

Rapid Communication

Establishment of the reef-forming tubeworm *Ficopomatus enigmaticus* (Fauvel, 1923) (Annelida: Serpulidae) in southern California

Bruno Pernet^{1*}, Michelle Barton¹, Kirk Fitzhugh², Leslie H. Harris², David Lizárraga¹, Ryan Ohl¹ and Christine R. Whitcraft¹

¹Department of Biological Sciences, California State University, Long Beach, 1250 Bellflower Blvd, Long Beach, CA 90840, USA

²Natural History Museum of Los Angeles County, Research & Collections, 900 Exposition Blvd., Los Angeles, CA 90007, USA

*Corresponding author

E-mail: bruno.pernet@csulb.edu

Received: 21 November 2015 / Accepted: 21 December 2015 / Published online: 8 January 2016

Handling editor: Melissa Frey

Abstract

The serpulid annelid *Ficopomatus enigmaticus* is found as a non-indigenous species in many subtropical and temperate habitats, where it often has major effects on the physical structure and community ecology of invaded habitats. In the northeastern Pacific, it has been present in northern California since about 1920, but clearly established populations have not previously been reported from southern California. We describe a large population of *F. enigmaticus* in the intertidal zone of the Los Angeles River, near Long Beach, California, and a much smaller population in the nearby Port of Los Angeles. Both reproductive adults and new recruits were common in the Los Angeles River population, suggesting that it is well established. We also describe previously unpublished observations of two additional populations in isolated lagoons in Santa Barbara County. Broader surveys aimed at establishing the distribution of this serpulid in central and southern California are needed to evaluate hypotheses on its pathway and timing of introduction to southern California, to evaluate risks of intraregional spread, and to begin to explore management strategies.

Key words: biological invasion, exotic species, Los Angeles River, polychaete

Introduction

The serpulid annelid *Ficopomatus enigmaticus* (Fauvel, 1923) was first described from Normandy, France, where it was recognized as a non-indigenous species. It has since been found in many subtropical and temperate locations, often in brackish water habitats (ten Hove and Weerdenburg 1978; Orensanz et al. 2002). Its native distribution is uncertain but is sometimes stated to be temperate regions of the Indian Ocean and Australia (e.g., Cohen and Carlton 1995; Orensanz et al. 2002; Dittmann et al. 2009). Members of the species typically form aggregations of tubes on hard substrates in shallow water; these aggregations may be up to several meters in maximum dimension (e.g., Obenat and Pezzani 1994; Bianchi and Morri 1996; Fornos et al. 1997). Where common, *F. enigmaticus* dramatically alters the physical structure of benthic habitats

(Fornos et al. 1997; Schwindt et al. 2004; McQuaid and Griffiths 2014), and has diverse direct and indirect effects on native planktonic (Bruschetti et al. 2008; Pan and Marcoval 2014) and benthic communities (Schwindt et al. 2001; Casariego et al. 2004; Heiman and Micheli 2010); it is thus often referred to as an ecosystem engineer. In addition to its effects on native communities, it can be an economically important fouling species, encrusting boat hulls and clogging power station cooling water intakes (Tebble 1953; Read and Gordon 1991).

In the northeast Pacific, newspaper reports indicate that *F. enigmaticus* has been present in San Francisco Bay since about 1920 (Carlton 1979; Cohen and Carlton 1995; Cohen et al. 2005a), though members of that population were only formally identified (as *Merceriella enigmatica*, an older name for the species) a few years later (Fauvel 1933). In 1994, it was reported as present

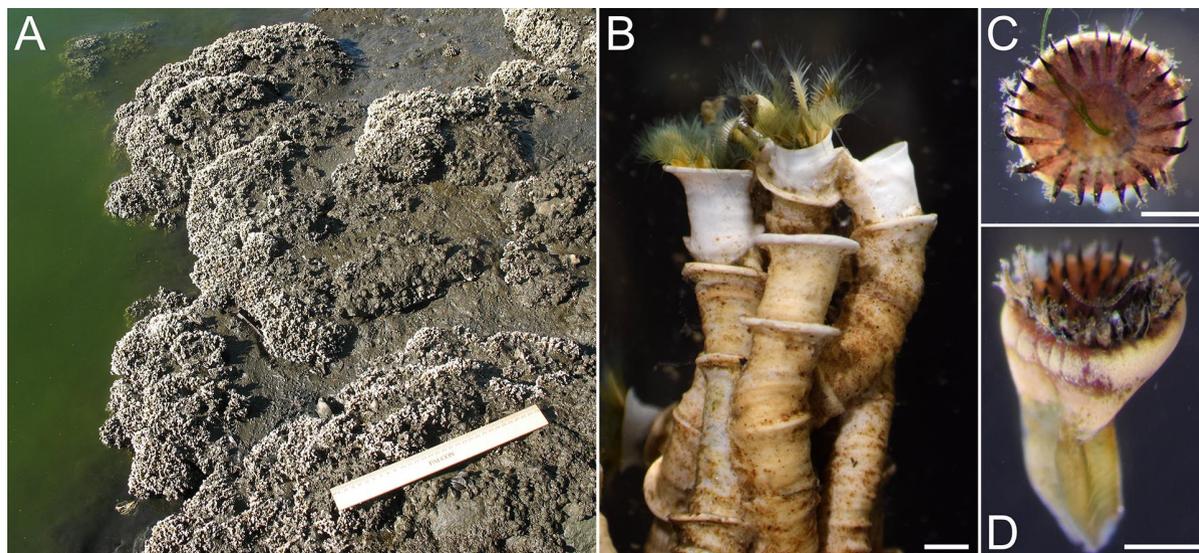


Figure 1. *Ficopomatus enigmaticus* from the east side of the Los Angeles River, near Golden Shore RV Resort (site #23). A. Aggregations of worms in the intertidal zone. The ruler in the foreground is 30 cm long. B. A small group of worms removed from an aggregation, showing the flanges (peristomes) that are typical of this species. Scalebar=1 mm. C. Apical view of the operculum, showing the ring of dark, incurved spines. Diatoms are visible on the spines, and a green alga is growing from the center of the operculum. Scalebar=400 μ m. D. Lateral view of an isolated operculum. Scalebar=400 μ m. Photographs by Bruno Pernet.

in Elkhorn Slough, an estuary ~150 km south of San Francisco Bay (Wasson et al. 2001). As of 1980, it had not been observed south of Point Conception (Abbott and Reish 1980). Since then, it has been reported as present in southern California on four occasions. Cohen et al. (2002, 2005b) collected two individuals of *F. enigmaticus* in August 2000 from a floating dock at a small boat marina in the Port of Los Angeles' Dominguez Channel; these specimens were identified by J.T. Carlton, but later lost (Cohen, pers. comm.). In August 2001, A. Cohen collected one more living individual and an empty tube at the same site; these were identified by LHH (Cohen, pers. comm.). Bastida-Zavala (2008) reported *F. enigmaticus* on settling plates set out in San Diego in 1999–2002 by the Smithsonian Environmental Research Center; this record, however, was apparently made in error, and in fact there is no evidence that *F. enigmaticus* has ever been seen in the San Diego area (Bastida-Zavala, pers. comm., 10 November 2015). The most recent report was of 86 individuals taken in Newport Bay in 2011 as part of the “Introduced Aquatic Species in Bays and Harbors 2011 Survey” (California Department of Fish and Wildlife 2014). This record is also apparently incorrect. LHH oversaw polychaete identifications for this survey, and no *F. enigmaticus* were reported by

her or the other two polychaete taxonomists at any station. Specimen counts of 86 were listed for three other polychaete species from Newport Bay samples, so the report of *F. enigmaticus* is likely to be due to an error in data entry.

In April 2014, one of us (BP) noticed dense aggregations of serpulids on cobbles and boulders along the edge of Golden Shore Marine Biological Preserve, at the mouth of the Los Angeles River, in Long Beach, California. He collected worms from these aggregations and identified them as *F. enigmaticus* by their distinctive tubes (which often bear flanges along their lengths) and opercula (which bear dark, incurved spines at their apical ends) (Figure 1). He noticed these aggregations again in August 2015. On that occasion he again collected worms, and LHH confirmed their identification as *F. enigmaticus*. Confirmation of their identity spurred us to survey the area to determine the extent of the population, and to determine if there were other populations in suitable habitats nearby.

Methods

From August–October 2015, we surveyed 54 intertidal sites in Los Angeles and Orange Counties, from Marina del Rey in the north to Newport Bay in the south (Figure 2, Supplemen-

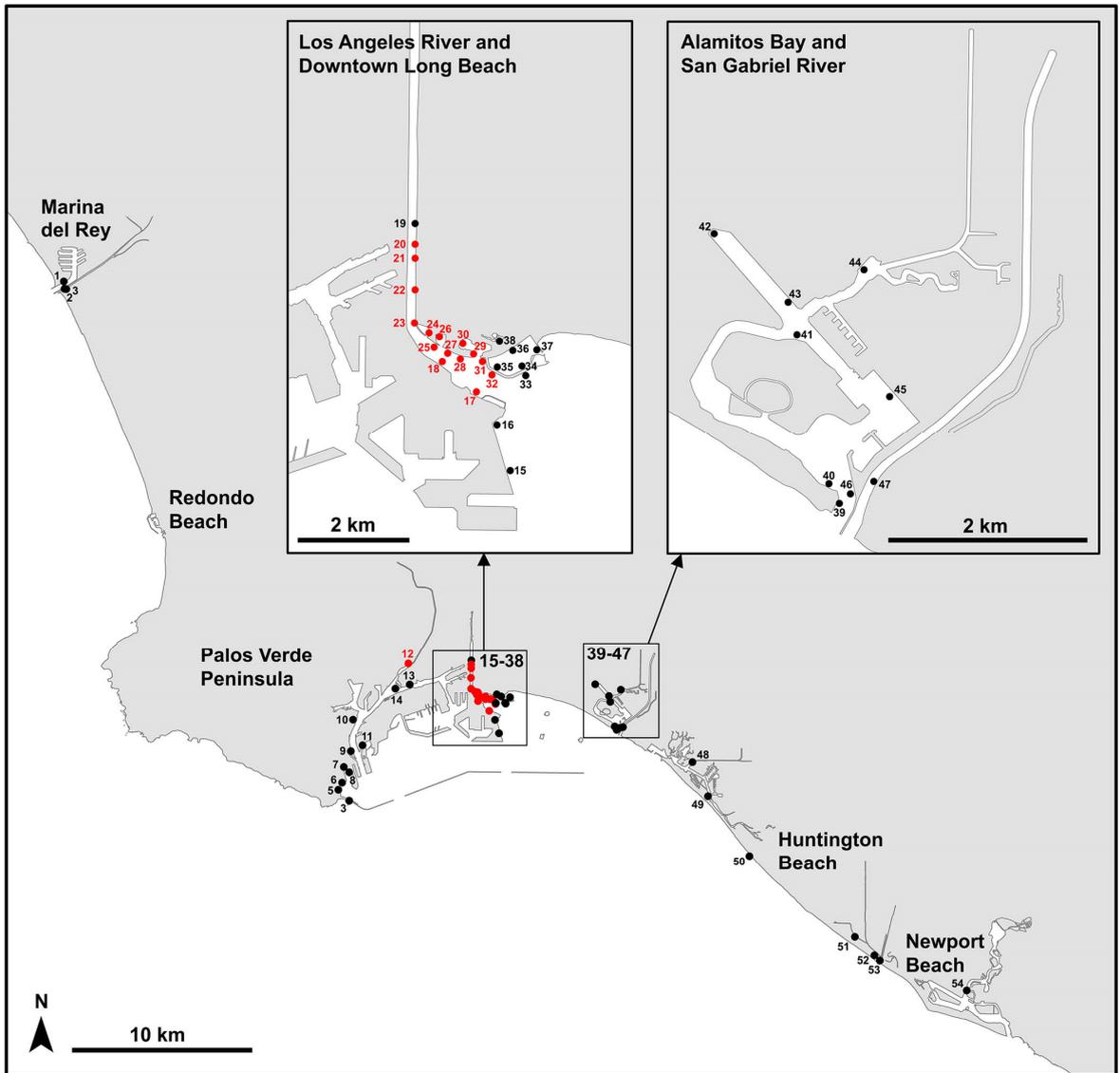


Figure 2. Sites sampled in Los Angeles and Orange Counties. Sites are numbered as in supplementary Table S1. Red points and numbers indicate sites at which *F. enigmaticus* was found; black points and numbers indicate sites at which *F. enigmaticus* was not found.

tary Table S1). All sites were relatively wave-protected, and all had hard substrate that seemed likely to be suitable for colonization by *Ficopomatus enigmaticus*. Surveys were carried out at or near the time of predicted low tide. At each site, we characterized substrate type, measured water temperature (with an alcohol or digital thermometer) and salinity (with a calibrated refractometer), and searched the area for ~5 min for the presence of serpulids. The tubes of *F. enigmaticus* are very distinctive and were easily identifiable in the field. We characterized populations of

F. enigmaticus at each site as “sparse” when primarily isolated individuals were identified, and “abundant” when worms were found in large aggregations. When we encountered serpulids that we could not immediately identify in the field, we collected them for later examination in the laboratory. At sites 23 and 24 (Table S1), we estimated the vertical range occupied by aggregations of *F. enigmaticus* using an automatic level (SAL series, CST/Berger, Watseka, Illinois, USA). These were compared to NOAA tide predictions to calculate elevation relative to mean lower low

water (MLLW). Samples of *F. enigmaticus* were collected from some sites and either fixed in 5% formalin in seawater and then preserved in 70% ethanol, or preserved directly in 95% ethanol. All samples were deposited in the polychaete collection of the Natural History Museum of Los Angeles County.

Results

We found *Ficopomatus enigmaticus* at 16 of the 54 sites surveyed (Figure 2, Table S1). Fifteen of these sites were along a continuous stretch of the Los Angeles River, from the Long Beach Shoreline Marina Jetty near the river mouth to a point ~3 km upriver, approximately midway between the Anaheim Street and Shoreline Drive bridges (note that we were unable to access the west side of the river except near its mouth). At these sites, *F. enigmaticus* were found in the intertidal, almost always on cobbles or boulders present as shoreline armor. Except at the extremes of this river range, where worms were present as isolated individuals, they were present in substantial aggregations of hundreds or thousands of worms. The largest aggregations (up to ~1 m in diameter) and most continuous cover of *F. enigmaticus* were found between Catalina Landing (site 26, near the river mouth) and West 3rd St. (site 22, upriver ~1.8 km). We estimated the vertical range occupied by *F. enigmaticus* at two of the Los Angeles River sites, 23 and 24, as between ~0.7 m above MLLW and ~0.5 m below MLLW. At both sites, hard substrate was rare immediately below 0.5 m below MLLW, and was replaced with mud.

The remaining site at which we found *F. enigmaticus* was deep in the Port of Los Angeles, on cobble and floating docks at the Leeward Bay Marina, in the Port's Dominguez Channel. At this site we found seven worms on concrete blocks in the intertidal zone and on the Styrofoam floats of floating docks. Most worms occurred as isolated individuals, but one group of three worms formed an aggregation on a concrete block. This site is ~12 shoreline km from the nearest site in the Los Angeles River at which we found *F. enigmaticus*.

We collected aggregations of *F. enigmaticus* from sites 23 and 24 (Figure 2; Table S1) repeatedly from August-October 2015 and examined tubes and worms in the laboratory. The smallest tubes observed were ~250 μ m internal diameter, and the largest ~2 mm internal diameter. When removed

from tubes, larger worms often released gametes into the petri dishes. The unfertilized eggs of two females averaged 41.8 (n=27) and 42.5 (n=22) μ m in diameter. We attempted to fertilize eggs five times in October 2015, and in each case swimming, feeding trochophore larvae were produced within 16 h at ~23°C.

The only other serpulid species we encountered in these surveys were *Hydroides elegans* (Haswell, 1883), *Hydroides gracilis* (Bush, 1905), and *Salmacina tribranchiata* (Moore, 1923). These species were all easily distinguished from *F. enigmaticus* by the absence of flanges on the tubes, or, for *S. tribranchiata*, by its diminutive size and branching tubes. Like *F. enigmaticus*, *H. elegans* is not indigenous to California (Carlton 1979; Bastida-Zavala 2008).

Discussion

A large population of *Ficopomatus enigmaticus* occupies the lower ~3 km of the Los Angeles River. Worms in this population form aggregations of tubes up to ~1 m in diameter in the mid-intertidal zone. In their zone of highest density, these aggregations occupy almost all available hard substrate (mainly cobbles and boulders). This population is clearly established, according to the criteria of Ruiz et al. (2000), which are a) multiple records of presence of the species, in either different locations or different years, and b) documentation of reproduction. Aggregations of *F. enigmaticus* were present at numerous sites in the lower ~3 km of the Los Angeles River, and were documented at one site (site 24, Table S1) in two consecutive years. Gravid adults (as determined by the spawning of viable gametes in the laboratory) are present at several Los Angeles River sites, as are tiny juveniles, indicative of recruitment. These observations suggest strongly that *F. enigmaticus* found in the Los Angeles River are reproductive.

Ficopomatus enigmaticus has been documented in the Los Angeles area twice before, in 2000 and 2001, when a total of four individuals – three living specimens and one empty tube – were collected from floating docks at Island Yacht Anchorage #1, a small boat marina in the Port of Los Angeles' Dominguez Channel (Cohen 2011). We did not sample at that site, but found a few individuals of *F. enigmaticus* at the Leeward Bay Marina (site 12), only ~0.5 shoreline km away. We were unable to sample more intensively in the Port of Los Angeles, so it is

entirely possible that *F. enigmaticus* occurs at other sites in that body of water. Further sampling is needed to determine the distribution of *F. enigmaticus* in the Port of Los Angeles.

It is unclear if the apparently low-density Port of Los Angeles population – which is ~12 km from the mouth of the Los Angeles River – is established, though repeated collections of living *F. enigmaticus* there (in 2000, 2001, and now 2015) suggest that that may indeed be the case. Alternatively, it may represent the result of rare larval dispersal events from the larger Los Angeles River population, or from larger, currently undocumented populations elsewhere in the Port. The planktonic feeding larvae of *F. enigmaticus* become competent to settle and metamorphose ~5–7 d after fertilization given adequate food and relatively warm temperatures (Gabilondo et al. 2013). However, larvae of several other serpulids can delay settlement and metamorphosis for 5–11 d after acquisition of competence, even if starved (Okamoto et al. 1995; Qian and Pechenik 1998). It is likely that competent larvae of *F. enigmaticus* have similar abilities, and the ability to delay settlement might permit wider dispersal during the larval phase. Further information on the development and behavior of larvae of *F. enigmaticus*, and on current patterns in the area, is needed in order to determine whether the Los Angeles River and Port of Los Angeles populations might be demographically connected by larval dispersal.

It is unclear why *F. enigmaticus* is limited in its local distribution to the Los Angeles River and the Port of Los Angeles (Figure 2), as many nearby sites have apparently suitable intertidal hard substrate. However, spatial variation in salinity likely plays a role. The 15 Los Angeles River sites where we found *F. enigmaticus* had among the lowest salinities (24–29) observed in our surveys; the Leeward Bay Marina had a slightly higher salinity (31). Although adults of *F. enigmaticus* can survive in full oceanic salinities (~35; Pernet, Langland, and Perria, unpubl. data), it is possible that they cannot grow rapidly, compete effectively with other sessile organisms, or reproduce at high salinities. Such effects may explain the disappearance of *F. enigmaticus* at sites oceanward of the mouth of the Los Angeles River. Indeed, previous work suggests that the optimal salinity range for growth and reproduction of *F. enigmaticus* is ~10–30 (reviewed by Dittmann et al. 2009). Salinity would not, of course, explain the fact that *F. enigmaticus* seems to disappear upstream of ~3 km from the mouth of the river. We

examined only one site above this point (site 19). Though salinity at that site (23) was the lowest of any site we sampled, it was well within the reported optimal range for *F. enigmaticus* (Dittmann et al. 2009). The absence of *F. enigmaticus* at this site may be due to indirect effects of salinity; alternatively, the tiny ciliated larvae of *F. enigmaticus* may not disperse effectively against downstream flowing surface currents.

It is not currently possible to identify when the Los Angeles River population became established. It was first noticed in April 2014 at our site 24, but at that time there were already large aggregations of tubes at that site, so it was undoubtedly present and simply unnoticed earlier. The “Southern California Exotics Expedition 2000” (Cohen et al. 2002, 2005b), a rapid survey of the region for non-indigenous species, primarily sampled communities on floating docks. They did sample at one site (their SCX-11) that was very close to our sites 29–32, all of which had *F. enigmaticus* present in 2015. Because *F. enigmaticus* occurs both in the intertidal zone and on floating docks, and members of the Expedition were actively looking for its tubes, it is likely that they would have seen it at SCX-11 if it were present within their search area.

Likewise, it is not currently possible to determine how *F. enigmaticus* first arrived in southern California, or from which source the propagules were derived. All of the sites we surveyed were in or very near to the Ports of Los Angeles and Long Beach, which are among the world’s busiest commercial shipping ports. Transport on or in commercial vessels is thus an obvious potential vector for the transport of *F. enigmaticus* to southern California. There is also substantial traffic of recreational vessels within California, and *F. enigmaticus* may have arrived in southern California from established northern California populations via that vector (Davidson et al. 2010; Zabin et al. 2014). It is also possible that the Los Angeles area populations we and Cohen et al. (2002, 2005b) describe were established by settlement of larvae originating from established populations to the north. That larvae with a planktonic duration of only ~1–2 weeks could directly travel ~550–700 km to reach the Los Angeles area from San Francisco Bay or Elkhorn Slough seems unlikely (e.g., Shanks 2009), even with the assistance of the predominantly southward-flowing California Current. However, if southward-dispersing larvae settled and established populations at geographically intermediate sites in southern Central California, or northern Southern

California, these might have served as “stepping-stone” populations that produced propagules that eventually colonized the Los Angeles area.

We are aware of unpublished observations of two geographically intermediate populations of *F. enigmaticus*, at least one of which is likely established, in northern Southern California. These populations were found at two sites in Santa Barbara County, ~170 km to the north of the Los Angeles River. First, specimens of *F. enigmaticus* were collected from Arroyo Burro Creek (a body of water ~420 m long and 10–15 m wide, isolated from the ocean by a sandbar; 34.4034 N; 119.7432 W) from hard surfaces and plant stems in 2008 by C. Swift (Cardno ENTRIX) and provided to LHH, who identified them and deposited specimens in the Natural History Museum of Los Angeles County. We visited Arroyo Burro Creek on 10 October 2015, and found living *F. enigmaticus* present in small aggregations on intertidal boulders and cobbles. Water temperature and salinity at the time of sampling were 27°C and 36, respectively. Second, in October 2015, dense aggregations of serpulids were collected by R. Thompson (Cardno, Santa Barbara, CA) from sheet piling material in Mission Creek Lagoon (~34.4126 N; 119.6882 W), a coastal lagoon ~7 km to the east of Arroyo Burro Creek. She provided LHH with photographs of the serpulids, which were easily identifiable as *F. enigmaticus*. The repeated sightings of this species over a period of seven years at Arroyo Burro Creek suggest that this population is established and self-sustaining. Thus, *F. enigmaticus* has likely been continuously present in Santa Barbara County since at least 2008.

Additional intensive surveying is needed to determine the current distribution of *F. enigmaticus* in southern California. Between Point Conception and the Mexican border, there are many creeks and rivers whose mouths may be suitable habitat for *F. enigmaticus* (e.g., Gaviota Creek, Atascadero Creek, Ventura River, Santa Clara River, San Mateo Creek, Santa Margarita River). The numerous coastal lagoons and estuaries in this region (e.g., Devereaux Lagoon, University of California Santa Barbara Lagoon, Mugu Lagoon, Malibu Lagoon, Agua Hedionda Lagoon, San Elijo Lagoon) may also contain suitable habitat for this species. Rapid visual surveys by LHH in 2014 failed to turn up any specimens in Malibu Lagoon, Agua Hedionda Lagoon, and San Elijo Lagoon. To our knowledge, none of the other sites have been surveyed specifically for the presence of *F. enigmaticus*. A detailed description of the current

distribution of this serpulid in southern California is crucial to evaluate hypotheses on its pathway and timing of introduction to the region, to evaluate risks of intraregional spread (e.g. Wasson et al. 2001; Davidson et al. 2010), and to begin to explore management strategies.

Acknowledgements

We thank Camm Swift (previously with Cardno ENTRIX, now retired) and Rosie Thompson (Cardno, Santa Barbara, CA) for their willingness to share unpublished information. James Carlton, Andrew Cohen, and two anonymous reviewers provided helpful comments on earlier versions of the manuscript. This paper is based on work supported by the National Science Foundation under Grant Nos. OCE-1060801 and DEB-1257355 (to BP).

References

- Abbott DP, Reish DJ (1980) Polychaeta: The Marine Annelid Worms. In: Morris RH, Abbott DP, Haderlie EC (eds), *Intertidal Invertebrates of California*. Stanford University Press (Redwood City), pp 448–489
- Bastida-Zavala JR (2008) Serpulids (Annelida: Polychaeta) from the Eastern Pacific, including a brief mention of Hawaiian serpulids. *Zootaxa* 1722: 1–61
- Bianchi CN, Morri C (1996) *Ficopomatus* 'reefs' in the Po River Delta (Northern Adriatic): their constructional dynamics, biology, and influences on the brackish-water biota. *Marine Ecology* 17: 51–66, <http://dx.doi.org/10.1111/j.1439-0485.1996.tb00489.x>
- Bruschetti M, Luppi T, Fanjul E, Rosenthal A, Iribarne O (2008) Grazing effect of the invasive reef-forming polychaete *Ficopomatus enigmaticus* (Fauvel) on phytoplankton biomass in a SW Atlantic coastal lagoon. *Journal of Experimental Marine Biology and Ecology* 354: 212–219, <http://dx.doi.org/10.1016/j.jembe.2007.11.009>
- California Department of Fish and Wildlife (2014) Introduced Aquatic Species in California Bays and Harbors 2011 Survey, 36 pp
- Carlton JT (1979) History, Biogeography, and Ecology of the Introduced Marine and Estuarine Invertebrates of the Pacific Coast of North America. Ph.D. Thesis. University of California, Davis (Davis)
- Casariello AM, Schwindt E, Iribarne O (2004) Evidence of habitat structure-generated bottleneck in the recruitment process of the SW Atlantic crab *Cyrtograpsus angulatus*. *Marine Biology* 145: 259–264, <http://dx.doi.org/10.1007/s00227-004-1325-7>
- Cohen AN (2011) The Exotics Guide: Non-native Marine Species of the North American Pacific Coast. Center for Research on Aquatic Bioinvasions, Richmond, CA, and San Francisco Estuary Institute, Oakland, CA. <http://www.exoticguide.org> (Accessed 17 October 2015)
- Cohen AN, Carlton JT (1995) Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. Report for the US Fish and Wildlife Service and the National Sea Grant College Program, Connecticut Sea Grant, 246 pp
- Cohen AN, Harris LH, Bingham BL, Carlton JT, Chapman JW, Lambert CC, Lambert G, Ljubenkov JC, Murray SN, Rao LC, Reardon K, Schwindt E (2002) Project Report for the Southern California Exotics Expedition 2000: A Rapid Assessment Survey of Exotic Species in Sheltered Coastal Waters. Report for the California Department of Fish and Game, State Water Resources Control Board, and National Fish and Wildlife Foundation, 28 pp

- Cohen AN, Calder DR, Carlton JT, Chapman JW, Harris LH, Kitayama T, Lambert CC, Lambert G, Piotrowski C, Shouse M, Solórzano LA (2005a) Rapid Assessment Shore Survey for Exotic Species in San Francisco Bay - May 2004. Final Report for the California State Coastal Conservancy, Association of Bay Area Governments/San Francisco Bay-Delta Science Consortium, National Geographic Society and Rose Foundation. San Francisco Estuary Institute, Oakland, CA, 32 pp
- Cohen AN, Harris LH, Bingham BL, Carlton JT, Chapman JW, Lambert CC, Lambert G, Ljubenkov JC, Murray SN, Rao LC, Reardon K, Schwindt E (2005b) Rapid assessment survey for exotic organisms in southern California bays and harbors, and abundance in port and non-port areas. *Biological Invasions* 7: 995–1002, <http://dx.doi.org/10.1007/s10530-004-3121-1>
- Davidson IC, Zabin CJ, Chang AL, Brown CW, Sytsma MD, Ruiz GM (2010) Recreational boats as potential vectors of marine organisms at an invasion hotspot. *Aquatic Biology* 11: 179–191, <http://dx.doi.org/10.3354/ab00302>
- Dittmann S, Rolston A, Benger SN, Kupriyanova EK (2009) Habitat requirements, distribution and colonisation of the tubeworm *Ficopomatus enigmaticus* in the Lower Lakes and Coorong. Report for the South Australian Murray-Darling Basin Natural Resources Management Board, Adelaide
- Fauvel P (1933) Histoire de la *Mercierella enigmatica* Fauvel, Serpulien d'eau saumâtre. *Archives de Zoologie Expérimentale et Générale* 75: 185–193
- Fornos JJ, Forteza V, Martínez-Taberner A (1997) Modern polychaete reefs in Western Mediterranean lagoons: *Ficopomatus enigmaticus* (Fauvel) in the Albufera of Menorca, Balearic Islands. *Palaeogeography, Palaeoclimatology, Palaeoecology* 128:175–186, [http://dx.doi.org/10.1016/S0031-0182\(96\)00045-4](http://dx.doi.org/10.1016/S0031-0182(96)00045-4)
- Gabilondo R, Graham H, Caldwell GS, Clare AS (2013) Laboratory culture and evaluation of the tubeworm *Ficopomatus enigmaticus* for biofouling studies. *Biofouling* 29: 869–878, <http://dx.doi.org/10.1080/08927014.2013.810214>
- Heiman KW, Micheli F (2010) Non-native ecosystem engineer alters estuarine communities. *Integrative and Comparative Biology* 50: 226–236, <http://dx.doi.org/10.1093/icb/icq036>
- Hove HA ten, Weerdenburg JCA (1978) A generic revision of the brackish-water serpulid *Ficopomatus* Southern 1921 (Polychaeta: Serpulinae), including *Mercierella* Fauvel 1923, *Sphaeropomatus* Treadwell 1934, *Mercierellopsis* Rioja 1945 and *Neopomatus* Pillai 1960. *Biological Bulletin* 154: 96–120, <http://dx.doi.org/10.2307/1540777>
- McQuaid KA, Griffiths CL (2014) Alien reef-building polychaete drives long-term changes in invertebrate biomass and diversity in a small, urban estuary. *Estuarine, Coastal and Shelf Science* 138: 101–106, <http://dx.doi.org/10.1016/j.ecss.2013.12.016>
- Obenat SM, Pezzani SE (1994) Life cycle and population structure of the polychaete *Ficopomatus enigmaticus* (Serpulidae) in Mar Chiquita Coastal Lagoon, Argentina. *Estuaries* 17: 263–270, <http://dx.doi.org/10.2307/1352574>
- Okamoto J, Watanabe A, Watanabe N, Sakata K (1995) Induction of larval metamorphosis in serpulid polychaetes by L-DOPA and catecholamines. *Fisheries Science* 61: 69–74
- Orensanz JM, Schwindt E, Pastorino G, Bortolus A, Casas G, Darrigran G, Elias R, Gappa JLL, Obenat S, Pascual M, Penchaszadeh P, Piriz ML, Scarabino F, Spivak ED, Vallarino EA (2002) No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic. *Biological Invasions* 4: 115–143, <http://dx.doi.org/10.1023/A:1020596916153>
- Pan J, Marcoval MA (2014) Top-down effects of an exotic serpulid polychaete on natural plankton assemblage of estuarine and brackish systems in the SW Atlantic. *Journal of Coastal Research* 30: 1226–1235, <http://dx.doi.org/10.2112/JCOASTRES-D-12-00163.1>
- Qian P-Y, Pechenik JA (1998) Effects of larval starvation and delayed metamorphosis on juvenile survival and growth of the tube-dwelling polychaete *Hydroides elegans* (Haswell). *Journal of Experimental Marine Biology and Ecology* 227: 169–185, [http://dx.doi.org/10.1016/S0022-0981\(97\)00267-0](http://dx.doi.org/10.1016/S0022-0981(97)00267-0)
- Read GB, Gordon DP (1991) Adventive occurrence of the fouling serpulid *Ficopomatus enigmaticus* (Polychaeta) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 25: 269–273, <http://dx.doi.org/10.1080/00288330.1991.9516478>
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* 31: 481–531, <http://dx.doi.org/10.1146/annurev.ecolsys.31.1.481>
- Schwindt E, Bortolus A, Iribarne OO (2001) Invasion of a reef-building polychaete: direct and indirect impacts on the native benthic community structure. *Biological Invasions* 3: 137–149, <http://dx.doi.org/10.1023/A:1014571916818>
- Schwindt E, Iribarne OO, Isla FI (2004) Physical effects of an invading reef-building polychaete on an Argentinean estuarine environment. *Estuarine, Coastal and Shelf Science* 59: 109–120, <http://dx.doi.org/10.1016/j.ecss.2003.06.004>
- Shanks AL (2009) Pelagic larval duration and dispersal distance revisited. *Biological Bulletin* 216: 373–385
- Tebble N (1953) A source of danger to harbour structures: encrustation by a tubed marine worm. *Journal of the Institute of Municipal Engineers* 80: 259–265
- Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. *Biological Conservation* 102: 143–153, [http://dx.doi.org/10.1016/S0006-3207\(01\)00098-2](http://dx.doi.org/10.1016/S0006-3207(01)00098-2)
- Zabin CJ, Ashton GV, Brown CW, Davidson IC, Systema MD, Ruiz GM (2014) Small boats provide connectivity for nonindigenous marine species between a highly invaded international port and nearby coastal harbors. *Management of Biological Invasions* 5: 97–112, <http://dx.doi.org/10.3391/mbi.2014.5.2.03>

Supplementary material

The following supplementary material is available for this article:

Table S1. Intertidal sites in Los Angeles and Orange Counties examined for the presence of *Ficopomatus enigmaticus*.

This material is available as part of online article from:

http://www.reabic.net/journals/bir/2016/Supplements/BIR_2016_Pernet_et_al_Supplement.xls