla spaldingi</i>	Point Lobos, Monterey Co. (subtidal)	October 2007	Bauder (2007)
	Point Loma (subtidal)	January 2009	Mitchell (2009)
<i>Doris pickensi</i>	Naples, Santa Barbara Co.	September 2012	JG
	Point Fermin	May 2007	JG
	Bird Rock, San Diego	January 2000	JG
<i>Doris tanya</i>	Bird Rock, San Diego	June 2010	Albers-Mead (2010b)
<i>Peltodoris mullineri</i>	Santa Catalina Island (subtidal)	July 2011	Grossman (2011)

Unless specified otherwise, collection localities are intertidal

^a AD A. Draeger personal communication to JG, JG J. H. R. Goddard personal observation, BG B. Green personal communication to JG, JJ J. Jacobs personal communication to JG, NPS National Park Service 1982–2006

on or including nudibranchs, around the Monterey Peninsula and throughout the SCB (Tables S2, S3). *Felimare californiensis* is also large, conspicuous, uniquely colored, and has long been a favorite among professionals and amateurs alike, so is unlikely to have been overlooked (D. Richards, J. Engle, S. Anderson, M. Passage, K. Kopp, pers. comms. to JG). Although there are relatively few post-1977 accounts of nudibranchs from certain historical intertidal sites of occurrence of *F. californiensis*, such as La Jolla and Laguna Beach (Tables S1, S2), both of these areas are popular destinations for recreational divers, including some especially interested in nudibranchs. Given the absence of subtidal reports of the species from either area in recent decades (Table S3), we can infer its absence intertidally at them as well.

The loss of *F. californiensis* from the SCB, with no counterpart among California's diverse opisthobranch fauna, suggests a specific cause linked to that region. Its persistence in Mexican waters and reappearance in the past decade on Santa Catalina Island, removed from large industrial and urban centers, suggests a human impact. At the regional scale of the SCB, the most severe and pervasive anthropogenic impacts are (1) water pollution, including wastewater discharge via ocean outfalls, and stormwater runoff from the large urban, agricultural, and industrial areas (Schiff et al. 2000; Lyon and Stein 2008); and (2) historical overfishing, overcollecting, and removal of ecologically important consumers (Tegner and Dayton 2000; Jackson et al. 2001; Roy et al. 2003; Sagarin et al. 2007). Overexploitation of large consumers has not been

limited to the SCB, and therefore, direct or indirect ecological effects of this factor can probably be ruled out as causing the decline of *F. californiensis*. This leaves water pollution as the most likely cause, the specific effects of which might have directly impacted the nudibranch or its sponge prey, or indirectly affected either one of them through effects on other members of their ecosystem. Not enough is known to evaluate the possibility of indirect effects of pollution in this case, although it is difficult to imagine them being so specific as to impact *F. californiensis* and not other shallow-water nudibranchs. Likewise, we would expect any direct effects of pollutants on sensitive life history stages of *F. californiensis* (e.g., Bay et al. 2003; Roepke et al. 2005; Puritz and Toonen 2011) to affect other species of nudibranchs, the majority of which have similar life histories with benthic, encapsulated embryonic development and planktotrophic larval development (Goddard 2004; Goddard and Green 2013). The direct effect of water pollution on the abundance or quality of the sponge prey of *F. californiensis* in the SCB, therefore, appears to be the most likely cause of its demise.

Available evidence suggests that in California, *F. californiensis* preys selectively on *Dysidea amblia*. In his redescription of this species, de Laubenfels (1932) mentions the abundance of *D. amblia* washed ashore following storms. However, although long-term declines have been described for intertidal cryptofauna, including sponges, in the SCB (Addressi 1994; Goodson 2004; Smith et al. 2006; J. Bakus, pers. comm. to AV, October 19, 2012), we know of no data on historical changes in the density of *D. amblia* in shallow waters to further evaluate its importance in the decline of *F. californiensis*. Dysideid sponges were not recorded in a regional survey of benthic macrofauna conducted from 1976 to 1978 in the SCB (Bakus and Green 1987), but were collected between 1978 and 1980 from sites in San Diego County (Thompson et al. 1985). Analysis of long-term monitoring of benthic invertebrate assemblages associated with soft sediments throughout the SCB reveals that anthropogenically disrupted assemblages now occur primarily on the inner shelf, in bays, and near river discharges (Schiff et al. 2000; Stein and Cadien 2009). We would expect a similar pattern to apply to shallow-water, sessile epifauna associated with hard substrates, but how dysideid sponges may have been affected is unknown.

Reports of *F. porterae*, which is still common in the SCB, preying on *D. amblia* (McDonald and Nybakken 1997) would seem to counter the argument that a decline in the sponge has resulted in the decline in *F. californiensis*. However, differentiating species of *Dysidea* is difficult, new species have recently been described from the Gulf of California (Carballo et al. 2006), and the taxonomy of the Dysideidae in California remains poorly understood

(R. W. M. van Soest, pers comm to MS, October 16, 2012). *Felimare porterae* and *F. californiensis* might, therefore, utilize different species of dysideids. Dysideids also harbor symbiotic cyanobacteria (Thacker and Starnes 2003). If *F. californiensis* is more dependent on them than *F. porterae*, then negative effects of pollutants on the symbionts, rather than the sponge itself, could explain the loss of *F. californiensis* compared to *F. porterae*, even if both nudibranchs consume the same sponge. Symbiotic cyanobacteria might (1) serve as sources of defensive metabolites for the nudibranch (e.g., see Unson and Faulkner 1993) or (2) provide chemical cues necessary for larval settlement and metamorphosis. Loss of the latter could conceivably shut down benthic recruitment of *F. californiensis* in the SCB even if larvae were being transported into the SCB from other areas.

Felimare californiensis was disappearing from California as water quality in the SCB reached a low point around the time the US Clean Water Act was passed in 1972 (Schiff et al. 2000). Its reappearance at Santa Catalina Island 20 years later, near the end of the 2002–2003 El Niño (McPhaden 2003), corresponds with steady improvements in concentrations of metals, nutrients, and regulated pesticides like DDT, especially from large point sources like municipal wastewater discharges (Schiff et al. 2000; Stein and Cadien 2009; Smail et al. 2012). The occurrence of *F. californiensis* at Santa Catalina Island over the past decade, combined with the 2011 sightings from Santa Cruz Island and Mission Bay, may, therefore, represent a nascent recovery of the species in the region. Time—and continued monitoring—will tell. A vast array of chemicals unregulated, illegally used, or not previously considered as contaminants (e.g., pharmaceuticals, hormones, and antibiotics) flow increasingly into the SCB through multiple pathways, presenting daunting environmental challenges (e.g., USGS 2012 and references therein; Vidal-Dorsch et al. 2012). Surface runoff and wastewater effluent from the region contain a plethora of contaminants whose chronic effects remain little known or unstudied. Compounding this are (1) characteristic cyclonic circulation and seasonally alternating poleward/equatorward flows in the SCB (Harms and Winant 1998; Dong et al. 2009), which promote retention of contaminated water masses, and (2) extensive dredging projects to maintain shipping and boating channels, which can resuspend and redistribute sediments contaminated with persistent pollutants (e.g., Parnell et al. 2008). Moreover, in simulations with larvae in the water column for at least a month, ocean-based circulation models for the SCB reveal that mainland sites tend to act as sources and the Channel Islands as sinks (Mitarai et al. 2009). Finally, Puritz and Toonen (2011) presented evidence that coastal pollution in the SCB acts as a barrier to pelagic larval dispersal in a common, non-

harvested seastar. Therefore, continued recovery of *F. californiensis* in the SCB will likely depend on further improvements to water quality on the inner shelf, no small task given a human population in coastal southern California >17 million in 2010 (US Census Bureau 2013).

Other factors that may have contributed to extinction of *F. californiensis* in the SCB include:

1. Overcollecting

Given its size and bright colors, overcollecting by school groups and the general public may have impacted local populations of *F. californiensis* at easily accessible sites. Although state Marine Life Refuges and Areas of Special Biological Significance were established in the late 1960s and 1970s, widespread collection of marine organisms continued, owing to a combination of rapidly growing human population, unclear refuge boundaries, and a lack of education and enforcement (e.g., Addressi 1994; Murray et al. 1999; Goodson 2004; Parnell et al. 2005). However, as pointed out by Roy et al. (2003), laws against collecting have been strictly enforced for decades at Cabrillo National Monument on Point Loma, which is also the only intertidal reserve in southern California with a human exclusion zone. James Lance found a total of 13 *F. californiensis* at Point Loma from 1956 to 1969, but none have been found since (Table S2), suggesting that overcollecting alone cannot account for the widespread loss of *F. californiensis*. Similarly, *F. californiensis* has not been found in decades at other long-established reserves like Corona del Mar (part of the Newport Beach Marine Life Refuge), Heisler Park Ecological Reserve in Laguna Beach, and the San Diego-La Jolla Ecological Reserve (Table S2, S3).

Felimare californiensis was also collected between the early 1960s and 1980 for feeding and biochemical studies conducted at the Scripps Institution of Oceanography (e.g., Paine 1963; McBeth 1970, 1971; Hochlowski et al. 1982). Although the size of McBeth's (1970, 1971) collections in the late 1960s from the La Jolla area is unknown and may have been substantial, the other collections were sparse and usually had <10 individuals.

With planktotrophic development and a relatively short adult lifespan, local populations of *F. californiensis* might be susceptible to short-term fluctuations in recruitment, but would be less likely to be extirpated by overcollecting, compared to nudibranchs lacking a larval stage. We, therefore, conclude that overcollecting may have contributed to the decline of *F. californiensis* in southern California, but was not a primary cause.

2. Habitat loss

Habitat loss likely directly accounts for the disappearance of *F. californiensis* from a few historical sites of occurrence. Development of the Ports of Los Angeles and

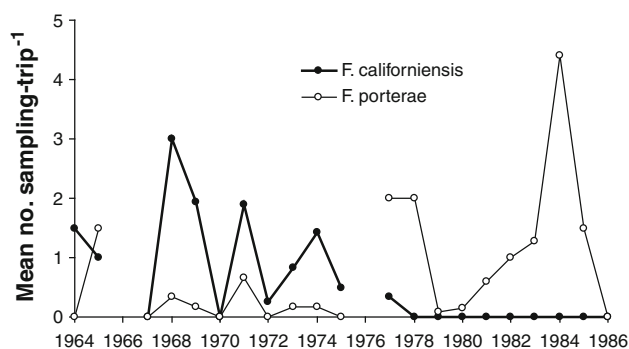


Fig. 4 Changes in abundance of *Felimare porterae* and *Felimare californiensis* found in San Diego, 1964–1986. Based on data collected by James Lance at Ladera Street, Hill Street, and South Casa Reef, San Diego (California Academy of Sciences and Goddard 2013)

Long Beach obliterated the broad cobble fields and tide flats once found at San Pedro (Dana 1840), and the extensive breakwaters there have blocked nearshore current flows in what used to be an open, south-facing embayment. Similarly, virtually nothing remains of the original shorelines in San Diego Bay and lower Newport Bay, where *F. californiensis* was found in 1885, and the 1930s and 1940s, respectively (Table S1). Maintenance of shipping and boating channels by dredging, combined with resuspension of persistent contaminants like DDT and PCBs, continues to physically and chemically degrade these sites and other embayments in the SCB (Schiff et al. 2000; Parnell et al. 2008). Thus, while habitat loss has undoubtedly contributed to the decline of *F. californiensis* in the SCB, it does not account for the disappearance of the nudibranch from relatively intact outer coast rocky sites, like La Jolla, Laguna Beach, and Malibu.

3. Competition

If *F. porterae* depends on the same sponge(s) as *F. californiensis*, then competitive exclusion by *F. porterae* may have contributed to the decline of *F. californiensis*. This seems unlikely given (1) the population dynamics of the nudibranchs and the highly heterogenous spatial nature of their benthic habitat, and (2) the documented examples of multiple species of nudibranchs—including chromodoridids—coexisting on the same prey species (e.g., Birkeland 1974; Rudman and Bergquist 2007). However, if competitive exclusion did occur, we might expect the abundance and prevalence of *F. porterae* to have increased coincident with the decline in *F. californiensis*, if not earlier.

Data collected by James Lance indicate that in San Diego, *F. porterae* did not become more abundant in the intertidal until after *F. californiensis* was already mostly gone (Fig. 4). Moreover, at South Casa Reef in La Jolla, where Lance sampled most frequently and both species were found, only one *F. porterae* was found in 16 sampling

trips from 1968 to 1975, compared to a total of 12 *F. californiensis* during the same period (California Academy of Sciences and Goddard 2013). Taken together, these results do not support the hypothesis that *F. californiensis* was competitively excluded by *F. porterae*, at least in San Diego.

Conclusions

In the 1980s, *Felimare californiensis* disappeared from its entire range in California and since 2003 has been consistently found only at Santa Catalina Island. No other nudibranch from California, including the two closest relatives of *F. californiensis*, has lost so much of its former range. The specific cause of the decline of *F. californiensis* is unknown, but consideration of both its remaining distribution and prey-specificity suggests that pollutants in the coastal waters of the SCB may have negatively affected the abundance or quality of its sponge prey, *Dysidea amblia*. More information on the distribution, abundance, and systematics of dysideids consumed by both *F. californiensis* and *F. porterae* in the SCB is needed to evaluate this hypothesis.

Localized habitat destruction and overcollecting likely contributed to the decline in *F. californiensis*, but were not primary causes. With regard to these latter factors, the recent records of *F. californiensis* in two Marine Protected Areas (MPAs) on Santa Catalina Island (Table S1), combined with the expanding network and increasing public acceptance of MPAs in the SCB (California Department of Fish and Game 2012), are encouraging. The records of *F. californiensis* since 2003 also suggest the species may be recovering. However, improvements to large, point sources of pollution notwithstanding (e.g., Schiff et al. 2000), surface runoff and water pollution by chemicals unregulated, illegally used, or not previously considered as contaminants continue to degrade inner shelf waters in the SCB, presenting daunting environmental challenges and possibly impeding the nascent recovery of *F. californiensis*.

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