UNIVERSITY OF CALIFORNIA

Los Angeles

Metazoan parasites of the California grunion *Leuresthes tenuis* and other New World silversides

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Biology

by

Bruno Passarelli

2021

ABSTRACT OF THE DISSERTATION

Metazoan parasites of the California grunion *Leuresthes tenuis*

and other New World silversides

by

Bruno Passarelli

Doctor of Philosophy in Biology

University of California, Los Angeles, 2021

Professor Donald G. Buth, Chair

Parasitism is one the most common lifestyles on earth. Parasites are important components of virtually all ecological communities and parasite research can help to elucidate many aspects of the ecology of their hosts. This dissertation focused on studying the metazoan parasites of the California grunion, *Leuresthes tenuis* and other fish hosts in the family Atherinopsidae.

In Chapter 1, the metazoan parasites of *L. tenuis* were investigated at five localities in southern California. A total of 2,902 parasites belonging to 26 taxa were recovered from 900 specimens of *L. tenuis* collected between 2016 and 2018. Comparisons of parasite communities showed that the parasite fauna of *L. tenuis* varied among localities. This variation suggests that *L. tenuis* may stay relatively close to their spawning grounds throughout their lives.

In Chapter 2, a redescription is provided of the parasitic copepod *Caligus olsoni*, associated with *L. tenuis* and other fishes in the northeast Pacific. *Caligus olsoni* was morphologically compared to another species, *Caligus serratus*. In light of the morphological similarities observed between these two species, we propose to treat *C. serratus* as a junior subjective synonym of *C. olsoni*. Based on previous reports, *C. olsoni* appeared to be highly host-specific. However, with the proposed synonymy of *C. olsoni* and *C. serratus*, *C. olsoni* has, in fact, low host specificity, with 16 fish host species currently reported from 12 families.

In Chapter 3, the parasite communities of *L. tenuis* and three other host species in the family Atherinopsidae were compared. A total of 5,677 parasites from 25 taxa were recovered from the four host species. The results showed significant differences in parasite communities in relation to host species. The three most abundant parasite taxa found in this study, which combined accounted for more than 78% of the total number of parasites recovered, were associated with two of the host species. Differences in parasite communities may be explained by variations in diet and feeding strategies among the hosts species investigated.

The dissertation of Bruno Passarelli is approved.

Ralph G. Appy

David K. Jacobs

Karen Martin

Michael Edward Shin

Donald G. Buth, Committee Chair

University of California, Los Angeles

2021

Dedication

To Ed Tarvyd and John Moss, who inspired me to become a biologist in my early days at Santa Monica College.

To my great-uncle Armando Mondadori for helping me to start this journey.

To all my family for their continuous love and support.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

LIST OF TABLES

Chapter 1

Chapter 2

Chapter 3

ACKNOWLEDGMENTS

First, I want to thank Don Buth for being a great advisor and human being. I am very lucky to have had Don mentoring me for the last six and a half years to become a better scientist and educator. I will always treasure his guidance, support, and friendship. Being part of the Buth lab made my experience at UCLA very worthwhile. I sincerely thank Ralph Appy (Cabrillo Marine Aquarium), David Jacobs (UCLA), Karen Martin (Pepperdine University), and Michael Shin (UCLA) for being part of my doctoral committee. The guidance and feedback that they provided is hugely appreciated. I also thank Malcolm Gordon (UCLA) for being part of my guidance committee. I'm fortunate to have committee members that I admire both as scientists and as people. I look forward to keep learning from them in the future.

This project was generously supported by the Eugene Cota-Robles Fellowship and the Department of Ecology and Evolutionary Biology Department funding award at UCLA.

I would like to acknowledge Jocelyn Yamadera, Tessa Villaseñor, and Melissa Carrillo for their tremendous help to all graduate students at the Ecology and Evolutionary Department at UCLA.

I would like to express my appreciation to Andrew Olson and Leon Olson who studied parasites of California and Gulf grunion before me. I'm happy to have had the opportunity to add to their work on grunion parasites.

Chapter 2 of this dissertation is a version of Passarelli, B. and Tang, D. Redescription of *Caligus olsoni* Pearse, 1953 (Copepoda: Caligidae), a parasite of California grunion *Leuresthes tenuis*, (Ayres, 1860) (Atherinopsidae) and other fishes in the northeast Pacific. *In preparation*. I contributed with the design of the study, collection of specimens, and writing of the manuscript.

Danny Tang (Orange County Sanitation District) contributed with the design of the study, illustration of specimens, and writing of the manuscript.

I cannot thank Ralph Appy enough for all the help he provided to my research over the years. Ralph helped with many aspects of my research, from input on research ideas, to helping with field collections, and identifying all the worms, no matter how featureless I thought they were, that I sent him. Anytime I had a research issue afflicting me, I always felt better after talking to Ralph. I am lucky to have him as a mentor.

I also thank Omar Amin (Institute of Parasitic Diseases and Parasitology Center) for his assistance in acanthocephalan identification, Ian Beveridge (University of Melbourne) for cestode identification, Julianne Passarelli (Cabrillo Marine Aquarium) and Danny Tang for copepod identification. My appreciation also goes to Samuel Gómez (Universidad Nacional Autónoma de México), Simon Jones (Pacific Biological Station), Geoff Keel and William Moser (Smithsonian Institution), Mark S. Okihiro (California Department of Fish and Wildlife), Regina Wetzer (Natural History Museum of Los Angeles County), Chelsea Williams and Johnathan Williams (Occidental College) for their assistance with samples of hosts and parasites.

This project would not have been possible if it wasn't for the continuous support of my colleagues and supervisors at Saddleback College. Tony Huntley planted the seed of this project and encouraged me even before I knew I wanted to pursue a Ph.D. Chris McDonald, Art Nitta (Deans of the Mathematics, Science, and Engineering Division at Saddleback College), Steve Teh, Karah Street, Marcelo Pires, Abby Sirulnik (Chairs of the Department of Biological Sciences at Saddleback College) have always supported me and accommodated my scheduling needs throughout my time at UCLA. I also thank Anita Bandekar, Tom Burrows, Karen Kelley, Nick Porter, and John Robinson for always helping me with my scientific equipment needs without any hesitation. I thank my colleagues Elizabeth Ininns, Monica Friedrich, Kat Shaw, and Terry Lopez for their support and encouragement. I also thank Suzanne Anderson, Sue Cook, and Ana Hancock for everything they do to keep the Mathematics, Science, and Engineering Division running smoothly. I couldn't have completed this project without their help and support.

I thank the staff at Cabrillo Marine Aquarium, in particular Bayne Westrick-Snapp for assisting with field collections in California and in Mexico, Zack Salas for assisting with field collections and grunion run footage, Mike Schaadt and Jeff Landesman for always welcoming and facilitating my research needs at CMA. I thank Ralph Appy, Kim Johnson (Rancho Santiago College), Jade Morris (volunteer), Kimo Morris (Santa Ana College), Julianne Passarelli, Marcelo Pires, and Michelle Smith (volunteer) for their assistance in collection of samples. I also thank Adriana Hernández-Álvarez (Universidad Autónoma de Baja California Sur), Kimo Morris, Jeff Watanabe (Ohlone College), and "Cactus Man" for assisting with field work in Mexico.

My appreciation goes to my master's thesis advisor Bruno Pernet (California State University Long Beach) for supporting my plan to pursue a Ph.D. and writing me a letter of recommendation for the Ph.D. program at UCLA. I also thank Bengt Allen (California State University, Long Beach) for comments and advice on multivariate analysis.

I also thank my fellow Buth Lab members Mason Gamble, Max Murray, Carly Myers, Fernando Postigo, Kelsi Rutledge, and Fabiola Torres-Toledo. Thanks to my fellow graduate students for being part of this journey with me, Shawn McEachin, Raquel Turba, Camila Medeiros, Marcel Vaz, Aji Anggoro, Dita Cahyani, Zack Gold, Chris Henry, Gaurav Kandlikar, Leila Fletcher, Scott O’Donnell, Hayley Stansell, Clive Lau, Page Zhang, Alayna Mead, Brandon MacDonald, Emily Ryznar, Tiara Moore, and many others.

I am very grateful for my friends Kimo Morris, Marcelo Pires, and Danny Tang for their encouragement, support, *and* solid scientific advice.

I owe my gratitude to Alicia Dale and Steve Klar for making it possible for me to be where I am today.

A very special thanks to my family in Brazil and in the United States for their continuous love and support. My parents Gilberto and Marieta, my step-mother Fernanda, my brother Cristiano, and my sister Patricia, my in-laws Marvin and Marjatta, Katrina, David, my nieces Bruna and Lilliana, and my nephew André. A very special thank you to Martin Dembitzer for sharing his words of wisdom and encouragement. A special thank you to my doggies Alley, Cairo, Phoebe, and Nile.

Most importantly, my deepest gratitude goes to my wife Julianne Passarelli for all her love and support. Juli, you are my main source of inspiration for being a better scientist and person. This journey was only possible because of you!

VITA

Previous Degrees Awarded

2002 A.A. in General Science, Santa Monica College

2007 B.Sc. in Marine Biology, California State University Long Beach

2010 M.Sc. in Biology, California state University Long Beach

Awards

2008-2010 California Sea Grant – Graduate Research Traineeship

2015-2019 UCLA – Eugene Cota-Robles Fellowship

2020 UCLA – Ecology and Evolutionary Biology Department Funding Award

Publications

2019 **Passarelli B.**, Pernet B. The marine live bait trade as a pathway for the introduction of nonindigenous species into California: patterns of importation and thermal tolerances of imported specimens. Management of Biological Invasions 10 (1): 80–95, **https://doi.org/10.3391/mbi.2019.10.1.05**

Select Presentations

2009 Western Society of Naturalists, Seaside, CA. Poster. "Tolerance of non-indigenous marine live bait to southern California coastal habitat thermal conditions."

2010 Western Society of Naturalists, San Diego, CA. Oral Presentation. "The marine live bait trade in California: a pathway for invasive species?"

2010 1st International Workshop on Symbiotic Copepoda. Cabrillo Marine Aquarium, San Pedro, CA. Oral presentation. "The parasitic fauna of two species of ghost shrimp (*Neotrypaea californiensis* and *N. gigas*) on the West Coast of the United States."

2011 Southern California Academy of Sciences (SCAS), Pomona, CA. Oral Presentation. "The marine live bait trade in California: a pathway for invasive species?"

2013 2nd International Workshop on Symbiotic Copepoda. University of Limpopo, South Africa. Oral presentation. "Prevalence and intensity of symbiotic copepods on *Neotrypaea* spp. in southern California mudflats."

2016 EEB Research Symposium. Poster. University of California Los Angeles, CA. "The marine live bait trade in southern California: a pathway for introduction of non-indigenous species of parasites."

2016 3rd International Workshop on Symbiotic Copepoda. James Cook University - Heron Island Marine Station, Australia. Oral Presentation. "Parasite fauna of the California grunion *Leuresthes tenuis*."

2017 13th International Conference on Copepoda. San Pedro, California. Poster. "Metazoan parasites of California grunion, *Leuresthes tenuis*, in southern California."

2018 Southern California Academy of Sciences (SCAS), Pomona, California. Poster. "Metazoan parasites of California grunion *Leuresthes tenuis* in southern California."

2018 EEB Research Symposium. Poster. University of California Los Angeles, CA. Poster. "Metazoan parasites of California grunion *Leuresthes tenuis* in southern California."

2020 Southern California Association of Ichthyology Taxonomists and Ecologists (SCAITE). Guest speaker. "Metazoan parasites of the California grunion *Leuresthes tenuis* and other New World silversides."

2021 Southern California Academy of Sciences (SCAS), virtual meeting. Presentation. "Metazoan parasites of the California grunion *Leuresthes tenuis* in the Southern California Bight".

Professional Experience

2007-2012 **Teaching Associate/Lecturer**
California State University Long Beach, Long Beach, CA
Department of Biological Sciences

2011-2013 **Adjunct Faculty**
Cypress College, Cypress, CA
Department of Biology

2016-2020 **Teaching Associate**
University of California Los Angeles
Department of Ecology and Evolutionary Biology

2011-present **Adjunct Faculty/Professor of Biology**
Saddleback College, Mission Viejo, CA
Department of Biological Sciences

Chapter 1

Metazoan parasites of the California grunion *Leuresthes tenuis* (Atherinopsidae) in southern California

Bruno Passarelli[1]

[1]Department of Ecology and Evolutionary Biology, University of California Los Angeles, California, 90095-7246, U.S.A.

ABSTRACT: The California grunion, *Leuresthes tenuis* (Ayres, 1860), is a beach-spawning fish endemic to California, U.S.A., and Baja California, Mexico. Southern California sandy beaches, crucial for grunion reproduction, have been continuously impacted for the last several decades due to high levels of urbanization, coastal construction, beach grooming, and pollution. Metazoan parasites can be used to study many aspects related to the ecology of their hosts, including movement patterns. In this study, 900 California grunion were collected at five localities in the Southern California Bight (SCB) between 2016 and 2018 and inspected for parasites. A total of 2,902 parasites belonging to 26 taxa were identified and quantitative descriptors (e.g. prevalence, mean intensity, mean abundance) were calculated for each taxon. Overall, 84.6% of grunion were infected with at least one species of parasite and, on average, 3.8 parasites were found per infected fish. The most abundant species of parasites were *Bomolochus* sp. (Copepoda), *Leuresthicola olsoni* (Monogenea), *Contracaecum (rudolphii)* (Nematoda), *Galactosomum* sp. (Digenea), *Asymphylodora atherinopsidis* (Digenea), *Lepocreadium manteri* (Digenea), *Caligus olsoni*, (Copepoda), and *Argulus melanostictus* (Branchiura). An analysis of similarity (ANOSIM) of parasite component communities (all parasites infecting all hosts in a sample) showed that the metazoan parasite fauna of California grunion varies among localities within the SCB. This variation in parasite assemblages is greater than what would be expected in freely migrating fish. This suggests that groups of California grunion may stay relatively close to their spawning grounds instead of moving extensively across their range in the SCB.

INTRODUCTION

Parasites are a fundamental component of ecological communities. They can regulate host populations with indirect effect on host fitness and mortality (Lafferty and Kuris 2009), alter host behavior (Lafferty and Morris 1996), and drive the evolution of hosts (Brooks 1985; Hafner and Nadler 1988; Klassen 1992). At the community level, parasites affect the dynamics of food webs (Lafferty 2008; Lafferty 2013) and community structure (Kuris and Lafferty 1994; Lafferty 2008; Morand 2015; Garcia-Vedrenne *et al*. 2016). Despite the growing evidence of the importance of parasites in ecosystems, parasites have been historically ignored in most ecological research (Marcogliese 2004; Gómez and Nichols; 2013, Rocha *et al*. 2016). However, to ignore parasites is to ignore most animal life, as parasitism is the most common consumer strategy on earth (Poulin and Morand 2000; Dobson *et al*. 2008). In fish ecology research, ignoring parasites is a mistake because parasites affect many variables used in fish ecology and fisheries and ignoring them may lead to biases and incorrect conclusions (Timi and Poulin 2020). Traditionally, the ecological implications of parasites have received attention in another branch of science, parasitology (Poulin 2007).

Parasites can be useful tools to study aspects of the ecology of their fish hosts. For example, parasites can be used to monitor the health of hosts and ecosystems (Marcogliese 2005; Sures *et al*. 2017) and to track and identify host populations (Kabata 1963; MacKenzie 2002; Mosquera *et al*.; 2003; Catalano *et al*. 2014). Because parasites are effective indicators of many aspects of host biology and the environment, they can also be used as important management and conservation tools (Marcogliese 2004; Gómez and Nichols 2013). Parasites have also been used to study differences in composition of parasite communities of various host species (Timi *et al*. 2010; Henríquez and González *et al*. 2012; Vidal-Martinez *et al*. 2019).

The California grunion *Leuresthes tenuis* (Ayres, 1860) is a species of New World Silverside (Atherinopsidae) endemic to southern California and northern Baja California (Walker 1952). The geographic range of *L. tenuis* extends from Tomales Bay, in northern California, to as far south as Bahía Magdalena, in southern Baja California (Love and Passarelli 2020), with a traditional habitat range between Point Conception, southern California, and Punta Abreojos, Baja California (Walker 1952; Johnson *et al*. 2009). In this traditional habitat range, especially in southern California, *L. tenuis* is one of the most iconic marine fishes because of their unique beach-spawning behavior, attracting thousands of people to observe spawning events known as "grunion runs" during their reproductive season in spring and summer (Walker 1952; Martin 2015; Martin *et al*. 2021). The sandy beach habitat that grunion uses to reproduce has been under intense impact for many decades in southern California because of urban development, resulting in a decrease in sandy beach habitat caused by coastal squeeze (Defeo *et al*. 2009; Schoeman *et al*. 2014; Martin *et al*. 2020). Over the last 10 years, an overall decline in the frequency of "intense" grunion runs has been observed in the Southern California Bight and this decline may indicate a decrease in the population size of *L. tenuis* (Martin *et al*. 2020). There are still many aspects of the ecology of *L. tenuis* that are not known.

The only time when adult *L. tenuis* can be reliably observed is during grunion runs (Martin *et al*. 2020) and, therefore, not much is known about the ecology of this species when they are not spawning. For example, little is known about their movement pattern along the coast. Tagging of *L. tenuis* by means of fin-clipping was attempted in the past with limited success because of the low recovery rates of marked specimens (Walker 1952). However, it is thought that *L. tenuis* stay close to the coast for their entire life, never moving far from the beaches where they spawn (Walker 1952). As an alternative to artificial tags, parasites have been effectively used as biological tags to identify fish stocks (Kabata 1963; Moser and Hsieh 1992; MacKenzie and Abaunza 1998; MacKenzie 2002, Catalano *et al*. 2014; Klapper *et al*. 2016). For example, parasites were successfully used to identify stocks of Pacific herring *Clupea harengus pallasi* Valenciennes, 1847, in northern California (Moser and Hsieh 1992) and to clarify residency and migration patterns of the Pacific sardine *Sardinops sagax* (Jenyns, 1842) along the west coast of North America (Jacobson *et al*. 2019). Thus, parasites can be used to test the hypothesis that *L. tenuis* stays relatively close to the beaches in which they spawn.

Two surveys have been previously conducted looking at the parasites of *L. tenuis*. The first survey (Olson 1955) was conducted in eight localities between Estero Beach, Baja California, and San Clemente, California. The second survey (Olson 1979) was conducted in the San Diego area. These previous surveys were conducted mostly in the San Diego area in southern California. Parasites reported in these surveys included ectoparasites (e.g. Branchiura, Copepoda, and Monogenea) and endoparasites (e.g. Cestoda, Digenena, Nematoda). No surveys of parasites of *L. tenuis* have been conducted north of San Clemente, Orange County. To gain a better understanding of the parasite communities of *L. tenuis* along the southern California coast, the sampling area needs to be expanded to include localities along the extent of the Southern California Bight. Besides expanding the study area, current data on parasites are needed because the earlier surveys were done several decades ago.

The goal of this study was to determine what parasites infect *L. tenuis* along the coast of southern California and to use parasite data to test the hypothesis that *L. tenuis* stay relatively close to the beaches in which they spawn. To achieve this goal, samples of *L. tenuis* were collected from five localities along the southern California coast between 2016 and 2018.

Parasites of *L. tenuis* were identified, quantified, and multivariate statistical analyses were used to determine differences among parasite communities among the five localities.

MATERIALS AND METHODS

Study area and parasitological examination of fish

A total of 900 California grunion were collected in five localities in southern California (Table 1.1, Figure 1.1). Thirty samples of 30 grunion each were collected during grunion runs between March 2016 and June 2018 (Table 1.2). Grunion were collected by hand during spawning events, placed in individual plastic bags, and frozen until inspection for parasites. After thawing, each fish and plastic bag were rinsed under running water to remove excess sand. The double-netting method (Madinabeitia and Nagasawa 2013) was used to collect parasites that may have been dislodged during sampling. Sex and standard length (SL) to the nearest millimeter (mm) were determined for each fish. Parasitological examination included body, fins, oral cavity, gill cavity, gills, heart, liver, spleen, gonads, body cavity, mesenteries, and digestive tract. Examination and identification of parasites were done using stereoscopic and compound microscopes. After fish were visually inspected, the double netting method of Madinabeitia and Nagasawa (2013) was used again with the remains of the body and head to maximize collection of parasites. Parasites were identified to the lowest taxonomical level possible and preserved in either 75% or 90% ethanol. A taxonomic summary is provided for the eight most abundant parasite species recovered from *L. tenuis* in this study and vouchers for these species were deposited at Cabrillo Marine Aquarium (CMA), San Pedro, California, U.S.A. (CMA 2021.01.0003 through CMA 2021.01.0010).

California grunion characteristics and general comparisons

Two separate t-tests were used to compare the size (SL) of *L. tenuis* between females and males and between infected and uninfected fish. A one-way ANOVA was used to compare the SL of *L. tenuis* among the five localities. Pearson's correlation analysis was used to test if there was a relationship between host SL and parasite abundance. Prior to this analysis, host SL was split into 6 class sizes (each class size = 10 mm). The correlation analysis was performed between mean SL for each class size and abundance (total number of parasites) for each parasite species. Pearson's correlation analysis was also used to test if there was a relationship between host SL and parasite prevalence.

Metazoan parasite component communities of the California grunion

Parasite component communities were determined by identifying and quantifying all the metazoan parasites found in each of the 30 samples of *L. tenuis*. Quantitative descriptors (prevalence, mean intensity, and mean abundance) and 95% confidence intervals were calculated for each species of parasite following Bush *et al*. (1997). Prevalence was calculated by dividing the number of infected hosts by the total number of specimens sampled. The 95% confidence intervals (95% C.I.) for prevalence were calculated using the Clopper-Pearson method. Mean intensity (± 95% C.I.) was calculated as the average number of parasites found in all infected hosts in a sample. Mean abundance (± 95% C.I.) was calculated as the average number of individuals of a parasite species present in a sample, including infected and non-infected hosts. The 95% confidence intervals (95% C.I.) for both mean intensity and mean abundance were calculated using the bias-corrected and accelerated (BCa) bootstrap method.

Multivariate analyses of component communities of the California grunion

All the parasites found in a sample of hosts composed a component community following Bush *et al*. (1997). Non-Metric Multidimensional Scaling (nMDS) was used to visualize similarity among component communities from all 5 localities. Bray-Curtis similarity indices were calculated among all samples and with samples from all possible pairs of localities. nMDS plots were generated with similarity matrices to visualize the groupings of samples using parasite abundance (total number of individuals of a species in a sample of hosts). The fit of the nMDS ordination was quantified by a value of stress. A permutation-based one-way analysis of similarity (ANOSIM) with Bray-Curtis similarity index was used using both parasite abundance and prevalence data to evaluate the similarity of parasite component communities from all 5 localities. Dispersal-weighting transformation was applied to abundance data before analysis to balance the contributions from abundant species with the contributions from less abundant species. In all multivariate analyses, only parasite species with a prevalence ≥ 10% in at least one locality were included. All maps, calculations of quantitative descriptors, visual, and statistical analyses were prepared using R software (R Core Development Team 2020).

RESULTS

Metazoan parasites of the California grunion

A total of 2,902 parasites belonging to 26 taxa were recovered from 900 specimens of *L. tenuis* collected at five localities in the Southern California Bight between 2016 and 2018. The parasites infecting *L. tenuis* included 11 species of ectoparasites: one branchiuran, seven copepods (five adults and two chalimus), two isopods, and one monogenean; and 15 species of endoparasites: two acanthocephalans, two cestodes (larval), five digeneans (two adults and three larval), and six nematodes (one adult and five larval) (Tables 1.3 and 1.4). Overall, 84.6% of specimens of *L. tenuis* were infected with at least one species of parasite and the mean intensity was 3.8 parasites per infected fish. The eight most abundant parasites included four ectoparasites and four endoparasites. Overall, the four most abundant ectoparasite species were *Bomolochus* sp. (Copepoda), *Leuresthicola olsoni* (Monogenea), *Caligus olsoni* (Copepoda), and *Argulus melanostictus* (Branchiura). The four most abundant endoparasite species were *Contracaecum (rudolphii)* (Nematoda), *Galactosomum* sp. (Digenea), *Asymphylodora atherinopisidis* (Digenea) and *Lepocreadium manteri* (Digenea) (Figure 1.2).

The following section includes a taxonomic summary for the four most abundant species of ectoparasites and the four most abundant species of endoparasites, listed alphabetically by parasite group, recovered from *L. tenuis* in this study.

<u>Ectoparasites</u>

BRANCHIURA
Family Argulidae
Argulus melanostictus Wilson, 1935

Localities: Goleta Beach, Malibu Beach, Cabrillo Beach, Seal Beach, and Pacific Beach
Site(s) of infection: Body, fins, also found with double netting method
Abundance (overall): 78 individuals
Prevalence (overall): 7.44%
Mean intensity (overall): 1.16
Voucher specimens: CMA2021.01.0003
Remarks: *A. melanostictus* was originally described by Wilson (1935) based on 2 free-swimming females recovered from plankton tows in Monterey Bay, California. In 1972, *A. melanostictus* was reported infecting *L. tenuis* between Del Mar, California and Estero Beach, Baja California, constituting the first host records (Olson 1972). This species was re-described based on specimens infecting California grunion *L. tenuis* collected at the type locality, Monterey Bay, California (Benz *et al.* 1995). In this study, the prevalence and abundance of *A. melanostictus* was highest at Goleta Beach (the northernmost locality) and lowest at Pacific Beach (the southernmost locality).
Type host: None, specimens were collected while swimming freely (Wilson 1935)
Type site of infection: None, specimens were collected while swimming freely (Wilson 1935)
Type locality: Monterey Bay, California
Type specimens: USNM No. 60430 (holotype)

COPEPODA
Family Bomolochidae
***Bomolochus* sp.** von Nordmann, 1832

Localities: Goleta Beach, Malibu Beach, Cabrillo Beach, Seal Beach, and Pacific Beach
Site(s) of infection: Opercular cavity, also found with double netting method
Abundance (overall): 636 individuals
Prevalence (overall): 46.3%
Mean intensity (overall): 1.52
Voucher specimens: CMA2021.01.0004
Remarks: The specimens recovered from the opercular cavity of *L. tenuis* belong to the genus *Bomolochus* von Nordmann, 1832. *Bomolochus cuneatus* Fraser, 1920 (as *Bomolochus pectinatus* Stock, 1955) has been reported from the gill chambers of California grunion collected from San Clemente, California to Estero Beach, Baja Mexico (Stock 1955; Olson 1972). In addition, *B. cuneatus* has been reported from other fish taxa (mostly surfperches) collected from western Canada to Mexico (Fraser 1920; Moser and Haldorson 1982; Kabata 1988). All bomolochid specimens collected in this study were keyed out to *Bomolochus nitidus* Wilson, 1911 (based on Ho and Lin's (2009) species key to females of *Bomolochus*). However, morphological differences indicate that these specimens are not conspecific to *B. nitidus* and further investigations are necessary to confirm identification. The specimens of *Bomolochus* from *L. tenuis* collected in this study are assigned as *Bomolochus* sp. pending morphological comparisons, and complemented with molecular analyses, with new material of *Bomolochus* from surfperches. Examination of Stock's (1955) specimens of *B. cuneatus* from California grunion would be also useful for identification.
Type host: NA
Type site of infection: NA
Type locality: NA
Type specimens: NA

Family Caligidae
Caligus olsoni Pearse, 1953

Localities: Goleta Beach, Malibu Beach, Cabrillo Beach, Seal Beach, and Pacific Beach
Site(s) of infection: Body surface, fins, also found with double netting method
Abundance (overall): 145 individuals
Prevalence (overall): 13.1%
Mean intensity (overall): 1.25
Voucher specimens: CMA2021.01.0005
Remarks: *C. olsoni* was first described by Pearse (1953) based on specimens infecting California grunion *L. tenuis* collected at Mission Bay and San Diego Bay, California. A redescription of this species is provided in this study (see Chapter 2). In this study, the prevalence and abundance of *C. olsoni* was highest at Pacific Beach (the southernmost locality) and lowest at Goleta Beach (the northernmost locality).
Type host: *Leuresthes tenuis*
Type site of infection: No details are given in original description (Pearse 1953)
Type locality: San Diego, California

Type specimens: USNM No. 93733 (syntype, female); 93734 (syntype, male)

MONOGENEA
Family Heteraxinidae
Leuresthicola olsoni Price, 1962

Localities: Goleta Beach, Malibu Beach, Cabrillo Beach, Seal Beach, and Pacific Beach
Site(s) of infection: Gills
Abundance (overall): 581 individuals
Prevalence (overall): 37.8%
Mean intensity (overall): 1.71
Voucher specimens: CMA2021.01.0006
Remarks: *Leuresthicola olsoni* was described based on specimens found on the gills of *L. tenuis* collected in San Diego, California (Price 1962).
Type host: *Leuresthes tenuis*
Type site of infection: Gills
Type locality: San Diego, California
Type specimens: USNM Helm. Coll. No. 49435 (holotype and paratype); 37744 (paratypes)

<u>Endoparasites</u>

DIGENEA
Family Lissorchiidae
Asymphylodora atherinopisidis Annereaux, 1947

Localities: Goleta Beach, Malibu Beach, Cabrillo Beach, Seal Beach, and Pacific Beach
Site(s) of infection: Posterior intestine
Abundance (overall): 196 individuals
Prevalence (overall): 15.3%
Mean intensity (overall): 1.38
Voucher specimens: CMA2021.01.0007
Remarks: *Asymphylodora atherinopisidis* was first described based on a single specimen collected from the intestine of jacksmelt *Atherinopsis californiensis* collected at Stinson's Beach, California (Annereaux 1947). This species was re-described based on specimens removed from the posterior intestine of *L. tenuis* collected between Estero Beach, Baja California and San Clemente, California (Olson 1977). Recently, however, it has been brought up that the "bipartite metraterm" structure in the original description of *A. atherinopsidis* Annereaux, 1947 may be, in fact, a terminal organ, which is a definitive feature of the family Monorchiidae. Because of its taxonomy uncertainty, *A. asymphylodora* has been deemed *incertae sedis* (Truong *et al.* 2021).
Type host: *Atherinopsis californiensis*
Type site of infection: Intestine
Type locality: Stinson's Beach, California
Type specimens: USNM Helm. Coll. No. 36953

Family Lepocreadiidae
Lepocreadium manteri Olson, 1978

Localities: Malibu Beach, Cabrillo Beach, Seal Beach, and Pacific Beach
Site(s) of infection: Anterior intestine.
Abundance (overall): 163 individuals
Prevalence (overall): 3.0%
Mean intensity (overall): 5.85
Voucher specimens: CMA2021.01.0008
Remarks: *L. manteri* was described by Olson (1978) based on specimens collected from the anterior intestine of *L. tenuis* collected between Estero Beach, Baja California and San Clemente, California. In this study the overall prevalence of *L. manteri* was highest (10.5%) in Pacific Beach (the southernmost locality). A single specimen of *L. manteri* was collected in Malibu Beach and no specimens were collected at Goleta Beach (the northernmost locality).
Type host: *Leuresthes tenuis*
Type site of infection: Anterior intestine
Type locality: San Diego Bay, California
Type specimens: USNM Helm. Coll. No. 73873 (holotype); 73784 and 73785 (paratypes)

Family Heterophyidae
Galactosomum sp. Looss, 1899

Localities: Goleta Beach, Malibu Beach, Cabrillo Beach, Seal Beach, and Pacific Beach
Site(s) of infection: Body cavity, also found with double netting method
Abundance (overall): 417 individuals
Prevalence (overall): 14.6 %
Mean intensity (overall): 3.18
Voucher specimens: CMA2021.01.0009
Remarks: *Galactosomum humbargari* was described by Park (1936) based on specimens collected from the small intestine of the California gull *Larus californicus* collected in Dillon Beach, California. In a laboratory experiment, cysts of *G. humbargari* recovered from *L. tenuis* were fed to the Caspian tern *Hydroprogne caspia* and recovered four days later at the young adult stage (Olson 1955). It is likely that the specimens of *Galactosomum* found in this study are *G. humbargari* but further investigations are necessary to confirm identification.
Type host: NA
Type site of infection: NA
Type locality: NA
Type specimens: NA

NEMATODA
Family Anisakidae
Contracaecum (rudolphii) Hartwich, 1964

Localities: Goleta Beach, Malibu Beach, Cabrillo Beach, Seal Beach, and Pacific Beach
Site(s) of infection: Mesenteries, also found with double netting method.
Abundance (overall): 510 individuals

Prevalence (overall): 18.6%
Mean intensity (overall): 2.89
Voucher specimens: CMA2021.01.0010
Remarks: The original description of *C. rudolphii* is not documented but is attributed to Hartwich, 1964. A redescription is provided in Arai and Smith (2016) based on specimens recovered from the body, cavity, intestinal lumen, and musculature of the mummichog *Fundulus heteroclitus* and the guppy *Poecilia reticulata* collected in Nova Scotia, Canada.
Type host: not documented
Type site of infection: not documented
Type locality: not documented
Type specimens: not documented

California grunion characteristics and general comparisons

The standard length (SL) of *L. tenuis* ranged between 111.1 mm and 168.3 mm and the overall (all localities) mean SL was 138.9 mm ± 10.8 SD. Of the 900 *L. tenuis* sampled, 353 were females and 547 were males. Females were larger (SL 145.2 mm ± 10.4 SD) than males (SL 134.8 mm ± 8.9 SD) and the difference in SL was significant (t = 15.41, df = 665.06, P < 0.001). Overall, fish infected with at least one species of parasite were significantly larger (139.6 mm + 10.8 SD) than uninfected fish (134.9 mm + 9.5 SD) (t = 5.27, df = 209.03, P < 0.001). Mean SL of *L. tenuis* varied significantly among localities (ANOVA, $F_{4,895}$ = 15.39, df = 895, P < 0.001). The largest fish were found in Seal Beach (n = 150, mean SL = 142.8 mm ± 10.1 SD) and the smallest fish were found in Pacific Beach (n = 210, mean SL = 134.6 mm ± 10.6 SD) (Figure 1.3). There was no correlation between parasite abundance and host SL for the eight most abundant parasite species. Prevalence was positively correlated with host SL for three out of the eight most abundant parasite species: *Bomolochus* sp. (r = 0.83, df =4, P = 0.04), *L. olsoni* (r = 0.91, df =4, P = 0.01), and *A. atherinopsidis* (r = 0.98, df =4, P <0.001).

Metazoan parasite component communities of the California grunion

The overall prevalence, mean intensity, and mean abundance of each parasite species infecting *L. tenuis* varied among the 5 localities (Table 1.5, Figures 1.4-1.5). Quantitative descriptors for the eight most abundant parasites infecting *L. tenuis*, arranged by locality, locality and year, and for each sample, are given in Chapter 1 - Supplemental Materials (Tables 1.S1-1.S24). Nine out of the 26 taxa of parasites infecting *L. tenuis* were recovered from samples collected at all five localities and two species were found in four out five localities. The nine parasite taxa found in all five localities were the ectoparasites *Argulus melanostictus* (Branchiura), *Bomolochus* sp. (Copepoda), *Caligus olsoni* (Copepoda) and *Leuresthicola olsoni* (Monogenea); and the endoparasites *Asymphylodora atherinopsidis* (Digenea), Didimozoidae type Pseudomonilicaecum (Digenea), Didimozoidae type Monilicaecum (Digenea), *Galactosomum* sp. (Digenea), and *Contracaecum (rudolphii)* (Nematoda). The two species found in four out five localities were *Lepocreadium manteri* (Digenea), recovered from all localities except for Goleta Beach and *Lacistorhynchus* sp. (Cestoda), recovered from all localities except for Pacific Beach.

The following are new host records for *L. tenuis*: Pseudomonilicaecum (Digenea; Didimozoidae), Pseudotorticaecum (Digenea; Didimozoidae), Trypanoryncha gen. sp. (Cestoda), *Oncophora* sp. (Nematoda), *Corynosoma* sp. (Acanthocephala), *Rhadinorhynchus* sp. (Acanthocephala), *Caligus macarovi* (Copepoda), *Caligus rotundigenitalis* (Copepoda), Pandaridae (chalimus) gen. sp. (Copepoda), Pennelidae (chalimus) gen. sp. (Copepoda) and Gnathiidae gen. sp. (Isopoda). Most of the parasite species that are new host records for *L. tenuis* were relatively rare (< 1% overall prevalence). The exceptions were the two larval didymozoids, which were found in all five localities and their overall prevalence was as high as 8.9% (type Pseudotorticaecum at Goleta Beach) and 7.6% (type Pseudomonolicaecum at Cabrillo Beach).

Multivariate analyses of component communities of the California grunion

Non-metric multidimensional scaling (nMDS) analysis was used to obtain a visual representation of the similarity among parasite component communities infecting *L. tenuis* collected at 5 localities in southern California. A Shepard diagram showing the distances of the nMDS against the dissimilarities in the Bray-Curtis matrices is given in Chapter 1 – Supplemental Materials (Figure 1-S1). The nMDS plot showed geographical variation among the parasite component communities of *L. tenuis* in the Southern California Bight (Figure 1.6). The stress score for the nMDS analysis was 0.122 (Table 1.6). Parasite component communities from samples collected at Goleta Beach were associated with higher abundance of *A. melanostictus* (Branchiura), *Bomolochus* sp. (Copepoda), and *L. olsoni* (Monogenea) and lower abundance of *C. olsoni* (Copepoda), *L. manteri* (Digenea), and *G. humburgari* (Digenea) in relation to the other localities. The opposite pattern was observed for parasite component communities from Pacific Beach, which were associated with higher abundance of *C. olsoni* (Copepoda), *L. manteri* (Digenea), and *Galactossomum* sp. (Digenea) and lower abundance of *A. melanostictus* (Branchiura), *Bomolochus* sp. (Copepoda), and *L. olsoni* (Monogenea) in relation to the other localities. Component communities from Malibu Beach, Cabrillo Beach, and Seal Beach were similar in relation to each other and were associated with most of the same species of parasite at intermediate abundances in relation to Goleta Beach and Pacific Beach.

At the component community level, the similarity varied significantly among all localities in relation to parasite abundance (ANOSIM, $R = 0.371$, $p < 0.001$) and prevalence (ANOSIM, $R = 0.390$, $p < 0.001$). Pairwise comparisons between localities indicated significant differences when comparing either Goleta Beach or Pacific Beach to any other locality but there were no significant differences among component communities from samples collected at Malibu Beach, Cabrillo Beach, and Seal Beach (Table 1.7).

DISCUSSION

Metazoan parasites of the California grunion

The results in this study indicate higher species richness (26 taxa) of metazoan parasites of *L. tenuis* in the Southern California Bight in relation to previous surveys (Olson 1955; Olson 1979). Olson (1955) reported 16 species of parasites infecting grunion at eight localities between Estero Beach, Baja California, and San Clemente, California, and Olson (1979) reported eight species of parasites from the greater San Diego area. The higher species richness in this study may be attributed to the detection of parasites that are rare (<1% overall prevalence) to *L. tenuis*, but could also be an artifact of the total number of fish hosts inspected for parasites. Olson (1979) had a much smaller sample size from a single sampling event.

Although differences in species richness were observed, many of the parasite species found in this study were also found in the Olson (1955) and Olson (1979) surveys. The only sampling area in common between this study and the earlier surveys is the San Diego area. Of the 8 most abundant species of parasites reported in this study (Fig. 1.2), 7 species (*Bomolochus* sp., *C. olsoni*, *L. olsoni*, *A. atherinopsidis*, *Contracaecum (rudolphii*), *Galactosomum humbargari* and *L. manteri*) were reported by Olson (1955) as either “abundant” or “common” and the same 7 species were also reported by Olson (1979). This suggests that the metazoan parasite fauna of *L. tenuis* has been relatively unchanged, in relation to the most common species of parasites, between 1955 and 2018. The similarity in metazoan parasite fauna of *L. tenuis* between this study and previous studies (Olson 1955; Olson 1979) may be explained by the fact that parasite assemblages (such as component communities) are long-lived assemblages that are formed over evolutionary time scales (Poulin 2004; Poulin 2007). Changes in component communities are related to processes such as colonization, extinction, and speciation of parasites that take place at very long (i.e. evolutionary) time scales (Poulin 2004; Poulin 2011). Although the most common species of parasites where similar, differences were observed in relation to parasite species found infecting *L. tenuis* occasionally between this and previous studies.

Olson (1955) reported the lernaeopodid copepod *Clavellopsis* sp., the isopods *Elthusa californica* (reported as *Livoneca californica*) and *Nerocila californica,* and the branchiuran *Argulus melanosticus* as occasional parasites of *L. tenuis*. Similarly, lernaeopodid copepods, cymothoid isopods, and gnathiid isopods found in this study were also rare (prevalence <1.0%). It is possible that the lernaeopodid copepods found in this study also belong to the genus *Clavellopsis*, as reported by Olson (1955), but it was not possible to confirm their identity because the only 2 specimens recovered were physically damaged. The branchiuran *A. melanostictus* was found infecting *L. tenuis* at higher prevalence in this study compared to Olson (1955), who reported this parasite at low prevalence between Estero Beach, Baja California and San Clemente, California, and in Olson (1979), in which *A. melanostictus* was not found in the greater San Diego area. In this study, *A. melanostictus* was more prevalent in localities in the northern SCB (20.6% at Goleta Beach and 10% at Malibu Beach) were sampled for grunion parasites for the first time in this study. The prevalence of *A. melanostictus* was < 5% at the other localities in the central SCB (2.4% at Cabrillo Beach and 4.0% at Seal Beach), and 1.9%, at Pacific Beach, which was similar to the overall prevalence (~1.4%) for *A. melanostictus* reported in Olson (1955). Some of the parasite species previously reported in Olson (1955) were not found in the current study. These parasites include the strigeid metacercaria (Digenea), larval distome (Digenea), tetraphyllidean plerocercoid (Cestoda), and *Nerocila californica* (Isopoda).

California grunion characteristics and general comparisons

The overall mean SL of *L. tenuis* (138.9 mm), the ratio between females and males (2 females:3 males), and the larger mean SL of females (145.2 mm) in relation to males (134.8 mm) indicate that the samples collected in this study are typical for this species. Host size may be an important variable affecting abundance of parasites in a host population. Although significant differences were observed in mean SL of *L. tenuis* among localities, the difference in mean SL between the locality with the largest fish (Seal Beach, SL = 142.8 mm ± 10.09 SD) and the locality with the smallest fish (Pacific Beach SL = 134.6 mm ± 10.57 SD) was small (<1cm). Mean SL of *L. tenuis* was not significantly correlated with parasite abundance for any of the eight most abundant species of parasite found in this study, showing that larger fish did not have a significant larger number of parasites in relation to smaller fish. Mean SL was significantly correlated with parasite presence for three out of the eight parasites species (*Bomolochus* sp., *L. olsoni*, and *A. atherinopsidis*) indicating that large specimens of *L. tenuis* are more likely to be infected by these species of parasites. However, none of these parasite species were found at their highest prevalence at Seal Beach (the locality where the largest fish were collected), suggesting that variables other than host SL (e.g. water temperature, presence/abundance of intermediate hosts) may be more relevant in affecting prevalence of parasite species. Currently, it is not known if size and age are correlated for *L. tenuis*. It is possible to determine age by counting marks that develop periodically in various hard parts of fishes (e.g. otoliths and scales) and then determining the relationship between body size and age. It would be useful, in the future, to investigative the relationship between body size and age for *L. tenuis* using a growth model (e.g. von Bertanlanffy growth factor).

Metazoan parasite component communities of the California grunion

The four most common species of ectoparasites were found at all localities but showed different patterns in relation to prevalence. The two most prevalent species found infecting *L. tenuis* in this study were the ectoparasites *Bomolochus* sp. (Copepoda) and *L. olsoni* (Monogenea) (Table 1.5). The overall prevalence of *Bomolochus* sp. ranged between 36.2% in Pacific Beach and 56.0% in Malibu Beach, while the overall prevalence of *L. olsoni* ranged between 18.6% in Pacific Beach and had the highest value for any parasite species at 61.7% in Goleta Beach, indicating a pattern of higher prevalence with an increase in latitude (Table 1.5, Fig. 1.4). The prevalence of *A. melanostictus* (Branchiura) at different localities was also higher with an increase in latitude, with a range between 1.9% in Pacific Beach and 20.6% in Goleta Beach. The opposite pattern was observed for *C. olsoni* (Copepoda), which showed lower prevalence with an increase in latitude with a range between 2.8% in Goleta Beach and 23.3% in Pacific Beach (Fig. 1.4). Both of these parasitic crustaceans infect the same location on the host (body and fins) and it is possible that they are competing for similar resources on the host, however, differences in temperature throughout the SCB may also be a factor. Although laboratory experiments are ideal to test hypothesis of correlation/competition between parasites competing for host resources (Poulin 2018), an experimental approach is not viable in this case because *L. tenuis* does not survive well in captivity.

Three out of the four most common species of endoparasites were found in all localities. The exception was *L. manteri* (Digenea) that was not found in the northern-most locality, Goleta

Beach. The prevalence of *L. manteri* was mostly very low (≤ 2% in the three central localities) but was near 10% in Pacific Beach. *Leuresthes tenuis* is the final host for *L. manteri* (Olson 1978), the first intermediate host is likely a gastropod (based on the life cycle of other species of *Lepocreadium*), and the second intermediate host is likely an annelid, but a turbellarian has also been reported (Stunkard 1972). It is possible that the distribution of one of the intermediate hosts of this parasite has an upper limit of its range near Malibu Beach. Only three species of endoparasites were commonly found (prevalence ≥10%) in at least one of the sampled localities. These species were *A. atherinopisidis* (Digenea), *Galactosomum* sp.(Digenea) and *Contracaecum rudolphii* (Nematoda). This low number of endoparasites may reflect the narrow diet of *L. tenuis* which is strictly carnivorous and consists mostly of mysid crustaceans (Horn *et al*. 2006; Higgins and Horn 2014). In this study, most of the "food" observed in the digestive tract of *L. tenuis* consisted of grunion eggs, which *L. tenuis* are capable of digesting (Santos *et al*. 2018).

The overall prevalence of *A. atherinopisidis* ranged between 7.62% in Pacific Beach and 22.8% in Goleta Beach, with similar values (ranging between 14.0% and 18.6%) at the three central localities. The life cycle for *A. atherinopsidis* is unknown but other species in the genus *Asymphylodora* use mollusks, typically gastropods, as intermediate hosts (Stunkard 1959).

The overall prevalence of *G. humbargari* was lower (between 5.3 and 8.6%) in the three central localities, 14.4% in Goleta Beach, and had the highest value (32.9%) in Pacific Beach. It is interesting to note that in the first survey of parasites of *L. tenuis* (Olson 1955), *G. humbargari* was the only species of parasite reported as "abundant" with 689 individuals collected from 225 fish at four localities, and a prevalence range between ~50% and ~90%. It is possible that the difference in prevalence observed between this study and the first survey is related with changes in the populations of the final hosts for *G. humbargari*. The type host of *G. humbargari* is the California gull *Larus californicus* (Park, 1936) but *G. humbargari* have a wide range of piscivore birds as their final hosts. The metacercariae of *G. humbargari* is also found in other New World silversides (e.g. *Atherinops affinis* and *Atherinopsis californiensis*) (Love and Moser 1983; Ralph Appy, pers. comm.).

The overall prevalence of *Contracaecum (rudolphii)* ranged between 13.3% in Pacific Beach and 27.2% in Goleta Beach, with a narrow range in the central localities (18.7%-20.0%). Nematodes of the genus *Contracaecum* have a global distribution and typically become adults in a variety of species of marine mammals and birds. Morphological measurements and morphological features (e.g. annulations, esophageal structure) comparing specimens of *Contracaecum* found in this study with other species of *Contracaecum* indicate that the species infecting *L. tenuis* may be *Contracaecum (rudolphii)* (Ralph Appy, pers. comm.).

Multivariate analyses of component communities of the California grunion

The component communities of parasites of *L. tenuis* showed geographical variation within the Southern California Bight (Figure 1.6 and Table 1.7). The dissimilarity was greater between communities obtained from *L. tenuis* collected at localities that were further apart from each other (i.e. Goleta Beach, in Santa Barbara, and Pacific Beach, in San Diego). Parasites component communities were more similar among the three central localities (Malibu Beach, Cabrillo Beach, and Seal Beach) based on the nMDS plot (Figure 1.6). ANOSIM analyses showed that the component communities of parasites infecting *L. tenuis* were significantly different among localities in the Southern California Bight (Table 1.7), indicating three groups of parasite communities: a northern group (Goleta samples), a central group (Malibu, Cabrillo

Beach, and Seal Beach samples), and a southern group (Pacific Beach samples). Component communities are long-lived assemblages in relation to the species of parasites but changes in quantitative descriptors (e.g. prevalence, abundance) may occur in much shorter time scales and may be related to environmental gradients (Timi 2007).

Previous research on the population structure of *L. tenuis* has indicated no substantial genetic divergence among samples of *L. tenuis* along the California coast (Johnson *et al*. 2019). Allozyme research has indicated that the population of *L. tenuis* approaches panmixia in southern California but also contains indication of isolation by distance (Gaida *et al*. 2003) within the same latitudinal gradients of the present study. The lack of substantial genetic divergence (Johnson *et al*. 2009) and the near panmixia observation (Gaida *et al*. 2003) may be an indication that the population of *L. tenuis* has been long established in southern California and this is supported by the similarity in the species of parasites most commonly found among localities in this study. However, allozyme genetic divergence was also found to be correlated with geographic distance (Gaida *et al*. 2003) and this is also supported by differences in parasite component communities among localities based on prevalence and abundance shown in the nMDS and ANOSIM analyses in this study, sampled on the same, or nearby, beaches as Gaida *et al.* (2013).

Conclusions

The metazoan parasite component communities of *L. tenuis* in the SCB observed in this study comprised of a total of 26 parasite taxa recovered from 900 fish collected at the five localities sampled between 2016 and 2018. The parasite communities of *L. tenuis* shared many species of parasites among localities but varied significantly in relation to prevalence and abundance of different species of parasites. This suggests that the geographic separation in observed in parasite communities may be a result of *L. tenuis* staying relatively close to the latitudes of their spawning grounds throughout their lives. The results found in this study agree with Walker (1949), who suggested that *L. tenuis* may spend their entire life close to the coast based on recapture of marked fish. On the other hand, within the past two decades, *L. tenuis* has expanded its spawning habitat to novel locations hundreds of kilometers north of the sampled sites (Roberts *et al.* 2007; Johnson *et al.* 2009; Martin *et al.* 2013).

In addition, Olson (1955) also suggested that differences in parasite quantitative descriptors (e.g. prevalence and abundance) among localities may be greater than would be expected in freely migrating populations. Future studies can further investigate the underlying causes (e.g. environmental gradients, anthropogenic impacts) of the variation in parasite component communities observed in this study. It would be especially interesting to investigate how climate change may affect the parasite communities of *L. tenuis* in the SCB and in the fish from the recent northern range expansion. Shallow subtidal and intertidal habitats are likely to see the most changes in parasite-host dynamics because these areas will experience the biggest changes in temperature. Predicting how climate change may influence host-parasite dynamics is an increasingly-important goal (Byers 2020). It would also be interesting to investigate the parasite fauna of different host species with known movement patterns within the SCB.

ACKNOWLEDGMENTS

I thank Dr. Donald Buth (University of California, Los Angeles), Dr. Ralph Appy (Cabrillo Marine Aquarium), Dr. David Jacobs (University of California, Los Angeles), Dr. Karen Martin (Pepperdine University), and Dr. Michael Shin (University of California, Los Angeles) for their comments on an earlier draft of this manuscript. I also would like to thank Dr. Ralph Appy, Jade Morris (volunteer), Dr. Kimo Morris (Santa Ana College), Dr. Julianne Passarelli (Cabrillo Marine Aquarium), Dr. Marcelo Pires (Saddleback College), Michelle Smith (volunteer), Kim Johnson (Rancho Santiago College), Zack Salas (Cabrillo Marine Aquarium), Bayne Westrick-Snapp (Cabrillo Marine Aquarium), and the staff at Cabrillo Marine Aquarium for their assistance in collection of samples. I would like to extend a special thanks to Dr. Omar Amin (Institute of Parasitic Diseases and Parasitology Center), Dr. Ralph Appy, Dr. Julianne Passarelli, and Dr. Danny Tang (Orange County Sanitation District) for help with identification of parasites and to Dr. Bengt Allen (California State University, Long Beach) for comments and advice on multivariate analysis. This study was done in partial completion of a doctoral degree in the Department of Ecology and Evolutionary Biology at the University of California, Los Angeles.

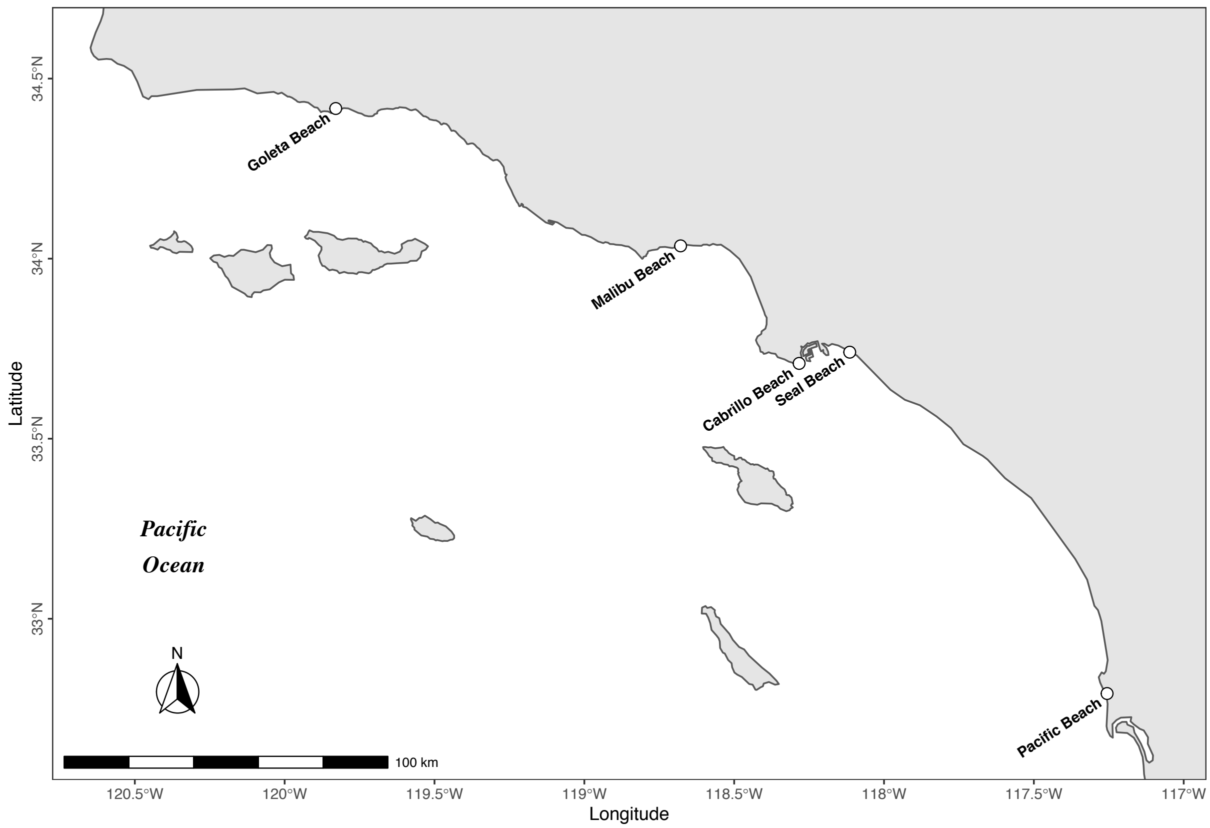

Figure 1.1. Map of the sampling localities of *L. tenuis* in southern California.

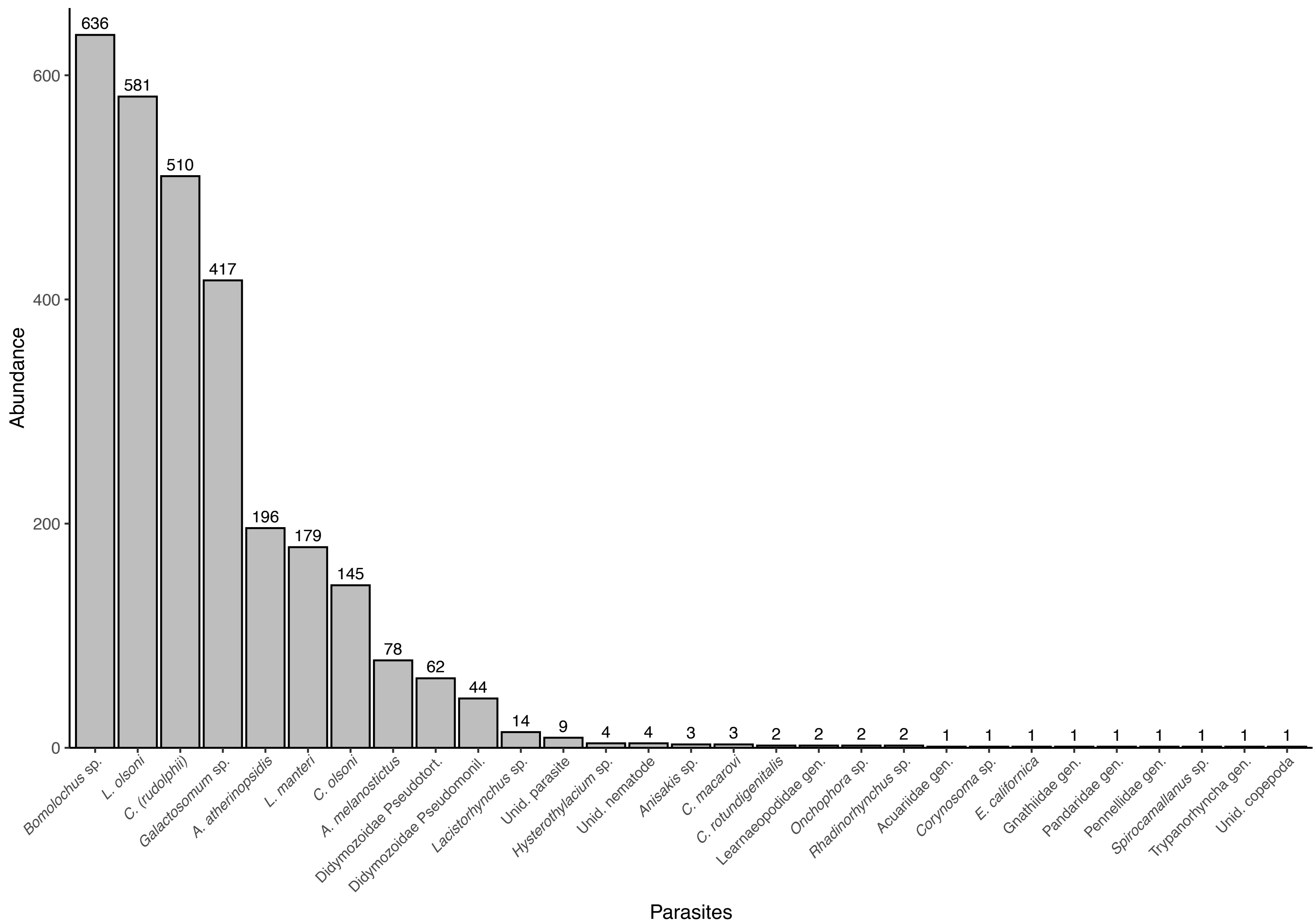

Figure 1.2. Rank abundance of metazoan parasites of *L. tenuis* from five localities in southern California between March 2016 and June 2018.

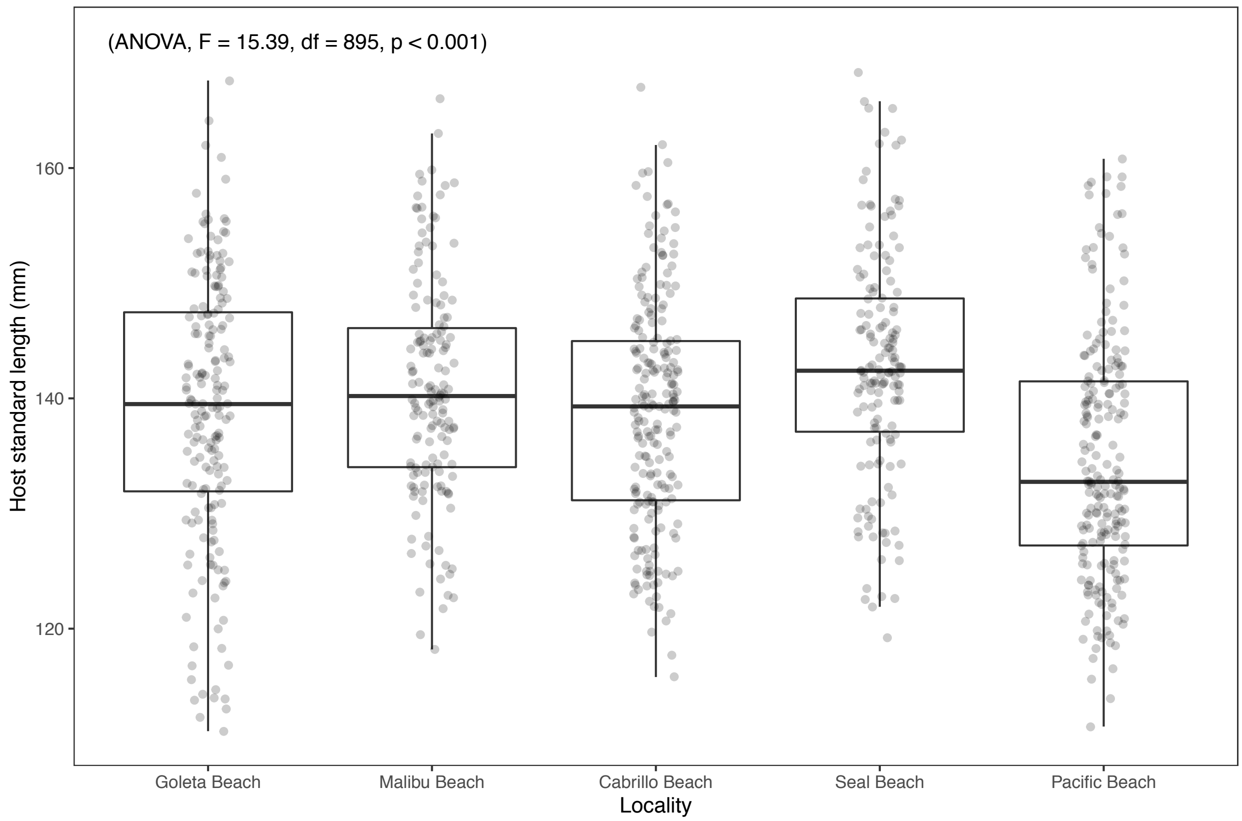

Figure 1.3. Standard length (SL) of *L. tenuis* from five sampling localities in southern California.

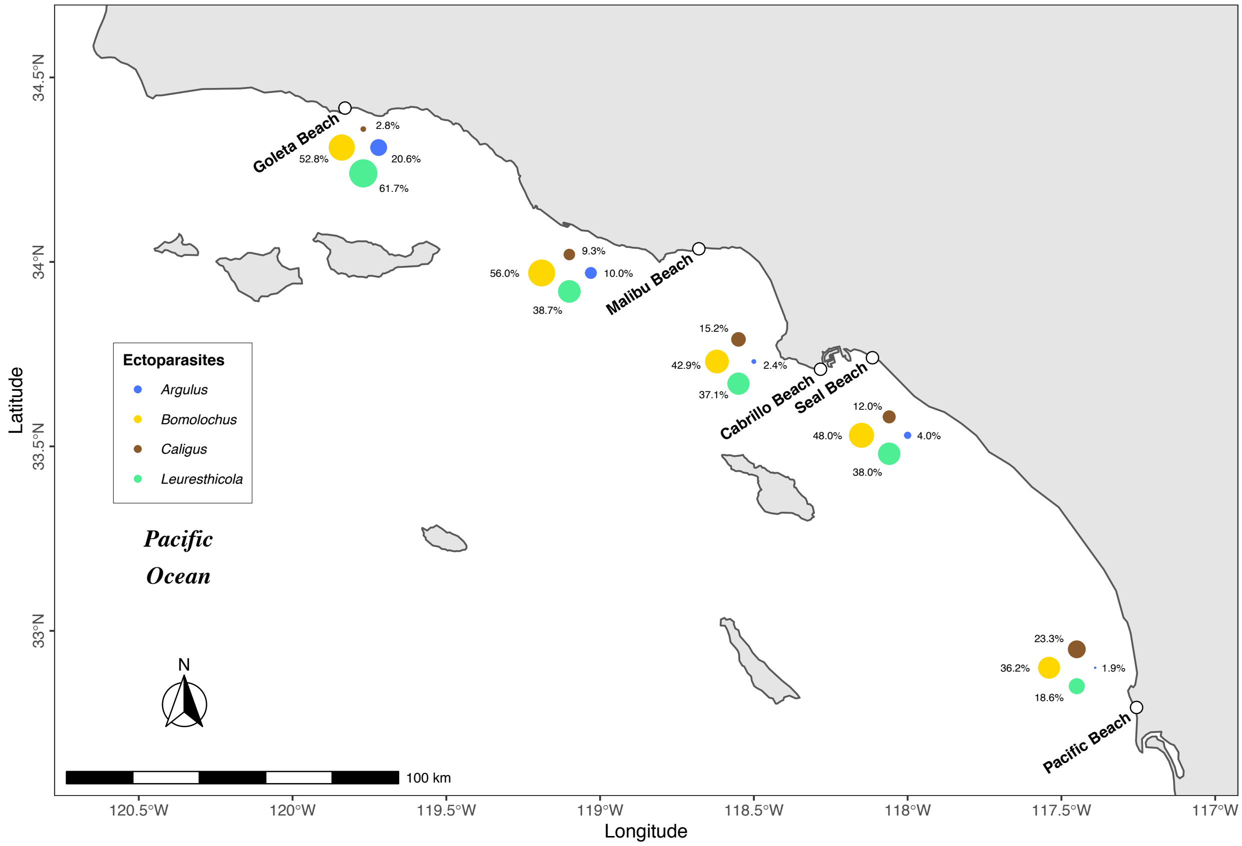

Figure 1.4. Overall prevalence for the four most common ectoparasites infecting *L. tenuis* in the SCB between 2016 and 2018. Differences in size of the circles indicate prevalence values (shown as percentages right next to the circles).

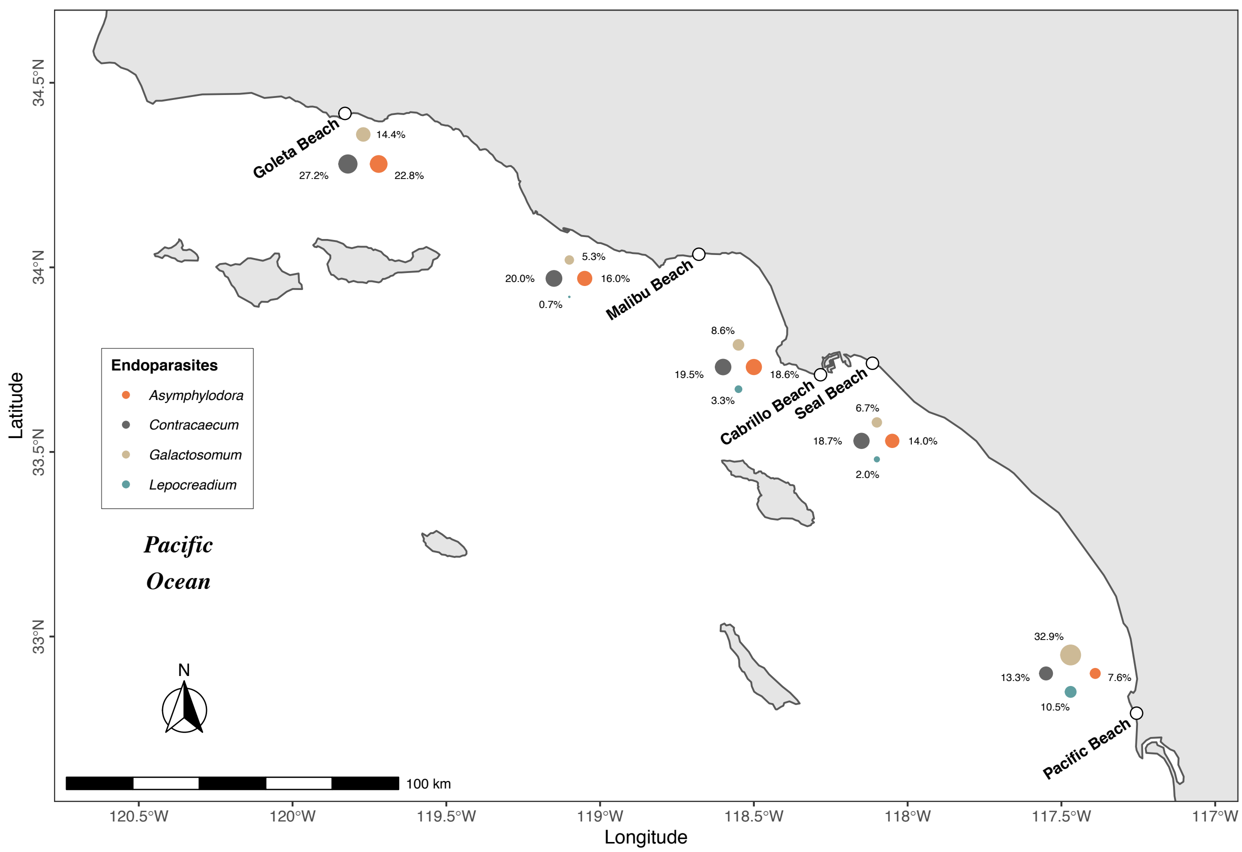

Figure 1.5. Overall prevalence for the four most common endoparasites infecting *L. tenuis* in the SCB between 2016 and 2018. Differences in size of the circles indicate prevalence values (shown as percentages right next to the circles).

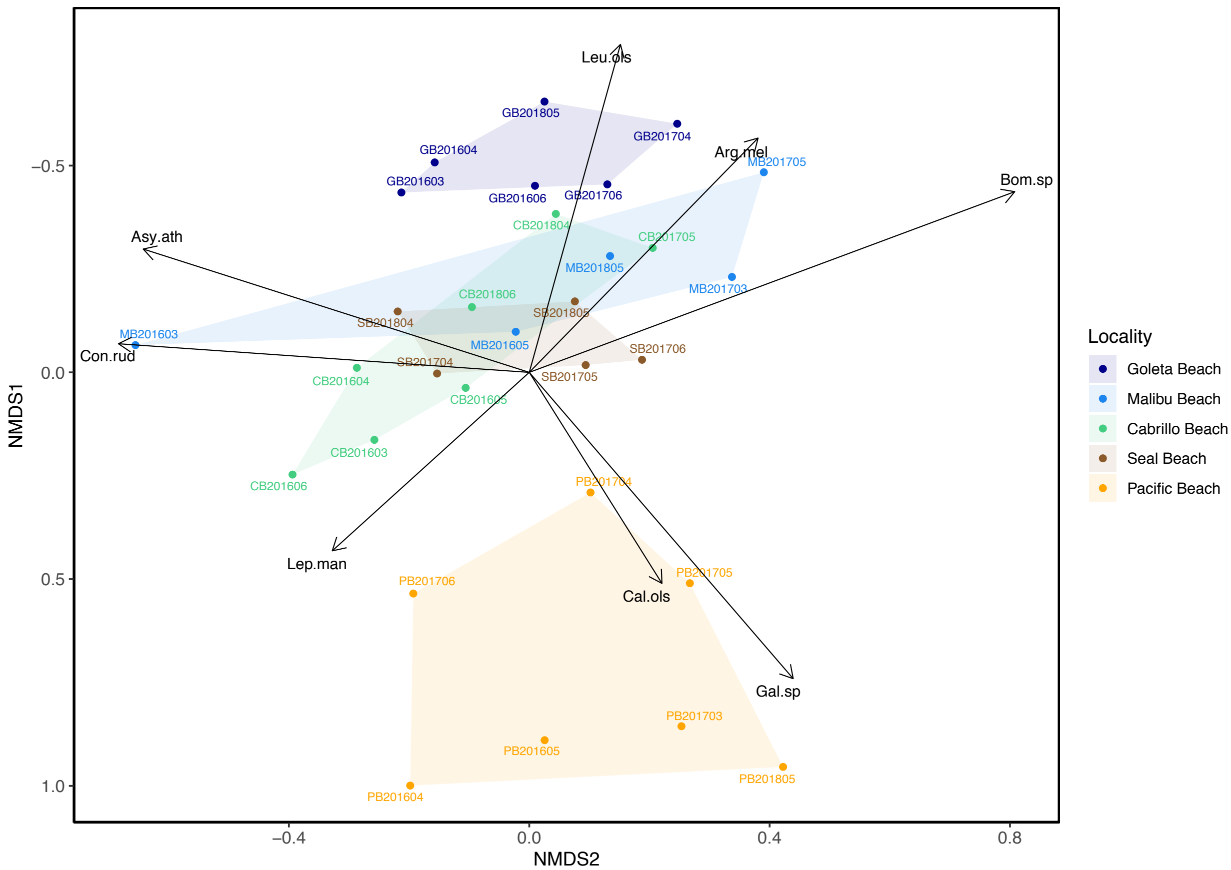

Figure 1.6. Nonmetric multidimensional scaling (nMDS) based on abundance of metazoan parasites infecting the California grunion *L. tenuis*. The plot shows similarity patterns among component communities from samples collected at five localities in southern California between 2016 and 2018. Black arrows represent the species of parasites driving the distribution of samples.

Species of parasites: Arg.mel = *Argulus melanostictus*, Asy.ath = *Asymphylodora atherinopsidis*, Bom.sp = *Bomolochus* sp., Cal.ols = *Caligus olsoni*, Con.rud = *Contracaecum (rudolphii)*, Gal.sp = *Galactosomum* sp., Lep.man = *Lepocreadium manteri*, Leu.ols = *Leuresthicola olsoni*. Localities: GB = Goleta Beach, MB = Malibu Beach, CB = Cabrillo Beach, SB = Seal Beach, PB = Pacific Beach. Numbers after localities denote year and month.

Table 1.1. GPS coordinates of sampling localities of *L. tenuis* in southern California.

Locality	Locality Code	County	Latitude	Longitude
Goleta Beach	GB	Santa Barbara	34°25'00.3"N	119°49'47.3"W
Malibu Beach	MB	Los Angeles	34°02'00.5"N	118°40'45.0"W
Cabrillo Beach	CB	Los Angeles	33°42'32.6"N	118°17'00.1"W
Seal Beach	SB	Los Angeles	33°44'24.6"N	118°06'51.9"W
Pacific Beach	PB	San Diego	32°47'32.0"N	117°15'20.1"W

Table 1.2. Sampling dates, number of hosts inspected (n), and mean standard length (SL) for the 30 samples of *L. tenuis* inspected for parasites.

Locality	Collection Date	n	Mean SL (mm) ± SD
Goleta Beach	3/25/2016	30	140.69 ± 9.31
	4/23/2016	30	134.48 ± 13.45
	6/21/2016	30	133.31 ± 12.29
	4/28/2017	30	145.07 ± 9.13
	6/11/2017	30	136.76 ± 11.64
	5/17/2018	30	143.44 ± 9.19
Malibu Beach	3/24/2016	30	141.51 ± 6.91
	5/22/2016	30	140.12 ± 9.23
	3/29/2017	30	139.88 ± 9.80
	5/26/2017	30	146.94 ± 8.80
	5/16/2018	30	135.69 ± 10.21
Cabrillo Beach	3/25/2016	30	137.16 ± 10.46
	4/23/2016	30	133.43 ± 10.00
	5/22/2016	30	135.75 ± 11.44
	6/22/2016	30	137.82 ± 8.78
	5/12/2017	30	145.58 ± 9.45
	4/2/2018	30	144.03 ± 5.39
	6/16/2018	30	137.41 ± 13.45
Seal Beach	4/12/2017	30	142.07 ± 10.20
	5/12/2017	30	144.54 ± 12.03
	6/10/2017	30	141.28 ± 10.09
	4/2/2018	30	144.49 ± 8.65
	5/31/2018	30	141.83 ± 9.35
Pacific Beach	4/25/2016	30	132.87 ± 9.73
	5/23/2016	30	133.57 ± 7.71
	3/30/2017	30	136.98 ± 8.31
	4/27/2017	30	140.05 ± 11.97
	5/27/2017	30	137.88 ± 8.87
	6/10/2017	30	134.56 ± 11.09
	5/1/2018	30	126.51 ± 10.81

Table 1.3. Taxonomic composition of ectoparasites of *Leuresthes tenuis* in five localities in the Southern California Bight between 2016 and 2018.

Parasite species
BRANCHIURA
Family Argulidae
Argulus melanostictus Wilson 1935
COPEPODA
Family Bomolochidae
Bomolochus sp. Fraser 1920
Family Caligidae
Caligus olsoni Pearse 1953
Caligus macarovi Gusev 1951
Caligus rotundigenitalis Yü 1933
Family Learnopodidae
Learnopodidae gen. sp.
Family Pandaridae
Pandaridae (chalimus) gen. sp.
Family Pennellidae
Pennellidae (chalimus) gen. sp.
ISOPODA
Elthusa californica (Schioedte & Meinert, 1884)
Gnathiidae gen. sp. Leach 1814
MONOGENEA
Family Heteraxinidae
Leuresthicola olsoni Price 1961

Table 1.4. Taxonomic composition of endoparasites of *Leuresthes tenuis* in five localities in the Southern California Bight between 2016 and 2018.

Parasite species
ACANTHOCEPHALA
Corynosoma sp. Lühe 1904
Rhadinorhynchus sp. Lühe 1911
CESTODA
Lacistorhynchus sp. Pintner, 1913
Trypanorhyncha gen. sp.
DIGENEA
Family Didymozoidae
Didymozoidae type 1 Monticelli, 1888
Didymozoidae type 2 Monticelli, 1888
Family Lepocreadiidae
Lepocreadium manteri Olson 1978
Family Lissorchiidae
Asymphylodora atherinopisidis Annereaux 1947
Family Heterophyidae
Galactosomum sp. Looss, 1899
NEMATODA
Acuariidae gen. sp. Railliet, Henry & Sisoff, 1912
Contracaecum (rudolphii) Hartwich, 1964
Anisakis sp. Dujardin, 1845
Hysterothylacium sp. Ward & Mogath, 1917
Onchophora melanocephala (Rudolphi, 1819)
Spirocamallanus pereirai Annereaux 1946

Table 1.5. Overall prevalence (P %), mean intensity (I), and mean abundance (A) of metazoan parasites of *Leuresthes tenuis* in five localities in southern California between March 2016 and June 2018.

	Locality														
	Goleta Beach			**Malibu Beach**			**Cabrillo Beach**			**Seal Beach**			**Pacific Beach**		
Parasite species	P (%)	I	A	P (%)	I	A	P (%)	I	A	P (%)	I	A	P (%)	I	A
BRANCHIURA															
Argulus melanostictus	20.6	1.22	0.25	10.0	1.00	0.10	2.38	1.20	0.03	4.00	1.33	0.05	1.90	1.00	0.02
COPEPODA															
Bomolochus sp.	52.8	1.76	0.93	56.0	1.62	0.91	42.9	1.46	0.62	48.0	1.43	0.69	36.2	1.29	0.47
Caligus olsoni	2.78	1.00	0.03	9.33	1.14	0.11	15.2	1.19	0.18	12.0	1.17	0.14	23.3	1.39	0.32
Caligus macarovi	---	---	---	---	---	---	---	---	---	0.67	1.00	0.01	0.48	1.00	0.005
Caligus rotundigenitalis	0.56	1.00	0.01	---	---	---	0.48	1.00	0.005	---	---	---	---	---	---
Lernaeopodidae gen. sp.	1.11	1.00	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Pandaridae (chalimus) gen. sp.	---	---	---	---	---	---	---	---	---	0.67	1.00	0.01	---	---	---
Pennellidae (chalimus) gen. sp.	0.48	1.00	0.005	---	---	---	---	---	---	---	---	---	---	---	---
ISOPODA															
Elthusa californica	0.56	1.00	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Gnathiidae gen. sp.	---	---	---	---	---	---	---	---	---	---	---	---	0.48	1.00	0.005
MONOGENEA															
Leuresthicola olsoni	61.7	2.14	1.32	38.7	1.48	0.57	37.1	1.56	0.58	38.0	1.65	0.63	18.6	1.44	0.28
ACANTHOCEPHALA															
Corynosoma sp.	0.56	1.00	0.01	---	---	---	---	---	---	---	---	---	---	---	---
Rhadinorhynchus sp.	0.56	1.00	0.01	---	---	---	---	---	---	0.67	1.00	0.01	---	---	---
CESTODA															
Lacistorhyncus sp.	2.22	1.00	0.02	0.67	1.00	0.01	0.95	1.00	0.01	1.33	1.00	0.01	---	---	---
Trypanorhyncha gen. sp.	---	---	---	---	---	---	---	---	---	---	---	---	0.48	1.00	0.005
DIGENEA															
Asymphylodora atherinopisidis	22.8	1.37	0.31	16.0	1.46	0.23	18.6	1.33	0.25	14.0	1.48	0.21	7.62	1.38	0.11
Didymozoidae Pseudomonilicaecum	4.44	1.12	0.05	2.67	1.25	0.03	7.62	1.19	0.09	1.33	1.00	0.10	3.33	1.00	0.03
Didymozoidae Monilicaecum	8.89	1.25	0.11	3.33	1.60	0.05	4.29	1.67	0.07	0.67	2.00	0.01	7.14	1.13	0.08
Galactossomum humbargari	14.4	1.27	0.18	5.33	1.38	0.07	8.57	1.44	0.12	6.67	3.20	0.21	32.9	4.57	1.50
Lepocreadium manteri	---	---	---	0.67	1.00	0.01	3.33	3.00	0.10	2.00	1.00	0.02	10.5	7.00	0.73
NEMATODA															
Acuaridae gen. sp.	---	---	---	---	---	---	---	---	---	---	---	---	0.48	1.00	0.005
Anisakis sp.	---	---	---	0.67	1.00	0.007	0.48	1.00	0.005	0.67	1.00	0.007	---	---	---
Contracaecum (rudolphii)	27.2	2.90	0.79	20.0	3.97	0.79	19.5	2.66	0.52	18.7	2.25	0.42	13.3	2.75	0.37
Hysterothylacium sp.	0.56	1.00	0.001	---	---	---	0.48	1.00	0.005	---	---	---	0.95	1.00	0.01
Onchophora melanocephala	---	---	---	---	---	---	0.48	1.00	0.005	---	---	---	0.48	1.00	0.005
Spirocamallanus pereirai	---	---	---	---	---	---	0.48	1.00	0.005	---	---	---	---	---	---

Table 1.6. Species scores from nMDS analysis with selected species of parasites (prevalence ≥ 10% in at least one locality).

Species	nMDS1	nMDS2	p-value
Ectoparasites			
Argulus melanostictus	-0.5649383	0.3880244	**0.002**
Bomolochus sp.	-0.4662639	0.6792247	**0.001**
Caligus olsoni	0.5892995	-0.2274121	**0.006**
Leuresthicola olsoni	-0.6832100	0.3738839	**0.001**
Endoparasites			
Asymphylodora atherinopsidis	-0.3643487	-0.6178216	**0.001**
Contracaecum (rudolphii)	-0.1247507	-0.5249707	**0.009**
Lepocreadium manteri	0.3010047	0.3742826	**0.037**
Galactosomum sp.	0.8083307	0.3460991	**0.001**

Table 1.7. Analysis of similarity (ANOSIM) results for comparison of parasite component communities among all localities and pairwise comparisons (distance method = Bray-Curtis, permutations = 9,999).

	Abundance		Prevalence	
Locality	R statistic	P-value	R statistic	P-value
All localities	0.371	**<0.001***	0.39	**<0.001***
Goleta Beach X Malibu Beach	0.285	**0.045***	0.307	**0.012***
Goleta Beach X Cabrillo Beach	0.448	**0.006***	0.434	**0.008***
Goleta Beach X Seal Beach	0.676	**0.003***	0.736	**0.002***
Goleta Beach X Pacific Beach	0.843	**0.001***	0.874	**<0.001***
Malibu Beach X Cabrillo Beach	0.071	0.25	0.0525	0.27
Malibu Beach X Seal Beach	0.116	0.16	0.044	0.31
Malibu Beach X Pacific Beach	0.64	**0.001***	0.659	**0.001***
Cabrillo Beach X Seal Beach	-0.176	0.96	-0.0618	0.67
Cabrillo Beach X Pacific Beach	0.613	**0.001***	0.466	**<0.001***
Seal Beach X Pacific Beach	0.478	**0.007***	0.521	**0.003***

CHAPTER 1 - SUPPLEMENTAL MATERIALS

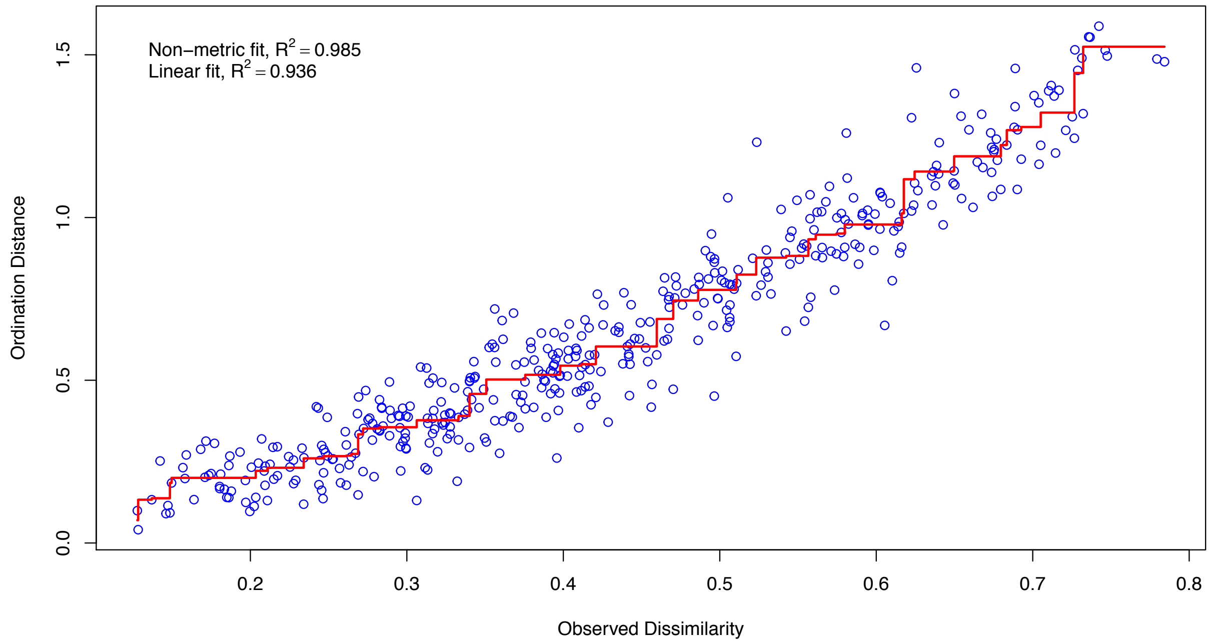

Figure 1.S1. Shepard diagram of the distances in the nMDS plot (Figure 1.6) against the dissimilarities in the Bray-Curtis matrix. The red line represents the fitted non-parametric regression.

Table 1.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Argulus melanostictus* infecting *Leuresthes tenuis* in five localities in southern California.

	Host		Parasite			
Locality	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	180	139.0	45	20.6 (14.9-27.2)	1.2 (1.1-1.4)	0.3 (0.2-0.3)
Malibu Beach	150	140.8	15	10.0 (5.7-16.0)	1.0 (NA)	0.1 (0.1-0.1)
Cabrillo Beach	210	138.7	6	2.4 (0.8-5.5)	1.2 (1.0-2.0)	0.0 (0.0-0.1)
Seal Beach	150	142.8	8	4.0 (1.5-8.5)	1.3 (1.0-1.8)	0.1 (0.0-0.1)
Pacific Beach	210	134.6	4	1.9 (0.5-4.8)	1.0 (NA)	0.0 (0.0-0.0)

Table 2.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Argulus melanostictus* infecting *Leuresthes tenuis* in five localities in southern California by locality and year.

		Host		Parasite			
Locality	**Year**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	2016	90	136.2	23	21.1 (13.2-31.0)	1.2 (1.0-1.6)	0.3 (0.1-0.4)
	2017	60	140.9	14	18.3 (9.5-30.4)	1.3 (1.0-1.6)	0.2 (0.1-0.4)
	2018	30	143.4	8	23.3 (9.9-42.3)	1.1 (1.0-1.7)	0.3 (0.1-0.4)
Malibu Beach	2016	60	140.8	3	5.0 (1.0-13.9)	1.0 (NA)	0.1 (0.0-0.1)
	2017	60	143.4	10	16.7 (8.3-28.5)	1.0 (NA)	0.2 (0.1-0.3)
	2018	30	135.7	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
Cabrillo Beach	2016	120	136.0	1	0.8 (0.0-4.6)	1.0 (NA)	0.0 (NA)
	2017	30	145.6	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	2018	60	140.7	5	6.7 (1.8-16.2)	1.3 (1.0-2.0)	0.1 (0.0-0.2)
Seal Beach	2016	--	--	--	--	--	--
	2017	90	142.6	6	4.4 (1.2-11.0)	1.5 (0.0-2.0)	0.1 (0.0-0.2)
	2018	60	143.2	2	3.3 (0.4-11.5)	1.0 (NA)	0.0 (0.0-0.1)
Pacific Beach	2016	60	133.2	0	0.0 (0.0-6.0)	0.0 (NA)	0.0 (NA)
	2017	120	137.4	3	2.5 (0.5-7.1)	1.0 (NA)	0.0 (0.0-0.1)
	2018	30	126.5	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)

Table 3.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Argulus melanostictus* infecting *Leuresthes tenuis* in five localities in southern California by sample.

		Host		Parasite			
Locality	**Collection date**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	3/25/2016	30	140.7	4	13.3 (3.8-30.7)	1.0 (NA)	0.1 (0.0-0.3)
	4/23/2016	30	134.5	13	30.0 (14.7-49.4)	1.4 (1.1-2.1)	0.4 (0.2-0.7)
	6/21/2016	30	133.3	6	20.0 (7.7-38.6)	1.0 (NA)	0.2 (0.1-0.3)
	4/28/2017	30	145.1	8	20.0 (7.7-38.6)	1.3 (1.0-1.8)	0.3 (0.1-0.5)
	6/11/2017	30	136.8	6	16.7 (5.6-34.7)	1.2 (1.0-2.0)	0.2 (0.1-0.4)
	5/17/2018	30	143.4	8	23.3 (9.9-42.3)	1.1 (1.0-1.6)	0.3 (0.1-0.4)
Malibu Beach	3/24/2016	30	141.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/22/2016	30	140.1	3	10.0 (2.1-26.5)	1.0 (NA)	0.1 (0.0-0.2)
	3/29/2017	30	139.9	4	13.3 (3.8-30.7)	1.0 (NA)	0.1 (0.0-0.2)
	5/26/2017	30	146.9	6	20.0 (7.7-38.6)	1.0 (NA-NA)	0.2 (0.1-0.3)
	5/16/2018	30	135.7	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.1)
Cabrillo Beach	3/25/2016	30	137.2	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/23/2016	30	133.4	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/22/2016	30	135.8	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	6/22/2016	30	137.8	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	5/12/2017	30	145.6	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/2/2018	30	144.0	5	13.3 (3.8-30.7)	1.3 (1.0-2.0)	0.2 (0.0-0.4)
	6/16/2018	30	137.4	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
Seal Beach	4/12/2017	30	142.1	2	3.3 (0.1-17.2)	2.0 (0.0-2.0)	0.1 (0.0-0.2)
	5/12/2017	30	144.5	2	6.7 (0.8-22.1)	1.0 (NA-NA)	0.1 (0.0-0.2)
	6/10/2017	30	141.3	2	3.3 (0.1-17.2)	2.0 (0.0-2.0)	0.1 (0.0-0.2)
	4/2/2018	30	144.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/31/2018	30	141.8	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
Pacific Beach	4/25/2016	30	132.9	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/23/2016	30	133.6	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	3/30/2017	30	137.0	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	4/27/2017	30	140.1	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	5/27/2017	30	137.9	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	6/10/2017	30	134.6	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/1/2018	30	126.5	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)

Table 4.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Bomolochus* sp. infecting *Leuresthes tenuis* in five localities in southern California.

	Host		Parasite			
Locality	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	180	139.0	168	52.8 (45.2-60.2)	1.8 (1.6-1.9)	0.9 (0.8-1.1)
Malibu Beach	150	140.8	136	56.0 (47.7-64.1)	1.6 (1.5-1.9)	0.9 (0.7-1.1)
Cabrillo Beach	210	138.7	131	42.9 (36.1-49.8)	1.5 (1.3-1.6)	0.6 (0.5-0.7)
Seal Beach	150	142.8	103	48.0 (39.8-56.3)	1.4 (1.3-1.6)	0.7 (0.6-0.8)
Pacific Beach	210	134.6	98	36.2 (29.7-43.1)	1.3 (1.2-1.4)	0.5 (0.4-0.6)

Table 5.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Bomolochus* sp. infecting *Leuresthes tenuis* in five localities in southern California by locality and year.

		Host		Parasite			
Locality	**Year**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	2016	90	136.2	62	42.2 (31.9-53.1)	1.6 (1.4-1.9)	0.7 (0.5-0.9)
	2017	60	140.9	80	68.3 (55.0-79.7)	2.0 (1.7-2.3)	1.3 (1.0-1.7)
	2018	30	143.4	25	53.3 (34.3-71.7)	1.6 (1.3-1.9)	0.8 (0.5-1.2)
Malibu Beach	2016	60	140.8	33	38.3 (26.1-51.8)	1.4 (1.2-1.7)	0.6 (0.4-0.8)
	2017	60	143.4	70	68.3 (55.0-79.7)	1.7 (1.4-2.1)	1.2 (0.9-1.5)
	2018	30	135.7	33	66.7 (47.2-82.7)	1.7 (1.4-2.0)	1.1 (0.8-1.5)
Cabrillo Beach	2016	120	136.0	49	30.0 (22.0-39.0)	1.4 (1.2-1.6)	0.4 (0.3-0.5)
	2017	30	145.6	35	73.3 (54.1-87.7)	1.6 (1.4-1.8)	1.2 (0.8-1.4)
	2018	60	140.7	47	53.3 (40.0-66.3)	1.5 (1.3-1.7)	0.8 (0.6-1.0)
Seal Beach	2016	--	--	--	--	--	--
	2017	90	142.6	59	48.9 (38.2-59.7)	1.3 (1.2-1.5)	0.7 (0.5-0.8)
	2018	60	143.2	44	46.7 (33.7-60.0)	1.6 (1.3-2.1)	0.7 (0.5-1.0)
Pacific Beach	2016	60	133.2	13	21.7 (12.1-34.2)	1.0 (NA-NA)	0.2 (0.1-0.3)
	2017	120	137.4	69	40.8 (32.0-50.2)	1.4 (1.3-1.6)	0.6 (0.4-0.7)
	2018	30	126.5	16	46.7 (28.3-65.7)	1.1 (1.0-1.4)	0.5 (0.3-0.7)

Table 6.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Bomolochus* sp. infecting *Leuresthes tenuis* in five localities in southern California by sample.

		Host		Parasite			
Locality	**Collection date**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	3/25/2016	30	140.7	13	30.0 (14.7-49.4)	1.4 (1.1-2.1)	0.4 (0.2-0.7)
	4/23/2016	30	134.5	20	43.3 (25.5-62.6)	1.5 (1.2-2.2)	0.7 (0.4-1.1)
	6/21/2016	30	133.3	29	53.3 (34.3-71.7)	1.8 (1.5-2.4)	1.0 (0.6-1.4)
	4/28/2017	30	145.1	38	70.0 (50.6-85.3)	1.8 (1.5-2.3)	1.3 (0.8-1.6)
	6/11/2017	30	136.8	42	66.7 (47.2-82.7)	2.1 (1.6-2.6)	1.4 (0.9-1.9)
	5/17/2018	30	143.4	25	53.3 (34.3-71.7)	1.6 (1.3-1.9)	0.8 (0.5-1.2)
Malibu Beach	3/24/2016	30	141.5	9	23.3 (9.9-42.3)	1.3 (1.0-1.8)	0.3 (0.1-0.5)
	5/22/2016	30	140.1	24	53.3 (34.3-71.7)	1.5 (1.2-1.9)	0.8 (0.5-1.1)
	3/29/2017	30	139.9	28	60.0 (40.6-77.3)	1.6 (1.2-2.5)	0.9 (0.6-1.5)
	5/26/2017	30	146.9	42	76.7 (57.7-90.1)	1.8 (1.5-2.4)	1.4 (1.0-1.9)
	5/16/2018	30	135.7	33	66.7 (47.2-82.7)	1.7 (1.4-1.9)	1.1 (0.8-1.4)
Cabrillo Beach	3/25/2016	30	137.2	13	30.0 (14.7-49.4)	1.4 (1.1-1.8)	0.4 (0.2-0.7)
	4/23/2016	30	133.4	12	26.7 (12.3-45.9)	1.5 (1.0-2.1)	0.4 (0.2-0.7)
	5/22/2016	30	135.8	16	43.3 (25.5-62.6)	1.2 (1.0-1.5)	0.5 (0.3-0.8)
	6/22/2016	30	137.8	8	20.0 (7.7-38.6)	1.3 (1.0-1.8)	0.3 (0.1-0.5)
	5/12/2017	30	145.6	35	73.3 (54.1-87.7)	1.6 (1.4-1.8)	1.2 (0.8-1.4)
	4/2/2018	30	144.0	27	56.7 (37.4-74.5)	1.6 (1.3-2.0)	0.9 (0.6-1.2)
	6/16/2018	30	137.4	20	50.0 (31.3-68.7)	1.3 (1.1-1.7)	0.7 (0.4-0.9)
Seal Beach	4/12/2017	30	142.1	16	40.0 (22.7-59.4)	1.3 (1.1-1.6)	0.5 (0.3-0.8)
	5/12/2017	30	144.5	18	43.3 (25.5-62.6)	1.4 (1.1-1.8)	0.6 (0.3-0.9)
	6/10/2017	30	141.3	25	63.3 (43.9-80.1)	1.3 (1.1-1.6)	0.8 (0.5-1.1)
	4/2/2018	30	144.5	18	36.7 (19.9-56.1)	1.6 (1.2-3.0)	0.6 (0.3-1.1)
	5/31/2018	30	141.8	26	56.7 (37.4-74.5)	1.5 (1.3-1.9)	0.9 (0.5-1.2)
Pacific Beach	4/25/2016	30	132.9	5	16.7 (5.6-34.7)	1.0 (NA)	0.2 (0.0-0.3)
	5/23/2016	30	133.6	8	26.7 (12.3-45.9)	1.0 (NA)	0.3 (0.1-0.4)
	3/30/2017	30	137.0	12	33.3 (17.3-52.8)	1.2 (1.0-2.0)	0.4 (0.2-0.7)
	4/27/2017	30	140.1	21	50.0 (31.3-68.7)	1.4 (1.1-1.9)	0.7 (0.4-1.0)
	5/27/2017	30	137.9	24	53.3 (34.3-71.7)	1.5 (1.2-1.8)	0.8 (0.5-1.1)
	6/10/2017	30	134.6	12	26.7 (12.3-45.9)	1.5 (1.0-2.1)	0.4 (0.2-0.7)
	5/1/2018	30	126.5	16	46.7 (28.3-65.7)	1.1 (1.0-1.4)	0.5 (0.3-0.7)

Table 7.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Caligus olsoni* infecting *Leuresthes tenuis* in five localities in southern California.

	Host		Parasite			
Locality	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	180	139.0	5	2.78 (0.1-6.4)	1.0 (NA)	0.03 (0.001-0.1)
Malibu Beach	150	140.8	16	9.33 (5.2-15.2)	1.1 (1.0-1.4)	0.1 (0.05-1.7)
Cabrillo Beach	210	138.7	38	15.2 (10.7-20.8)	1.2 (1.1-1.6)	0.2 (1.1-2.6)
Seal Beach	150	142.8	21	12.0 (7.3-18.3)	1.2 (1.0-1.4)	0.1 (0.01-0.2)
Pacific Beach	210	134.6	68	23.3 (17.8-29.6)	1.4 (1.2-2.1)	2.1(0.2-0.5)

Table 8.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Caligus olsoni* infecting *Leuresthes tenuis* in five localities in southern California by locality and year.

		Host		Parasite			
Locality	**Year**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	2016	90	136.2	2	2.2 (0.3-7.8)	1.0 (NA)	0.0 (0.0-0.1)
	2017	60	140.9	3	5.0 (1.0-13.9)	1.0 (NA)	0.1 (0.0-0.1)
	2018	30	143.4	0	0.0 (0.0-11.6)	--	--
Malibu Beach	2016	60	140.8	5	8.3 (2.8-18.4)	1.4 (1.0-2.0)	0.1 (0.0-0.3)
	2017	60	143.4	3	5.0 (1.0-13.9)	1.0 (NA)	0.1 (0.0-0.1)
	2018	30	135.7	6	20.0 (7.7-38.6)	1.0 (NA)	0.2 (0.1-0.3)
Cabrillo Beach	2016	120	136.0	24	20.0 (13.3-28.3)	1.2 (1.0-1.7)	0.2 (0.2-0.4)
	2017	30	145.6	1	3.3 (0.1-17.2)	1.0 (NA-NA)	0.0 (0.0-0.1)
	2018	60	140.7	7	11.7 (4.8-22.6)	1.1 (1.0-2.0)	0.1 (0.1-0.3)
Seal Beach	2016	--	--	--	--	--	--
	2017	90	142.6	12	13.3 (7.1-22.1)	1.1 (1.0-1.4)	0.1 (0.1-0.2)
	2018	60	143.2	6	10.0 (3.8-20.5)	1.3 (1.0-1.8)	0.1 (0.0-0.3)
Pacific Beach	2016	60	133.2	5	8.3 (2.8-18.4)	1.0 (NA)	0.1 (0.0-0.2)
	2017	120	137.4	33	27.5 (19.7-36.4)	1.2 (1.0-1.4)	0.3 (0.2-0.4)
	2018	30	126.5	11	36.7 (19.9-56.1)	2.2 (1.3-4.9)	0.8 (0.4-1.8)

Table 9.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Caligus olsoni* infecting *Leuresthes tenuis* in five localities in southern California by sample.

		Host		Parasite			
Locality	**Collection date**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	3/25/2016	30	140.7	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/23/2016	30	134.5	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	6/21/2016	30	133.3	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/28/2017	30	145.1	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	6/11/2017	30	136.8	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	5/17/2018	30	143.4	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
Malibu Beach	3/24/2016	30	141.5	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	5/22/2016	30	140.1	6	13.3 (3.8-30.7)	1.5 (1.0-2.0)	0.2 (0.0-0.4)
	3/29/2017	30	139.9	3	10.0 (2.1-26.5)	1.0 (NA)	0.1 (0.0-0.2)
	5/26/2017	30	146.9	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/16/2018	30	135.7	6	20.0 (7.7-38.6)	1.0 (NA)	0.2 (0.1-0.3)
Cabrillo Beach	3/25/2016	30	137.2	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	4/23/2016	30	133.4	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	5/22/2016	30	135.8	7	20.0 (7.7-38.6)	1.2 (1.0-1.8)	0.2 (0.1-0.4)
	6/22/2016	30	137.8	18	46.7 (28.3-65.7)	1.3 (1.0-2.2)	0.6 (0.4-1.0)
	5/12/2017	30	145.6	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	4/2/2018	30	144.0	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	6/16/2018	30	137.4	6	16.7 (5.6-34.7)	1.2 (1.0-2.0)	0.2 (0.1-0.4)
Seal Beach	4/12/2017	30	142.1	4	13.3 (3.8-30.7)	1.0 (NA)	0.1 (0.0-0.2)
	5/12/2017	30	144.5	5	13.3 (3.8-30.7)	1.3 (1.0-2.0)	0.2 (0.0-0.3)
	6/10/2017	30	141.3	4	13.3 (3.8-30.7)	1.0 (NA)	0.1 (0.0-0.2)
	4/2/2018	30	144.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/31/2018	30	141.8	8	20.0 (7.7-38.6)	1.3 (1.0-1.8)	0.3 (0.1-0.5)
Pacific Beach	4/25/2016	30	132.9	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	5/23/2016	30	133.6	4	13.3 (3.8-30.7)	1.0 (NA)	0.1 (0.0-0.3)
	3/30/2017	30	137.0	5	16.7 (5.6-34.7)	1.0 (NA)	0.2 (0.0-0.3)
	4/27/2017	30	140.1	12	33.3 (17.3-52.8)	1.2 (1.0-2.1)	0.4 (0.2-0.7)
	5/27/2017	30	137.9	5	16.7 (5.6-34.7)	1.0 (NA)	0.2 (0.0-0.3)
	6/10/2017	30	134.6	17	43.3 (25.5-62.6)	1.3 (1.1-1.8)	0.6 (0.3-0.9)
	5/1/2018	30	126.5	24	36.7 (19.9-56.1)	2.2 (1.3-4.9)	0.8 (0.4-1.8)

Table 10.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Leuresthicola olsoni* infecting *Leuresthes tenuis* in five localities in southern California.

	Host		Parasite			
Locality	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	180	139.0	239	61.7 (54.1 - 68.8)	2.14 (1.89 - 2.46)	1.32 (1.1 - 1.58)
Malibu Beach	150	140.8	86	38.7 (30.8 - 47.0)	1.48 (1.32 - 1.69)	0.57 (0.44 - 0.71)
Cabrillo Beach	210	138.7	122	37.1 (30.6 - 44.1)	1.56 (1.41 - 1.79)	0.58 (0.46 - 0.72)
Seal Beach	150	142.8	94	38.0 (30.2 - 46.3)	1.65 (1.39 - 2.03)	0.63 (0.47 - 0.81)
Pacific Beach	210	134.6	40	17.1 (12.3 - 22.9)	1.11 (1.03 – 1.26)	0.19 (0.13 - 0.25)

Table 11.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Leuresthicola olsoni* infecting *Leuresthes tenuis* in five localities in southern California by locality and year.

		Host		Parasite			
Locality	**Year**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	2016	90	136.2	110	62.2 (51.4-72.2)	2.0 (1.7-2.3)	1.2 (1.0-1.5)
	2017	60	140.9	68	53.3 (40.0-66.3)	2.1 (1.7-3.0)	1.1 (0.8-1.7)
	2018	30	143.4	59	76.7 (57.7-90.1)	2.6 (1.9-3.4)	2.0 (1.4-2.7)
Malibu Beach	2016	60	140.8	24	31.7 (20.3-45.0)	1.3 (1.1-1.6)	0.4 (0.3-0.6)
	2017	60	143.4	38	38.3 (26.1-51.8)	1.7 (1.4-2.0)	0.6 (0.4-0.9)
	2018	30	135.7	24	53.3 (34.3-71.7)	1.5 (1.2-1.9)	0.8 (0.5-1.1)
Cabrillo Beach	2016	120	136.0	47	25.0 (17.5-33.7)	1.6 (1.3-2.0)	0.4 (0.3-0.6)
	2017	30	145.6	24	53.3 (34.3-71.7)	1.5 (1.2-1.9)	0.8 (0.5-1.2)
	2018	60	140.7	51	53.3 (40.0-66.3)	1.6 (1.3-1.9)	0.9 (0.6-1.1)
Seal Beach	2016	--	--	--	--	--	--
	2017	90	142.6	48	35.6 (25.7-46.3)	1.5 (1.2-1.9)	0.5 (0.4-0.8)
	2018	60	143.2	46	41.7 (29.1-55.1)	1.8 (1.4-2.6)	0.8 (0.5-1.2)
Pacific Beach	2016	60	133.2	16	20.0 (10.8-32.3)	1.3 (1.1-1.6)	0.3 (0.1-0.4)
	2017	120	137.4	22	18.3 (11.9-26.4)	1.0 (--)	0.2 (0.1-0.3)
	2018	30	126.5	2	6.7 (0.8-22.1)	1.0 (--)	0.1 (0.0-0.2)

Table 12.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Leuresthicola olsoni* infecting *Leuresthes tenuis* in five localities in southern California by sample.

		Host		Parasite			
Locality	**Collection date**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	3/25/2016	30	140.7	39	73.3 (54.1 - 87.7)	1.8 (1.4-2.2)	1.3 (0.9-1.7)
	4/23/2016	30	134.5	32	56.7 (37.4 - 74.5)	1.9 (1.5-2.3)	1.1 (0.7-1.5)
	6/21/2016	30	133.3	39	56.7 (37.4 - 74.5)	2.3 (1.7-3.1)	1.3 (0.8-1.9)
	4/28/2017	30	145.1	41	56.7 (37.4 - 74.5)	2.4 (1.7-3.8)	1.4 (0.8-2.3)
	6/11/2017	30	136.8	27	50.0 (31.3 - 68.7)	1.8 (1.3-3.3)	0.9 (0.5-1.6)
	5/17/2018	30	143.4	59	76.7 (57.7 - 90.1)	2.6 (1.9-3.5)	2.0 (1.3-2.7)
Malibu Beach	3/24/2016	30	141.5	10	23.3 (9.9 - 42.3)	1.4 (1.0-2.4)	0.3 (0.1-0.6)
	5/22/2016	30	140.1	14	40.0 (22.7 - 59.4)	1.2 (1.0-1.5)	0.5 (0.2-0.7)
	3/29/2017	30	139.9	17	40.0 (22.7 - 59.4)	1.4 (1.1-1.9)	0.6 (0.3-0.9)
	5/26/2017	30	146.9	21	36.7 (19.9 - 56.1)	1.9 (1.5-2.6)	0.7 (0.4-1.1)
	5/16/2018	30	135.7	24	53.3 (34.3 - 71.7)	1.5 (1.2-1.9)	0.8 (0.5-1.1)
Cabrillo Beach	3/25/2016	30	137.2	8	23.3 (9.9 - 42.3)	1.1 (1.0-1.7)	0.3 (0.1-0.5)
	4/23/2016	30	133.4	15	30.0 (14.7 - 49.4)	1.7 (1.1-2.3)	0.5 (0.2-0.9)
	5/22/2016	30	135.8	14	23.3 (9.9 - 42.3)	2.0 (1.4-2.8)	0.5 (0.2-0.9)
	6/22/2016	30	137.8	10	23.3 (9.9 - 42.3)	1.4 (1.0-2.7)	0.3 (0.1-0.7)
	5/12/2017	30	145.6	24	53.3 (34.3 - 71.7)	1.5 (1.2-1.9)	0.8 (0.5-1.2)
	4/2/2018	30	144.0	32	70.0 (50.6 - 85.3)	1.5 (1.3-1.9)	1.1 (0.7-1.4)
	6/16/2018	30	137.4	19	36.7 (19.9 - 56.1)	1.7 (1.3-2.5)	0.6 (0.3-1.0)
Seal Beach	4/12/2017	30	142.1	11	23.3 (9.9 - 42.3)	1.6 (1.0-2.0)	0.4 (0.1-0.7)
	5/12/2017	30	144.5	21	40.0 (22.7 - 59.4)	1.8 (1.2-2.7)	0.7 (0.4-1.2)
	6/10/2017	30	141.3	16	43.3 (25.5 - 62.6)	1.2 (1.0-1.8)	0.5 (0.3-0.8)
	4/2/2018	30	144.5	15	40.0 (22.7 - 59.4)	1.3 (1.0-1.8)	0.5 (0.3-0.8)
	5/31/2018	30	141.8	31	43.3 (25.5 - 62.6)	2.4 (1.6-3.5)	1.0 (0.5-1.7)
Pacific Beach	4/25/2016	30	132.9	5	16.7 (5.64 – 34.7)	1.4 (1.0-2.0)	0.2 (0.1-0.5)
	5/23/2016	30	133.6	7	23.3 (9.9 - 42.3)	1.3 (1.0-1.7)	0.3 (0.1-0.5)
	3/30/2017	30	137.0	2	6.7 (0.8 - 22.1)	1.0 (NA)	0.1 (0.0-0.2)
	4/27/2017	30	140.1	5	16.7 (5.6 - 34.7)	1.0 (NA)	0.2 (0.0-0.3)
	5/27/2017	30	137.9	5	16.7 (5.6 - 34.7)	1.0 (NA)	0.2 (0.0-0.3)
	6/10/2017	30	134.6	10	33.3 (17.3 - 52.8)	1.0 (NA)	0.3 (0.1-0.5)
	5/1/2018	30	126.5	2	6.7 (0.8 - 22.1)	1.0 (NA)	0.1 (0.0-0.2)

Table 13.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Asymphylodora atherinopsidis* infecting *Leuresthes tenuis* in five localities in southern California.

	Host		Parasite			
Locality	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	180	139.0	55	22.8 (16.9-29.6)	1.3 (1.1-1.9)	0.3 (0.2-0.4)
Malibu Beach	150	140.8	33	15.3 (10.0-22.1)	1.4 (1.2-1.8)	0.2 (0.1-0.3)
Cabrillo Beach	210	138.7	50	17.6 (12.7-23.5)	1.4 (1.2-1.7)	0.2 (0.2-0.3)
Seal Beach	150	142.8	31	14.0 (8.9-20.6)	1.5 (1.2-1.9)	0.2 (0.1-0.3)
Pacific Beach	210	134.6	22	7.6 (4.4-12.1)	1.4 (1.1-2.0)	0.1 (0.1-0.2)

Table 14.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Asymphylodora atherinopsidis* infecting *Leuresthes tenuis* in five localities in southern California by locality and year.

		Host		Parasite			
Locality	**Year**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	2016	90	136.2	30	27.8 (18.9-38.2)	1.2 (1.1-1.5)	0.3 (0.2-0.5)
	2017	60	140.9	16	16.7 (8.3-28.5)	1.6 (1.0-4.0)	0.3 (0.1-0.7)
	2018	30	143.4	9	20.0 (7.7-38.6)	1.5 (1.0-2.3)	0.3 (0.1-0.6)
Malibu Beach	2016	60	140.8	23	25.0 (14.7-37.9)	1.5 (1.2-2.0)	0.4 (0.2-0.6)
	2017	60	143.4	1	1.7 (0.0-8.9)	1.0 (NA)	0.0 (0.0-0.1)
	2018	30	135.7	9	23.3 (9.9-42.3)	1.3 (1.0-1.7)	0.3 (0.1-0.5)
Cabrillo Beach	2016	120	136.0	25	15.8 (9.8-23.6)	1.3 (1.1-1.7)	0.2 (0.1-0.3)
	2017	30	145.6	5	16.7 (5.6-34.7)	1.0 (NA-NA)	0.2 (0.0-0.3)
	2018	60	140.7	20	21.7 (12.1-34.2)	1.5 (1.1-2.3)	0.3 (0.2-0.6)
Seal Beach	2016	--	--	--	--	--	--
	2017	90	142.6	14	13.3 (7.1-22.1)	1.2 (1.0-1.9)	0.2 (0.1-0.3)
	2018	60	143.2	17	15.0 (7.1-26.6)	1.9 (1.4-2.4)	0.3 (0.1-0.5)
Pacific Beach	2016	60	133.2	6	8.3 (2.8-18.4)	1.2 (1.0-2.0)	0.1 (0.0-0.2)
	2017	120	137.4	14	7.5 (3.5-13.8)	1.6 (1.0-2.6)	0.1 (0.0-0.2)
	2018	30	126.5	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)

Table 15.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Asymphylodora atherinopsidis* infecting *Leuresthes tenuis* in five localities in southern California by sample.

		Host		Parasite			
Locality	**Collection date**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	3/25/2016	30	140.7	9	30.0 (14.7-49.4)	1.0 (NA)	0.3 (0.1-0.4)
	4/23/2016	30	134.5	14	30.0 (14.7-49.4)	1.6 (1.1-2.1)	0.5 (0.2-0.8)
	6/21/2016	30	133.3	7	23.3 (9.9-42.3)	1.0 (NA)	0.2 (0.1-0.4)
	4/28/2017	30	145.1	3	10.0 (2.1-26.5)	1.0 (NA)	0.1 (0.0-0.2)
	6/11/2017	30	136.8	13	23.3 (9.9-42.3)	1.9 (1.0-5.5)	0.4 (0.1-1.4)
	5/17/2018	30	143.4	9	20.0 (7.7-38.6)	1.5 (1.0-2.5)	0.3 (0.1-0.6)
Malibu Beach	3/24/2016	30	141.5	16	33.3 (17.3-52.8)	1.6 (1.1-2.2)	0.5 (0.2-0.9)
	5/22/2016	30	140.1	7	16.7 (5.6-34.7)	1.4 (1.0-2.0)	0.2 (0.1-0.5)
	3/29/2017	30	139.9	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/26/2017	30	146.9	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	5/16/2018	30	135.7	9	23.3 (9.9-42.3)	1.3 (1.0-1.8)	0.3 (0.1-0.5)
Cabrillo Beach	3/25/2016	30	137.2	7	23.3 (9.9-42.3)	1.0 (NA)	0.2 (0.1-0.4)
	4/23/2016	30	133.4	6	10.0 (2.1-26.5)	2.0 (0.0-2.0)	0.2 (0.0-0.4)
	5/22/2016	30	135.8	6	16.7 (5.6-34.7)	1.2 (1.0-2.0)	0.2 (0.1-0.4)
	6/22/2016	30	137.8	6	13.3 (3.8-30.7)	1.5 (1.0-3.0)	0.2 (0.0-0.5)
	5/12/2017	30	145.6	5	16.7 (5.6-34.7)	1.0 (NA)	0.2 (0.0-0.3)
	4/2/2018	30	144.0	10	23.3 (9.9-42.3)	1.4 (1.0-2.4)	0.3 (0.1-0.6)
	6/16/2018	30	137.4	10	20.0 (7.7-38.6)	1.7 (1.0-3.2)	0.3 (0.1-0.8)
Seal Beach	4/12/2017	30	142.1	8	20.0 (7.7-38.6)	1.3 (1.0-3.0)	0.3 (0.1-0.5)
	5/12/2017	30	144.5	4	13.3 (3.8-30.7)	1.0 (NA)	0.1 (0.0-0.3)
	6/10/2017	30	141.3	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	4/2/2018	30	144.5	9	13.3 (3.8-30.7)	2.3 (2.0-3.0)	0.3 (0.1-0.6)
	5/31/2018	30	141.8	8	16.7 (5.6-34.7)	1.6 (1.0-3.0)	0.3 (0.1-0.6)
Pacific Beach	4/25/2016	30	132.9	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	5/23/2016	30	133.6	4	10.0 (2.1-26.5)	1.3 (1.0-2.0)	0.1 (0.0-0.3)
	3/30/2017	30	137.0	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.1)
	4/27/2017	30	140.1	7	13.3 (3.8-30.7)	1.8 (1.0-4.0)	0.2 (0.1-0.7)
	5/27/2017	30	137.9	5	10.0 (2.1-26.5)	1.7 (1.0-3.0)	0.2 (0.0-0.5)
	6/10/2017	30	134.6	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/1/2018	30	126.5	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)

Table 16.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Galactosomum* sp. infecting *Leuresthes tenuis* in five localities in southern California.

	Host		Parasite			
Locality	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	180	139.0	33	14.4 (9.66-20.4)	1.27 (1.09-1.57)	0.18 (0.12-0.27)
Malibu Beach	150	140.8	11	5.33 (2.33-10.2)	1.38 (1.00-1.78)	0.07 (0.03-0.13)
Cabrillo Beach	210	138.7	26	8.57 (5.16-13.2)	1.44 (1.10-2.29)	0.12 (0.07-0.21)
Seal Beach	150	142.8	32	6.67 (3.24-11.9)	3.2 (1.57-6.00)	0.21 (0.07-0.48)
Pacific Beach	210	134.6	315	32.9 (26.5-39.7)	4.57 (3.39-6.51)	1.5 (1.05-2.32)

Table 17.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Galactosomum* sp. infecting *Leuresthes tenuis* in five localities in southern California by locality and year.

		Host		Parasite			
Locality	**Year**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	2016	90	136.2	20	20.0 (12.3-29.8)	1.1 (1.0-1.4)	0.2 (0.1-0.3)
	2017	60	140.9	7	6.7 (1.8-16.2)	1.8 (1.0-3.0)	0.1 (0.0-0.3)
	2018	30	143.4	6	13.3 (3.8-30.7)	1.5 (1.0-3.0)	0.2 (0.0-0.5)
Malibu Beach	2016	60	140.8	9	10.0 (3.8-20.5)	1.5 (1.0-1.9)	0.2 (0.1-0.3)
	2017	60	143.4	1	1.7 (0.0-8.9)	1.0 (NA-NA)	0.0 (0.0-0.1)
	2018	30	135.7	1	3.3 (0.1-17.2)	1.0 (NA-NA)	0.0 (0.0-0.1)
Cabrillo Beach	2016	120	136.0	19	10.0 (5.3-16.8)	1.6 (1.1-2.8)	0.2 (0.1-0.3)
	2017	30	145.6	2	6.7 (0.8-22.1)	1.0 (NA-NA)	0.1 (0.0-0.2)
	2018	60	140.7	5	6.7 (1.8-16.2)	1.3 (1.0-2.0)	0.1 (0.0-0.2)
Seal Beach	2016	--	--	--	--	--	--
	2017	90	142.6	19	6.7 (2.5-13.9)	3.2 (1.0-7.2)	0.2 (0.0-0.6)
	2018	60	143.2	13	6.7 (1.8-16.2)	3.3 (1.0-8.0)	0.2 (0.0-0.8)
Pacific Beach	2016	60	133.2	123	43.3 (30.6-56.8)	4.7 (2.7-10.6)	2.1 (1.1-4.6)
	2017	120	137.4	129	26.7 (19.0-35.5)	4.0 (2.8-6.3)	1.1 (0.7-1.8)
	2018	30	126.5	63	36.7 (19.9-56.1)	5.7 (3.7-10.5)	2.1 (1.1-4.4)

Table 18.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Galactosomum* sp. infecting *Leuresthes tenuis* in five localities in southern California by sample.

		Host		Parasite			
Locality	**Collection date**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	3/25/2016	30	140.7	7	16.7 (5.6-34.7)	1.4 (1.0-2.0)	0.2 (0.1-0.5)
	4/23/2016	30	134.5	6	20.0 (7.7-38.6)	1.0 (NA-NA)	0.2 (0.1-0.3)
	6/21/2016	30	133.3	7	23.3 (9.9-42.3)	1.0 (NA-NA)	0.2 (0.1-0.4)
	4/28/2017	30	145.1	3	6.7 (0.8-22.1)	1.5 (0.0-2.0)	0.1 (0.0-0.3)
	6/11/2017	30	136.8	4	6.7 (0.8-22.1)	2.0 (0.0-3.0)	0.1 (0.0-0.5)
	5/17/2018	30	143.4	6	13.3 (3.8-30.7)	1.5 (1.0-3.0)	0.2 (0.0-0.5)
Malibu Beach	3/24/2016	30	141.5	6	13.3 (3.8-30.7)	1.5 (1.0-2.0)	0.2 (0.0-0.4)
	5/22/2016	30	140.1	3	6.7 (0.8-22.1)	1.5 (0.0-2.0)	0.1 (0.0-0.3)
	3/29/2017	30	139.9	0	0.0 (0.0-11.6)	NA (NA)	0.0 (NA)
	5/26/2017	30	146.9	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	5/16/2018	30	135.7	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
Cabrillo Beach	3/25/2016	30	137.2	7	10.0 (2.1-26.5)	2.3 (1.0-5.0)	0.2 (0.0-0.9)
	4/23/2016	30	133.4	4	10.0 (2.1-26.5)	1.3 (1.0-2.0)	0.1 (0.0-0.3)
	5/22/2016	30	135.8	3	10.0 (2.1-26.5)	1.0 (NA)	0.1 (0.0-0.2)
	6/22/2016	30	137.8	5	10.0 (2.1-26.5)	1.7 (1.0-3.0)	0.2 (0.0-0.5)
	5/12/2017	30	145.6	2	6.7 (0.8-22.1)	1.0 (NA-NA)	0.1 (0.0-0.2)
	4/2/2018	30	144.0	4	10.0 (2.1-26.5)	1.3 (1.0-2.0)	0.1 (0.0-0.3)
	6/16/2018	30	137.4	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
Seal Beach	4/12/2017	30	142.1	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	5/12/2017	30	144.5	10	6.7 (0.8-22.1)	5.0 (0.0-9.0)	0.3 (0.0-1.5)
	6/10/2017	30	141.3	8	10.0 (2.1-26.5)	2.7 (1.0-6.0)	0.3 (0.0-1.0)
	4/2/2018	30	144.5	0	0.0 (0.0-11.6)	NA (NA)	0.0 (NA)
	5/31/2018	30	141.8	13	13.3 (3.8-30.7)	3.3 (1.0-8.0)	0.4 (0.1-1.7)
Pacific Beach	4/25/2016	30	132.9	41	30.0 (14.7-49.4)	4.6 (1.5-10.3)	1.4 (0.4-3.5)
	5/23/2016	30	133.6	82	56.7 (37.4-74.5)	4.8 (2.2-14.5)	2.7 (1.1-8.5)
	3/30/2017	30	137.0	47	23.3 (9.9-42.3)	6.7 (3.3-12.3)	1.6 (0.6-3.5)
	4/27/2017	30	140.1	19	30.0 (14.7-49.4)	2.1 (1.2-5.0)	0.6 (0.3-1.6)
	5/27/2017	30	137.9	45	33.3 (17.3-52.8)	4.5 (2.2-11.8)	1.5 (0.6-4.2)
	6/10/2017	30	134.6	18	20.0 (7.7-38.6)	3.0 (1.2-11.0)	0.6 (0.2-1.9)
	5/1/2018	30	126.5	63	36.7 (19.9-56.1)	5.7 (3.7-10.8)	2.1 (1.0-4.3)

Table 19.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Lepocreadium manteri* infecting *Leuresthes tenuis* in five localities in southern California.

	Host		Parasite			
Locality	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	180	139.0	0	0.0 (0.0-2.0)	0.0 (NA)	0.0 (NA)
Malibu Beach	150	140.8	1	0.1 (0.02-3.7)	1.0 (NA)	0.01 (0.0-0.02)
Cabrillo Beach	210	138.7	21	3.3 (0.8-5.5)	3.4 (1.0-13.0)	0.1 (0.0-0.3)
Seal Beach	150	142.8	3	2.0 (0.4-5.7)	1.0 (NA-NA)	0.0 (0.0-0.0)
Pacific Beach	210	134.6	154	10.5 (6.7-15.4)	7.0 (3.9-14.1)	0.7 (0.4-1.5)

Table 20.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Lepocreadium manteri* infecting *Leuresthes tenuis* in five localities in southern California by locality and year.

		Host		Parasite			
Locality	**Year**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	2016	90	136.2	0	0.0 (0.0-4.0)	0.0 (NA)	0.0 (NA)
	2017	60	140.9	0	0.0 (0.0-6.0)	0.0 (NA)	0.0 (NA)
	2018	30	143.4	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
Malibu Beach	2016	60	140.8	0	0.0 (0.0-6.0)	0.0 (NA)	0.0 (NA)
	2017	60	143.4	0	0.0 (0.0-6.0)	0.0 (NA)	0.0 (NA)
	2018	30	135.7	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
Cabrillo Beach	2016	120	136.0	15	2.5 (0.5-7.1)	5.0 (1.0-13.0)	0.1 (0.0-0.6)
	2017	30	145.6	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	2018	60	140.7	2	3.3 (0.4-11.5)	1.0 (NA)	0.0 (0.0-0.1)
Seal Beach	2016	--	--	--	--	--	--
	2017	90	142.6	0	0.0 (0.0-4.0)	0.0 (NA)	0.0 (NA)
	2018	60	143.2	3	5.0 (1.0-13.9)	1.0 (NA-NA)	0.1 (0.0-0.1)
Pacific Beach	2016	60	133.2	123	20.0 (10.8-32.3)	10.3 (4.6-20.8)	2.1 (0.8-4.8)
	2017	120	137.4	15	5.8 (2.4-11.6)	2.1 (1.0-7.0)	0.1 (0.0-0.4)
	2018	30	126.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)

Table 21.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Lepocreadium manteri* infecting *Leuresthes tenuis* in five localities in southern California by sample.

		Host		Parasite			
Locality	**Collection date**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	3/25/2016	30	140.7	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/23/2016	30	134.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	6/21/2016	30	133.3	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/28/2017	30	145.1	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	6/11/2017	30	136.8	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/17/2018	30	143.4	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
Malibu Beach	3/24/2016	30	141.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/22/2016	30	140.1	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	3/29/2017	30	139.9	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/26/2017	30	146.9	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/16/2018	30	135.7	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
Cabrillo Beach	3/25/2016	30	137.2	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/23/2016	30	133.4	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	5/22/2016	30	135.8	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	6/22/2016	30	137.8	14	6.7 (0.8-22.1)	7.0 (0.0-13.0)	0.5 (0.0-2.2)
	5/12/2017	30	145.6	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/2/2018	30	144.0	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	6/16/2018	30	137.4	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
Seal Beach	4/12/2017	30	142.1	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/12/2017	30	144.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	6/10/2017	30	141.3	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/2/2018	30	144.5	1	3.3 (0.1-17.2)	1.0 (NA)	0.0 (0.0-0.1)
	5/31/2018	30	141.8	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
Pacific Beach	4/25/2016	30	132.9	98	20.0 (7.7-38.6)	16.3 (3.0-31.9)	3.3 (1.0-9.1)
	5/23/2016	30	133.6	25	20.0 (7.7-38.6)	4.2 (2.0-6.8)	0.8 (0.3-1.8)
	3/30/2017	30	137.0	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	4/27/2017	30	140.1	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)
	5/27/2017	30	137.9	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	6/10/2017	30	134.6	13	16.7 (5.6-34.7)	2.6 (1.0-9.0)	0.4 (0.1-1.6)
	5/1/2018	30	126.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)

Table 22.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Contracaecum (rudolphii)* infecting *Leuresthes tenuis* in five localities in southern California.

	Host		Parasite			
Locality	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	180	139.0	132	25.6 (19.4-32.6)	2.9 (2.0-4.4)	0.7 (0.5-1.2)
Malibu Beach	150	140.8	117	19.3 (13.3-26.6)	4.0 (2.1-10.1)	0.8 (0.4-2.0)
Cabrillo Beach	210	138.7	100	19.0 (14.0-25.0)	2.5 (1.9-3.5)	0.5 (0.3-0.7)
Seal Beach	150	142.8	62	18.0 (12.2-25.1)	2.3 (1.8-3.0)	0.4 (0.3-0.6)
Pacific Beach	210	134.6	71	11.9 (7.9-17.1)	2.8 (1.8-5.1)	0.3 (0.2-0.7)

Table 23.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Contracaecum (rudolphii)* infecting *Leuresthes tenuis* in five localities in southern California by locality and year.

		Host		Parasite			
Locality	Year	n	Mean SL (mm)	n	Prevalence %	Mean Intensity	Mean Abundance
Goleta Beach	2016	90	136.2	115	36.7 (26.8-47.5)	3.5 (2.4-5.4)	1.3 (0.8-2.1)
	2017	60	140.9	9	13.3 (5.9-24.6)	1.1 (1.0-1.6)	0.2 (0.1-0.3)
	2018	30	143.4	8	16.7 (5.6-34.7)	1.6 (1.0-2.0)	0.3 (0.1-0.5)
Malibu Beach	2016	60	140.8	81	30.0 (18.8-43.2)	4.5 (2.1-14.8)	1.4 (0.5-4.6)
	2017	60	143.4	32	13.3 (5.9-24.6)	4.0 (1.5-14.8)	0.5 (0.2-1.9)
	2018	30	135.7	4	10.0 (2.1-26.5)	1.3 (1.0-2.0)	0.1 (0.0-0.3)
Cabrillo Beach	2016	120	136.0	71	20.8 (14.0-29.2)	2.8 (1.9-4.2)	0.6 (0.3-1.0)
	2017	30	145.6	7	16.7 (5.6-34.7)	1.4 (1.0-2.0)	0.2 (0.1-0.5)
	2018	60	140.7	22	16.7 (8.3-28.5)	2.2 (1.5-4.2)	0.4 (0.2-0.8)
Seal Beach	2016	--	--	--	--	--	--
	2017	90	142.6	32	15.6 (8.8-24.7)	2.3 (1.6-3.0)	0.4 (0.2-0.6)
	2018	60	143.2	30	21.7 (12.1-34.2)	2.3 (1.5-3.7)	0.5 (0.2-0.9)
Pacific Beach	2016	60	133.2	44	15.0 (7.1-26.6)	4.9 (2.1-10.1)	0.7 (0.3-1.8)
	2017	120	137.4	27	13.3 (7.8-20.7)	1.7 (1.3-2.5)	0.2 (0.1-0.4)
	2018	30	126.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)

Table 24.S1. Prevalence (P), mean intensity (MI), and mean abundance (MA) of *Contracaecum (rudolphii)* infecting *Leuresthes tenuis* in five localities in southern California by sample.

		Host		Parasite			
Locality	**Collection date**	**n**	**Mean SL (mm)**	**n**	**Prevalence %**	**Mean Intensity**	**Mean Abundance**
Goleta Beach	3/25/2016	30	140.7	47	50.0 (31.3-68.7)	3.1 (1.9-5.3)	1.6 (0.8-2.8)
	4/23/2016	30	134.5	43	23.3 (9.9-42.3)	6.1 (1.8-14.0)	1.4 (0.3-3.8)
	6/21/2016	30	133.3	25	36.7 (19.9-56.1)	2.3 (1.6-3.2)	0.8 (0.4-1.4)
	4/28/2017	30	145.1	5	13.3 (3.8-30.7)	1.3 (1.0-2.0)	0.2 (0.0-0.4)
	6/11/2017	30	136.8	4	13.3 (3.8-30.7)	1.0 (NA)	0.1 (0.0-0.3)
	5/17/2018	30	143.4	8	16.7 (5.6-34.7)	1.6 (1.0-2.0)	0.3 (0.1-0.5)
Malibu Beach	3/24/2016	30	141.5	63	30.0 (14.7-49.4)	7.0 (2.0-24.2)	2.1 (0.5-7.9)
	5/22/2016	30	140.1	18	30.0 (14.7-49.4)	2.0 (1.3-2.4)	0.6 (0.3-1.0)
	3/29/2017	30	139.9	29	20.0 (7.7-38.6)	4.8 (1.5-15.2)	1.0 (0.2-4.1)
	5/26/2017	30	146.9	3	6.7 (0.8-22.1)	1.5 (0.0-2.0)	0.1 (0.0-0.3)
	5/16/2018	30	135.7	4	10.0 (2.1-26.5)	1.3 (1.0-2.0)	0.1 (0.0-0.3)
Cabrillo Beach	3/25/2016	30	137.2	9	20.0 (7.7-38.6)	1.5 (1.0-2.3)	0.3 (0.1-0.6)
	4/23/2016	30	133.4	29	26.7 (12.3-45.9)	3.6 (1.3-6.6)	1.0 (0.3-2.1)
	5/22/2016	30	135.8	10	16.7 (5.6-34.7)	2.0 (1.0-5.0)	0.3 (0.1-0.9)
	6/22/2016	30	137.8	23	20.0 (7.7-38.6)	3.8 (1.8-8.8)	0.8 (0.2-2.0)
	5/12/2017	30	145.6	7	16.7 (5.6-34.7)	1.4 (1.0-2.0)	0.2 (0.1-0.5)
	4/2/2018	30	144.0	7	10.0 (2.1-26.5)	2.3 (2.0-3.0)	0.2 (0.1-0.6)
	6/16/2018	30	137.4	15	23.3 (9.9-42.3)	2.1 (1.1-5.0)	0.5 (0.2-1.3)
Seal Beach	4/12/2017	30	142.1	16	23.3 (9.9-42.3)	2.3 (1.2-3.4)	0.5 (0.2-1.1)
	5/12/2017	30	144.5	9	13.3 (3.8-30.7)	2.3 (1.0-4.0)	0.3 (0.1-0.8)
	6/10/2017	30	141.3	7	10.0 (2.1-26.5)	2.3 (0.0-3.0)	0.2 (0.0-0.6)
	4/2/2018	30	144.5	8	16.7 (5.6-34.7)	1.6 (1.0-3.0)	0.3 (0.1-0.5)
	5/31/2018	30	141.8	22	26.7 (12.3-45.9)	2.8 (1.3-4.5)	0.7 (0.3-1.5)
Pacific Beach	4/25/2016	30	132.9	25	23.3 (9.9-42.3)	3.6 (1.7-7.7)	0.8 (0.3-2.2)
	5/23/2016	30	133.6	19	6.7 (0.8-22.1)	9.5 (0.0-17.0)	0.6 (0.0-2.4)
	3/30/2017	30	137.0	5	10.0 (2.1-26.5)	1.7 (1.0-3.0)	0.2 (0.0-0.5)
	4/27/2017	30	140.1	7	13.3 (3.8-30.7)	1.8 (1.0-3.0)	0.2 (0.0-0.5)
	5/27/2017	30	137.9	2	6.7 (0.8-22.1)	1.0 (NA)	0.1 (0.0-0.2)
	6/10/2017	30	134.6	13	23.3 (9.9-42.3)	1.9 (1.1-3.7)	0.4 (0.2-1.0)
	5/1/2018	30	126.5	0	0.0 (0.0-11.6)	0.0 (NA)	0.0 (NA)

REFERENCES

Annereaux, R. F. 1946. A new nematode, *Procamallanus pereirai*, with a key to the genus. *Transactions of the American Microscopical Society* 65: 299–303.

Annereaux, R. F. 1947. Three new trematodes from marine fishes of California. *Transactions of the American Microscopical Society* 66: 249–255.

Benz, G. W., Otting, R. L. and Case, A. 1995. Redescription of *Argulus melanostictus* (Branchiura: Argulidae), a parasite of California grunion (*Leuresthes tenuis*: Atherinidae), with notes regarding chemical control of *A. melanostictus* in a captive host population. *The Journal of Parasitology* 81: 754–761.

Brooks, D. R. 1985. Historical ecology - a new approach to studying the evolution of ecological associations. *Annals of the Missouri Botanical Garden* 72: 660–680.

Bush, A. O., Lafferty, K. D., Lotz, J. M., and Shostak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *The Journal of Parasitology* 83: 575–583.

Byers, J. E. 2020. Effects of climate change on parasites and disease in estuarine and nearshore environments. *PLOS Biology* 18: e3000743.

Catalano, S. R., Whittington, I. D., Donnellan, S. C., and Gillanders, B. M. 2014. Parasites as biological tags to assess host population structure: Guidelines, recent genetic advances and comments on a holistic approach. *International Journal for Parasitology: Parasites and Wildlife* 3: 220–226.

Defeo, O., McLachlan, A., Schoeman, D. S., Schlacher, T. A., Dugan, J., Jones, A., Lastra, M., Scapini, F. 2009. Threats to sandy beach ecosystems: A review. *Estuarine, Coastal and Shelf Science* 81: 1–12.

Dobson, A., Lafferty, K. D., Kuris, A. M., Hechinger, R. F., and Jetz, W. 2008. Homage to Linnaeus: How many parasites? How many hosts? *Proceedings of the National Academy of Sciences* 105: 11482–11489.

Fraser, C. M. 1920. Copepods parasitic on fish from the Vancouver Island region. *Proceedings and transactions of the Royal Society of Canada* (5) (3) 13: 45–67.

Gaida, I. H., Buth, D. G., Matthews, S. D., Snow, A. L., Luo, S. B., and Kutsuna, S. 2003. Allozymic variation and population structure of the California grunion, *Leuresthes tenuis* (Atheriniformes: Atherinopsidae). *Copeia* 2003: 594–600.

Garcia-Vedrenne, A. E., Quintana, A. C. E., DeRogatis, A. M., Martyn, K., Kuris, A. M., and Hechinger, R. F. 2016. Social organization in parasitic flatworms—four additional echinostomoid trematodes have a soldier caste and one does not. *The Journal of Parasitology* 102: 11–20.

Gómez, A., and Nichols, E. 2013. Neglected wild life: Parasitic biodiversity as a conservation target. *International Journal for Parasitology: Parasites and Wildlife* 2: 222–227.

Hafner, M. S., and Nadler, S. A. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. *Nature* 332: 258–259.

Henriquez, V. P., González, M. T., Licandeo, R., and Carvajal, J. 2011. Metazoan parasite communities of rock cod *Eleginops maclovinus* along southern Chilean coast and their use as biological tags at a local spatial scale. *Journal of Fish Biology* 79: 1851–1865.

Higgins, B. A., and Horn, M. H. 2014. Suction among pickers: jaw mechanics, dietary breadth and feeding behaviour in beach-spawning Leuresthes spp. compared with their relatives. *Journal of Fish Biology* 84: 1689–1707.

Ho, J. S. and C. L. Lin. 2009. *Bomolochus bramus* n. sp. (Copepoda, Poecilostomatoida, Bomolochidae) from the pomfrets (Bramidae) off Taiwan, with a list of nominal species and key to valid species of *Bomolochus* von Nordmann, 1832. *Zootaxa* 2092:47-57.

Horn, M. H., Gawlicka, A. K., German, D. P., Logothetis, E. A., Cavanagh, J. W., and Boyle, K. S. 2006. Structure and function of the stomachless digestive system in three related species of New World silverside fishes (Atherinopsidae) representing herbivory, omnivory, and carnivory. *Marine Biology* 149: 1237–1245.

Jacobson, K., Baldwin, R., Banks, M., and Emmett, R. 2019. Use of parasites to clarify residency and migration patterns of Pacific sardine (*Sardinops sagax*) in the California Current. *Fishery Bulletin* 117: 72–86.

Johnson, P. B., Martin, K. L., Vandergon, T. L., Honeycutt, R. L., Burton, R. S., and Fry, A. 2009. Microsatellite and mitochondrial genetic comparisons between northern and southern populations of California grunion (*Leuresthes tenuis*). *Copeia* 2009: 465–474.

Kabata, Z. 1963. Parasites as biological tags. *International Commission on Northwest Atlantic Fisheries, Special Publication* 31–37.

Kabata, Z. 1988. Copepoda and Branchiura. In: L. Margolis and Z. Kabata (eds.), Guide to the parasites of fishes of Canada. Part II – Crustacea: 3-127. (Canadian Special Publication in Fisheries and Aquatic Sciences, Ottawa).

Klapper, R., Kochmann, J., O'Hara, R. B., Karl, H., and Kuhn, T. 2016. Parasites as biological tags for stock discrimination of beaked redfish (*Sebastes mentella*): parasite infra-communities vs. limited resolution of cytochrome markers. *PLoS ONE*, *11*, e0153964.

Klassen, G. J. 1992. Coevolution: A history of the macroevolutionary approach to studying host-parasite associations. *The Journal of Parasitology* 78: 573–587.

Kuris, A. M., and Lafferty, K. D. 1994. Community structure: larval trematodes in snail hosts. *Annual Review of Ecology and Systematics* 25: 189–217.

Lafferty, K. D. 2008. Ecosystem consequences of fish parasites*. *Journal of Fish Biology* 73: 2083–2093.

Lafferty, K. D. 2013. Parasites in marine food webs. *Bulletin of Marine Science* 89: 123–134.

Lafferty, K. D., and Kuris, A. M. 2009. Parasitic castration: the evolution and ecology of body snatchers. *Trends in Parasitology* 25: 564–572.

Lafferty, K. D., and Morris, A. K. 1996. Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* 77: 1390.

Love, M. S., and Passarelli, J. K. 2020. *Miller and Lea's Guide to the Coastal Marine Fishes of California*, 2nd ed. Davis, CA: UC Agriculture and Natural Resources Publications.

MacKenzie, K. 2002. Parasites as biological tags in population studies of marine organisms: an update. *Parasitology* 124: S153–S163.

MacKenzie, K., and Abaunza, P. 1998. Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods. *Fisheries Research* 38: 45–56.

Madinabeitia, I., and Nagasawa, K. 2013. Double-netting: an alternative approach for the recovery of parasitic copepods from finfishes. *Journal of Natural History* 47: 529–541.

Marcogliese, D. J. 2004. Parasites: Small players with crucial roles in the ecological theater. *EcoHealth* 1, 151–164.

Marcogliese, D. J. 2005. Parasites of the superorganism: Are they indicators of ecosystem health? *International Journal for Parasitology* 35, 705–716.

Martin, K. L. M. 2015. Beach-Spawning Fishes. CRC Press, Boca Raton.

Martin, K. L. M., Pierce, E. A., Quach, V. V., and Studer, M. 2020. Population trends of beach-spawning California grunion Leuresthes tenuis monitored by citizen scientists. ICES Journal of Marine Science 77 (6): 2226-2233.

Martin, K. L. M., Schaadt, M. and Lawrenz-Miller, S. 2021. The Walker Scale: Details of a method for assessing beach-spawning runs of California Grunion *Leuresthes tenuis* (Atheriniformes: Atherinopsidae). *Ichthyology and Herpetology* 109, 4 (in press).

Morand, S. 2015. (macro-) Evolutionary ecology of parasite diversity: From determinants of parasite species richness to host diversification. *International Journal for Parasitology: Parasites and Wildlife* 4: 80–87.

Moser, M. and L. C. Haldorson. 1982. Parasites of two species of surfperch (Embiotocidae) from seven Pacific coast locales. *The Journal of Parasitology* 68:733-735.

Moser, M., and Hsieh, J. 1992. Biological tags for stock separation in Pacific herring *Clupea harengus pallasi* in California. *The Journal of Parasitology* 78: 54.

Mosquera, J., de Castro, M. and Gómez-Gesteira, M. 2003. Parasites as biological tags of fish populations: Advantages and limitations. *Comments on Theorethical Biology* 8, 69–91.

Olson, A. C. 1955. Parasites of the Grunion, *Leuresthes tenuis* (Ayres). Ph.D. Dissertation. Oregon State College, Corvallis, Oregon.

Olson, A. C. 1972. *Argulus melanostictus* and other parasitic crustaceans on the California grunion, *Leuresthes tenuis* (Osteichthyes: Atherinidae). *The Journal of Parasitology* 58, 1201.

Olson, A. C. 1977. *Asymphylodora atherinopsidis* (Trematoda: Monorchiidae) from the California grunion, *Leuresthes tenuis*, including a redescription. *The Journal of Parasitology* 63, 295.

Olson, A. C. 1978. *Lepocreadium manteri* sp. n. (Trematoda: Lepocreadiidae) from the California grunion, Leuresthes tenuis, and its hyperparasitic microsporidan. *Proceedings of the Helminthological Society of Washington* 45: 155–157.

Olson, L. J. 1979. Host-parasite associations of the grunions *Leuresthes sardina* and *Leuresthes tenuis* from the Gulf of California and California. Ph.D. Dissertation. The University of Arizona. Tucson, Arizona.

Park, J. T. 1936. New trematodes from birds, *Plagiorchis noblei* sp. nov. (Plagiorchidae) and *Galactosomum humbargari* sp. nov. (Heterophyidae). *Transactions of the American Microscopical Society* 55: 360–365.

Pearse, A. S. 1953. A new copepod parasite from the grunion. *The Journal of Parasitology* 39, 332.

Poulin, R. 2004. Macroecological patterns of species richness in parasite assemblages. *Basic and Applied Ecology* 5: 423–434.

Poulin, R. 2007. *Evolutionary Ecology of Parasites*, Second Edition. Princeton: Princeton University Press.

Poulin, R. 2018. Best practice guidelines for studies of parasite community ecology. *Journal of helminthology* 93: 8–11.

Poulin, R., and Morand, S. 2000. The diversity of parasites. *The Quarterly Review of Biology* 75: 277–293.

Price, E. W. 1962. North American monogenetic trematodes. XI. The Family Heteraxinidae. *The Journal of Parasitology* 48: 402.

R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Roberts D., Lea, R. N. and Martin, K. L. M. 2007. First record of the occurrence of the California Grunion, *Leuresthes tenuis*, in Tomales Bay, California; a northern extension of the species. California Fish & Game 93: 107-110.

Rocha, C. F. D., Bergallo, H. G., and Bittencourt, E. B. 2016. More than just invisible inhabitants: parasites are important but neglected components of the biodiversity. *Zoologia* 33 (3): e20150198.

Santos, A. J., Frederick, A. R., Higgins, B. A., Carrillo, A., Carter, A. L., Dickson, K. A., Carter, A. L., Horn, M. H. 2018. The beach-spawning California grunion Leuresthes tenuis eats and digests conspecific eggs. *Journal of Fish Biology* 93: 282–289.

Schoeman, D. S., Schlacher, T. A., and Defeo, O. 2014. Climate-change impacts on sandy-beach biota: crossing a line in the sand. *Global Change Biology* 20: 2383–2392.

Stock, J. H. 1955. A new *Bomolochus* (Copepoda parasitica) from the California grunion. *Beaufortia*, 5 (49): 55-59.

Stunkard, H. W. 1959. The morphology and life-history of the digenetic trematode, *Asymphylodora amnicolae* n. sp.; the possible significance of progenesis for the phylogeny of the Digenea. *Biological Bulletin* 117: 562–581.

Stunkard, H. W. 1972. Observations on the morphology and life-history of the digenetic trematode, *Lepocreadium setiferoides* (Miller and Northup, 1926) Martin, 1938. *Biological Bulletin* 142: 326–334.

Sures, B., Nachev, M., Selbach, C., and Marcogliese, D. J. 2017. Parasite responses to pollution: what we know and where we go in 'Environmental Parasitology.' *Parasites and Vectors* 10(1): 65.

Timi, J. T. 2007. Parasites as biological tags for stock discrimination in marine fish from South American Atlantic waters. *Journal of Helminthology* 81: 107–111.

Timi, J. T., Lanfranchi, A. L., and Luque, J. L. 2010. Similarity in parasite communities of the teleost fish *Pinguipes brasilianus* in the southwestern Atlantic: Infracommunities as a tool to detect geographical patterns. *International Journal for Parasitology* 40: 243–254.

Timi, J. T., and Poulin, R. 2020. Why ignoring parasites in fish ecology is a mistake. *International Journal for Parasitology* 50: 1–7.

Truong, T. N., Warren, M. B., Ksepka, S. P., Curran, S. S., and Bullard, S. A. 2021. *Posthovitellinum psiloterminae* n. gen., n. sp. (Digenea: Lissorchiidae) Infecting the Intestine of *Cyclocheilos enoplos* (Cypriniformes: Cyprinidae) in the Mekong River, Vietnam. *Journal of Parasitology* 107: 431–445.

Vervoort, W. 1964. Notes on Bomolochidae (Copepoda), I. A redescription of *Parabomolochus* sp. (Fraser, 1920) and notes on its synonymy. *Crustaceana*, 6: 291–302.

Vidal-Martínez, V. M., Velázquez-Abunader, I., Centeno-Chalé, O. A., May-Tec, A. L., Soler-Jiménez, L. C., Pech, D., Mariño-Tapia, I., Enriquez, C., Zapata-Pérez, O., Herrera-Silveira, J., Hernández-Mena, D. I., Herzka, S. Z., Ordoñez-López, U., Aguirre-Macedo, M. L. 2019. Metazoan parasite infracommunities of the dusky flounder (*Syacium papillosum*) as bioindicators of environmental conditions in the continental shelf of the Yucatan Peninsula, Mexico. *Parasites and Vectors* 12: 277.

Walker, B. W. 1949. Periodicity of spawning by the grunion, *Leuresthes tenuis*, an Atherine Fish. Ph.D. Dissertation. University California Los Angeles. Los Angeles, California.

Walker, B. W. 1952. A Guide to the Grunion. *The American Biology Teacher* 76: 409–420.

Wilson, C. B. 1935. Parasitic copepods from the Pacific Coast. *American Midland Naturalist* 16: 776–797.

Chapter 2

Redescription of *Caligus olsoni* Pearse, 1953 (Copepoda: Caligidae), a parasite of California grunion *Leuresthes tenuis*, (Ayres, 1860) (Atherinopsidae) and other fishes in the northeast Pacific

Bruno Passarelli[1] and Danny Tang[2]

[1]Department of Ecology and Evolutionary Biology, University of California Los Angeles, California, 90095-7246, U.S.A.
[2]Environmental Laboratory and Ocean Monitoring Division, Orange County Sanitation District, 10844 Ellis Avenue, Fountain Valley, California 92708-7018, U.S.A.

ABSTRACT: Adult male and female *Caligus olsoni* Pearse, 1953 are redescribed based on detailed examination of type specimens and recently collected specimens of both sexes obtained from its type host, the California grunion *Leuresthes tenuis* (Ayres 1860), collected in southern California, U.S.A., and three other hosts: two atherinopsids (jacksmelt, *Atherinopsis californiensis* Girard, 1854, collected in southern California, U.S.A. and Gulf grunion, *Leuresthes sardina* (Jenkins and Everman, 1889), collected in the Gulf of California, Mexico) and one sciaenid (white seabass, *Atractoscion nobilis* (Ayres, 1860), collected in southern California, U.S.A.). We compared *C. olsoni* to another species in the *Caligus pseudorhombi* species-group, *Caligus serratus* Shiino, 1965. The descriptions of *C. serratus* by Shiino (1965) and Morales-Serna *et al*. (2013) match our specimens of *C. olsoni* in nearly every detail. In light of the morphological similarities observed between *C. olsoni* and *C. serratus*, we propose to treat *C. serratus* as a junior subjective synonym of *C. olsoni*. We provide an updated record on the species of *Caligus* reported from fish hosts collected in California, U.S.A., and an updated list of fish hosts for *C. olsoni*.

INTRODUCTION

The family Caligidae Burnmeister, 1835, also known as sea lice, is the most species-rich family of parasitic copepods of marine fishes, with over 30 valid genera and 509 valid species (Dojiri and Ho 2013; Walter and Boxshall 2021). Although severe infestations in wild populations of hosts are uncommon, many species of sea lice, especially of the genera *Caligus* and *Lepeophtheirus*, are pests in aquaculture of marine and brackish water fishes, resulting in significant economic losses (Costello 2009; Shinn *et al.* 2015). *Caligus* Müller, 1785 is the largest genus in the family Caligidae with 267 valid described species (Walter and Boxshall 2021). To help navigate this relatively large genus, Boxshall and El-Rashidy (2009) and Boxshall (2018) defined five distinct species groups within the genus *Caligus*, based around the following species: *C. bonito* Wilson, 1905, *C. confusus* Pillai, 1961, *C. diaphanus* von Nordmann, 1832, *C. macarovi* Gusev, 1951 and *C. productus* Dana, 1852. Recently, Ohtsuka and Boxshall (2019) proposed a sixth species group based on *C. pseudorhombi*. Presently, 12 species of *Caligus*, from various species groups, have been reported from 14 fish families along the California coast (Table 2.1).

Caligus olsoni Pearse, 1953 is a parasite of the California grunion *Leuresthes tenuis* (Ayres, 1860). Prior to this study, *C. olsoni* has been reported to infect only its type host, *L. tenuis*, in nearshore waters of California and Baja California (Pearse 1953; Olson 1955, 1972) and the type host's sister species, the Gulf grunion *Leuresthes sardina* (Jenkins and Everman, 1889), in the Gulf of California, Mexico (Olson 1979). While these reports on *C. olsoni* suggest that this species is relatively host specific, a morphologically similar species, *Caligus serratus* Shiino 1965, has been reported to infect many species of marine fishes in California and Baja California (Morales-Serna *et al.* 2013, 2014). *C. serratus* was redescribed by Morales-Serna *et* *al.* (2013) but *C. olsoni* was not considered in their study. *Caligus olsoni* is one of the species included in the *C. pseudorhombi* species group recently proposed by Ohtsuka and Boxshall (2019). Although not listed in Ohtsuka and Boxshall (2019), *C. serratus* is also likely to be part of the *C. pseudorhombi* species group, especially considering morphological similarities shared with *C. olsoni*. However, the original description of *C. olsoni* (Pearse, 1953) is not up to modern standards, thus it is necessary to redescribe *C. olsoni* to include morphological details important in denoting species identity and allowing for meaningful comparisons to morphologically similar species.

We recently obtained specimens of *C. olsoni* from California grunion *L. tenuis* and three other host species collected in California, U.S.A. and in the northern Gulf of California, Mexico. In light of the advances in taxonomic descriptions in the several decades since *C. olsoni* was first described, here we redescribe *C. olsoni* based on detailed examinations of both the syntypes and our newly collected specimens representing both sexes.

MATERIALS AND METHODS

Most of the specimens of *C. olsoni* were obtained from samples of *L. tenuis* collected during grunion spawning runs in southern California between March 2015 and June 2018. Hosts were collected by hand, placed individually in plastic bags, and frozen until inspection. Additionally, specimens of *C. olsoni* were obtained from three other hosts: two atherinopsids (jacksmelt, *A. californiensis* Girard, 1854 collected in southern California, U.S.A., and Gulf grunion, *L. sardina* collected in the northern Gulf of California, Mexico) and one sciaenid (white seabass, *A. nobilis* (Ayres, 1860) collected in southern California, U.S.A.). Host species, localities, collection dates, and specimens of *C. olsoni* examined are listed on Table 2.2. All copepod samples were preserved in 70% or 95% ethanol upon removal from the host.

Type material of *C. olsoni* deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., as well as specimens of *C. serratus* from Morales-Serna *et al.* (2011) and *Caligus clemensi* Parker and Margolis, 1964 collected off British Columbia, Canada, were also examined for comparative purposes: 1 female syntype mounted on a glass slide (USNM 93733), 1 male syntype mounted on a glass slide (USNM 93734), and 1 poorly preserved female voucher mounted on a glass slide (USNM 93735) of *C. olsoni* from *L. tenuis*, collected by A. C. Olson on 4 July 1950 in San Diego Bay, California, U.S.A. Seven females and 8 males of *Caligus serratus* from Morales-Serna *et al.* (2011), collected from *Sphoeroides annulatus* (Jenyns, 1842), Santa María La Reforma lagoon, Sinaloa, Mexico. Twelve females and 19 males of *C. clemensi*, from farmed Atlantic salmon, *Salmo salar* Linnaeus, 1758, collected by S. Jones in March 2018 from British Columbia, Canada.

Copepod specimens were examined using an Olympus SZX10 dissection microscope and an Olympus BX53 compound microscope equipped with differential interference contrast optics. Selected specimens were soaked in lactophenol for at least 24 hours and then 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 attached to the Olympus BX53 compound microscope. Drawings were subsequently inked in with Sakura Pigma Micron™ pens on 110 g/m^2 tracing paper, digitized with a CanoScan LiDE 500F scanner, and assembled into figure plates using

Adobe Photoshop. Copepod morphological terminology follows Huys and Boxshall (1991) and Dojiri and Ho (2013). Common and scientific names of fishes follow Page *et al.* (2013). Voucher specimens of *C. olsoni* were deposited at Cabrillo Marine Aquarium (CMA), San Pedro, California, U.S.A. (CMA 2021.01.0001 and CMA 2021.01.0002).

RESULTS

Redescription

Order Siphonostomatoida Thorell, 1859
Family Caligidae Burmeister, 1835
Genus *Caligus* Müller, 1785

***Caligus olsoni* Pearse, 1953**
Syn. *Caligus serratus* Shiino, 1965
(Figs. 2.1–2.5)

Adult female (Figs. 2.1-2.3): Body (Figure 2.1A) 3.72 (3.35–4.33) mm long (excluding caudal setae) (n=6). Cephalothoracic shield subcircular, slightly longer than wide [2.07 (1.90–2.30) mm × 1.77 (1.60–2.03) mm], with well-developed, paired frontal plates each bearing 1 discoid lunule on ventrolateral surface; posterior margin of thoracic zone extending well beyond posterior limit of lateral zone; anterior margin of frontal plates, outer margin of cephalic and lateral zones, and lateral margin of posterior sinuses of thoracic zone fringed with hyaline membrane. Free fourth pedigerous somite nearly 3 times wider than long [190 (140–240) µm × 540 (470–630) µm] and indistinctly separated from genital complex. Genital complex as long as wide [1.02 (0.85–1.28) mm × 1.09 (0.90–1.33) mm] and about half the length of cephalothoracic shield, with convex anterolateral margins and straight posterior margin. Abdomen composed of 1 somite, 403 (355–440) µm × 323 (290–355) µm, and noticeably constricted anteriorly at juncture with genital complex. Caudal ramus (Fig. 1B) slightly longer than wide [152 (110–180) µm × 121 (100–135) µm], with 6 plumose setae (seta I absent) and short row of setules along inner margin; outer margin of seta VI also with longitudinal row of fine spinules (visible in ventral view). Egg sacs (Fig. 2.1A) uniseriate.

Antennule (Fig. 2.1C) 2-segmented. Proximal segment rhomboid, bearing 23 pappose setae (setules not drawn in Fig. 2.1C), 2 naked setae, and 2 plumose setae (setules not drawn in Fig. 2.1C) along anterior margin. Distal segment cylindrical, bearing 12 naked setae (2 setae near posterodistal corner share a common base) and 2 aesthetascs.

Antenna (Fig. 2.1D) 3-segmented, comprising coxa, basis and 1-segmented endopod incorporating distal claw. Coxa with posteriorly-directed acuminate process. Basis rectangular, with adhesion pad on dorsal surface. Endopod long, uncinate, bearing stout naked seta proximally, thin naked seta at mid-length, and short ridge at curvature of tip.

Postantennal process (Fig. 2.1D) with slightly curved tip, 1 pair of setulose papillae at base, and 1 setulose papilla posterior to base.

Mandible (Fig. 2.1E) modified into elongate stylet bearing distolateral hyaline membrane and 12 distomedial teeth.

Maxillule (Fig. 2.1D) composed of trisetose papilla and elongate, apically rounded dentiform process. Sclerite anterior to papilla tapered medially into truncate tip.

Maxilla (Fig. 2.1F), brachiform, 2-segmented, composed of elongate, unarmed syncoxa and slender basis. Basis with large subapical flabellum and long apical calamus and shorter apical canna; calamus furnished with finely serrated margins on proximal half and finely serrated membranes on distal half; canna with finely serrated margins.

Maxilliped (Fig. 2.2A) large, subchelate, 3-segmented, comprising long protopod (corpus) and subchela consisting of free endopodal segment (shaft) and claw. Protopod with 2 unequal naked setae and 1 large and 2 small ridges in myxal area plus 2 patches of fine striations on outer margin (proximal patch situated on swelling). Shaft with proximal pore and tiny element at mid-length. Claw with long, naked basal seta and fine striations on both posterior and anterior surfaces (striations on posterior surface only are illustrated in Fig. 2.2A).

Tines of sternal furca (Fig. 2.2B) two times longer than box, slightly divergent, and apically rounded.

Legs 1 to 3 (Figs. 2.2C, E and 2.3A) biramous; leg 4 (Fig. 2.3C) uniramous. Armature formula of legs 1–4 (Roman numerals = spines; Arabic numerals = setae) are listed in Table 2.3.

Leg 1 (Fig. 2.2C) intercoxal sclerite elongate and unornamented. Protopod with 1 proximolateral setulose papilla, 1 outer and 1 inner plumose setae, and 1 mid-lateral pore. First exopodal segment with 1 small, naked distolateral spine and inner row of setules. Second exopodal segment with 4 apical elements (3 spines, 1 seta), 1 pore near apical margin, and 3 inner plumose setae; outer apical spine naked and as long as other apical spines; middle and inner apical spines (Fig. 2.2D) each with outer row of serrations and subapical accessory process; apical seta with thin flange along inner margin; proximal two-thirds of outer margin of each inner seta with longer and more widely spaced setules than on distal third. Endopod vestigial, naked, and digitiform.

Leg 2 (Fig. 2.2E) intercoxal sclerite subquadrate, with hyaline membrane along distal margin. Coxa with 1 inner plumose seta and 1 sensillum on anterior surface. Basis with 1 outer naked seta, 1 long sensillum and hyaline membrane along inner border, and large hyaline membrane (not drawn in Fig. 2.2E) covering posterolateral surface and extending over exopod. Exopod 3-segmented. First segment with 1 inner plumose seta, inner row of setules, and small pectinate membrane at base of long distolateral spine; outer and inner margins of spine ornamented with sclerotized flange. Second segment with 1 inner plumose seta, short inner row of setules, 1 short distolateral spine, and 1 minute pore on anterior surface; spine with sclerotized flange on outer margin. Third segment with 5 inner plumose setae, 1 apical spine, and 2 naked outer spines; outer distal spine apically rounded and about twice as long as outer proximal spine; apical spine with finely serrated flange 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 margin, and multiple rows of setules along outer margin. Third segment with 6 plumose setae, short row of setules along inner margin, and patch of setules at base of outermost seta.

Leg 3 (Fig. 2.3A) protopod large, modified to form apron, with sclerotized, striated ridge on mid-lateral margin, several minute pores on ventral surface, 3 marginal membranes (1 along mid-lateral margin, 2 closely set along inner distal margin), row of tiny spinules along base of mid-lateral membrane, 1 outer plumose seta situated on dorsal surface near base of exopod, 1 inner plumose seta inserted between inner distal pair of marginal membranes, and 2 unequal sensilla along distal margin. Exopod 3-segmented. First segment (Fig. 2.3B) with 1 long apical spine furnished with hyaline flange on outer margin, 1 minute pore, 1 sensillum on outer distal corner of basal swelling, and sclerotized flange near distal margin. Second segment with 1 inner plumose seta, 1 outer naked spine, and setules along outer margin. Third segment with 4 plumose setae, 3 naked spines, 1 minute pore, and setules along outer margin. Endopod 2-segmented. First segment expanded to form large, setulose velum and armed with 1 inner plumose seta. Second segment with 6 plumose setae and setules along outer margin.

Leg 4 (Fig. 2.3C) protopod as long as exopod and armed with 1 distolateral plumose seta. First exopodal segment with finely spinulate membrane at base of long outer spine; latter extending to base of mid-lateral spine on second exopodal segment and furnished with finely spinulate flange along both margins. Second exopodal segment armed with 1 long mid-lateral spine plus 1 very short and 2 long apical spines; mid-lateral and outer apical spines each with finely spinulate flange along margins and coarsely serrated membrane at base (half of outer apical spine covered by membrane); middle and inner apical spines each with several rows of fine spinules along outer margin and large pectinate membrane at base.

Leg 5 (Fig. 2.3D) vestigial, comprised of 2 setiferous lobes on ventrodistal corners of genital complex; outer lobe (protopod) with 1 sparsely plumose seta and inner lobe (exopod) with 2 sparsely plumose setae.

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

Adult male (Figs. 2.4-2.5): Body (Fig. 2.3E) 3.21 (2.70–3.58) mm long (excluding caudal setae) (n=6). Cephalothoracic shield slightly longer than wide [2.03 (1.68–2.28) mm × 1.67 (1.38–1.83) mm], ornamented as in female. Free fourth pedigerous somite wider than long [213 (185–250) µm × 475 (400–520) µm] and indistinctly demarcated from genital complex. Genital complex oblong, 492 (420–550) µm × 507 (440–540) µm. Abdomen composed of 2 unequal somites; first somite 124 (100–145) µm × 309 (280–330) µm; second somite 295 (260–330) µm × 338 (300–360) µm. Caudal ramus longer than wide [180 (155–190) µm × 137 (120–145) µm], armed as in female.

All limbs as in female, except for the following. Antennule with 2 additional setae on ventrodistal surface of proximal segment (position of each seta indicated by black circle in Fig. 2.1C). Antenna (Figs. 2.3F and 2.4A, B) 3-segmented, comprising coxa, basis, and 1-segmented endopod incorporating distal claw. Coxa elongated and naked. Basis as long as coxa, with 3 large corrugated pads. Endopod forming bifurcate terminal claw, furnished with 2 sclerotized flanges and 2 naked setae. Postantennal process (Fig. 2.4C) relatively longer, with strongly recurved tip. Maxillule (Fig. 2.4D) with slightly longer dentiform process and subquadrate sclerite at base. Maxilliped (Fig. 2.4E, F) with robust protopod bearing prominent denticulated myxal process, 2 unequal elements (these elements, 1 proximal and 1 distal to the myxal process, are typically protracted rather than retracted as figured), and 4 sets of denticles on anteromedial surface (composition of each set from inner edge towards the center of protopod: highly sclerotized denticulated shelf, patch of denticles, longitudinal row of denticles, and 1 pair of denticles); free endopodal segment with 1 tiny proximal element and 1 hyaline subdistal element; claw with naked basal seta and transverse striations on outer margin. Leg 5 (Fig. 2.5A) with plumose seta on outer lobe (protopod) and 1 unipinnate and 1 bipinnate setae on inner lobe (exopod). Leg 6 (Fig. 2.5A) forming genital operculum, with 1 tiny outer element.

Morphological variability. Seven of 16 females collected on 8 April 2019 from *L. sardina* at El Golfo de Santa Clara site, with small posterolateral lobes on genital complex. One male specimen collected on 31 May 2018 from *L. tenuis* at Seal Beach site, with small digitiform process on posterolateral margins of genital complex and longer outer element on leg 6 (Fig. 2.5B). One male specimen collected on 27 April 2017 from *L. tenuis* at Pacific Beach site, with small digitiform process on left side only of genital complex. Six male specimens collected on 8 April 2019 from *L. sardina* at El Golfo de Santa Clara site, with narrow subtriangular process on posterolateral margins of genital complex as described by Morales-Serna *et al.* (2013); 1 male specimen from same collection of *L. sardina*, with posterolateral process on right side only of genital complex.

DISCUSSION

Detailed comparison of our specimens of *Caligus* from three atherinopsid and one sciaenid host species, including California Grunion, collected in southern California waters and the northern Gulf of Mexico to Pearse's (1953) syntype specimens of *C. olsoni* from California grunion collected on Mission Beach and in San Diego Bay, California, revealed that our material is conspecific with *C. olsoni*. It was also evident that *C. olsoni* was poorly characterized by Pearse (1953), and as such, salient morphological characters of *C. olsoni* are supplemented as follows. The female has a subtriangular sclerite at the base of the elongate, apically rounded maxillulary process, 2 naked setae plus 1 large and 2 small ridges along the inner margin of the corpus maxillipedis, and 1 unisetose and 1 bisetose lobe on leg 5. The male has 3 corrugated pads on the basis and a bifurcate endopodal claw ornamented with 2 sclerotized flanges on the antenna; a long, recurved postantennal process; a subquadrate sclerite at the base of a relatively longer maxillulary process; 2 unequal setae, a denticulated myxal process, and 4 groups of denticles on the corpus, plus a seta on the shaft and a basal seta and transverse striations on the claw of the maxilliped; a unisetose and a bisetose lobe on leg 5; a minute outer element on leg 6; and posterolateral processes on the genital complex, which are commonly present in samples from Mexico. Both sexes have serrations and an accessory process on the middle and inner apical spines on the second exopodal segment of leg 1; a vestigial endopod on leg 1; a long outer spine on the first exopodal segment and a shorter outer spine on the second exopodal segment of leg 2; a tiny outer proximal spine and a short, digitiform outer distal spine on the third exopodal segment of leg 2; a short row of setules, multiple rows of setules, and cluster of setules along the outer margin of the first, second, and third endopodal segments, respectively, of leg 2; a row of minute spinules along the outer margin of the leg 3 protopod; a 3-segmented exopod and a 2-

segmented endopod on leg 3 as in most members of *Caligus*; a very short, outer apical spine on the compound distal exopodal segment of leg 4 that is partially obscured by a large, coarsely serrated membrane at its base; and a longitudinal row of fine spinules along the ventrolateral margin of the plumose caudal seta VI.

Ohtsuka and Boxshall (2019) recently established the *Caligus pseudorhombi* species-group to accommodate *C. acanthopagri* Ho, Lin, and Chen, 1994, *C. bifurcus* Shen, 1958, *C. buechlerae* Hewitt, 1964, *C. chinglonglini* Ohtsuka and Boxshall, 2019, *C. dieuzeidei* Brian, 1932, *C. hobsoni* Cressey, 1969, *C. kajii* Ohtsuka and Boxshall, 2019, *C. latigenitalis* Shiino, 1954, *C. ligatus* Lewis, 1964, *C. longirostris* Heegaard, 1962, *C. musaicus* Cavaleiro, Santos, and Ho, 2010, *C. nuenonnae* Andrews, Bott, Battaglene, and Nowak, 2009, *C. olsoni*, *C. pectinatus* Shiino, 1965, *C. pseudorhombi* Boxshall, 2018, *C. priacanthi* Pillai, 1961, *C. pterois* Kurian, 1949, *C. similis* Ho, Kim, and Nagasawa, 2005, and *C. xystercus* Cressey, 1991. Members of this group are characterized by having: (1) a markedly reduced proximal spine and a relatively small distal spine on the outer margin of the third exopodal segment of leg 2 in both sexes; (2) a 2-segmented leg 4 exopod with 4 spines on the compound distal segment in both sexes; (3) a genital complex that is as long as wide, without posterolateral lobes, and about twice as long as the abdomen in the female; (4) an abdomen that is about as long as wide in the female; (5) 1 to 3 pointed or rounded processes on the myxal surface of the male maxilliped (except for *C. longirostris* Hewitt, 1964); (6) a subquadrate genital complex, with legs 5 and 6 situated close together at the posterolateral corner, in the male; and (7) an abdomen composed of 1 or, typically, 2 somites in the male. *C. clemensi*, *C. serratus*, and *C. teres* Wilson, 1905 should be classified in this group as each species possesses many of the features listed above. We note here that not all species assigned to this group by Ohtsuka and Boxshall (2019) share the full suite of features. For example, the genital complex in the female is nearly 5 times longer than the abdomen in *C. xystercus*, about 4 times longer than the abdomen in *C. hobsoni*, or nearly as long as the abdomen in *C. bifurcus*. In addition, leg 5 is not situated in the same transverse plane as the distal setal element(s) on the genital operculum of leg 6 in the male of *C. buechlerae*, *C. olsoni*, and *C. similis* as compared to other members of the group.

Examination of specimens of both sexes of *C. clemensi* from British Columbia, Canada, revealed this species shares many features in common with *C. olsoni*, such as the overall structure of the male antenna, shape of the maxillule, armature of the female corpus maxillipedis, shape and armature of the male maxilliped, shape of the sternal furca, structure of leg 1 including the ornamentation pattern of the 3 inner apical setae on the second exopodal segment, structure of leg 2, structure of leg 3 including the row of spinules on the outer margin of the protopod, presence of a well-developed serrated membrane at the base of each apical spine on the second exopodal segment of leg 4, and presence of a longitudinal row of fine spinules along the outer margin of caudal seta VI. *C. clemensi* has been reported on the skin and fins of Pacific herring, *Clupea pallasi* Valenciennes, 1847 (as *Clupea harengus pallasi*) (Clupeiformes; Clupeidae) sampled off northern California, Oregon, Washington, Alaska, and British Columbia (Arthur and Arai 1980) and on the external surface of a wide range of fishes belonging to the Chimaeridae, Clupeidae, Gadidae, Gasterosteidae, Hexagrammidae, Salmonidae, and Scorpaenidae captured along the Pacific coast of Canada (Kabata 1988). Parker and Margolis (1964) illustrated a rectangular abdomen in the female of *C. clemensi*, but the abdomen is slightly constricted proximally in the females of *C. clemensi* we examined. Kabata (1972) illustrated transverse ridges on the medial surface of the maxillulary dentiform process of an immature adult female of *C. clemensi*, but no ridges were observed in the adult females of *C. clemensi* we examined.

Caligus clemensi differs from *C. olsoni* by having a longer abdomen, larger lunules, a thicker spiniform process on the antennal coxa, a small proximal process on the postantennal process, and a smooth medial margin on the corpus maxillipedis in the female. In addition, both sexes of *C. clemensi* have a larger outer apical spine on the second exopodal segment of leg 4 and the male of *C. clemensi* has a small bifid apex on 1 of the 2 tips of the antennal claw, a single large patch of denticles on the corpus maxillipedis, and 2 minute distal spines on leg 6.

Within the *C. pseudorhombi* species-group, *C. olsoni* closely resembles *C. serratus* and *C. teres*, particularly in the shared possession of a waist-like constriction at the base of the female abdomen, a coarsely serrated membrane at the base of the mid-lateral spine on the distal exopodal segment of leg 4, a very short, outer apical spine on the distal exopodal segment of leg 4 that is partially obscured by a coarsely serrated membrane at its base, and a pair of posterior processes on the male genital complex. Shiino (1965) described *C. serratus* based on specimens of both sexes removed from jacksmelt captured off La Jolla, California. Morales-Serna *et al*. (2011) analyzed the seasonal occurrence of 5 parasitic copepods, including *C. serratus*, on bullseye puffer occurring in the Santa María La Reforma lagoon, Mexico. Morales-Serna *et al*. (2013) redescribed *C. serratus* based on specimens of both sexes removed from Pacific agujon needlefish collected in Chamela Bay, Mexico. The description of *C. serratus* by Shiino (1965) and Morales-Serna *et al*. (2013) matches our specimens of *C. olsoni* in nearly every detail. The posteriorly-directed process on the coxa of the female antenna of *C. serratus* was neither mentioned nor illustrated by Shiino (1965). His description may have been based on an aberrant specimen since the antennal process is present in the 3 female specimens of *C. serratus* examined by Morales-Serna *et al.* (2013) and in the 7 female specimens of *C. serratus* we had examined from the collection of Morales-Serna *et al*. (2011). This feature is also present in our single female specimen of *C. olsoni* collected from jacksmelt (type-host of *C. serratus*) captured off Long Beach, California. Shiino (1965) and Morales-Serna *et al.* (2013) did not report the outer bulge and small proximomedial seta on the female corpus maxillipedis, the inner pair of small denticles on the male corpus maxillipedis, the row of minute spinules along the outer margin of the leg 3 protopod, and the longitudinal row of fine spinules along the outer margin of caudal seta VI on their specimens of *C. serratus*. They most likely overlooked those features as they are present in the specimens of both sexes of *C. serratus* we had examined from the collection of Morales-Serna *et al.* (2011), as well as in our female specimen of *C. olsoni* from jacksmelt. Shiino (1965) did not report the pair of posterior processes on the genital complex of his 3 male specimens of *C. serratus*, but these structures are present (singly or paired) in 2 of 56 male specimens of *C. olsoni* in our collection from California, in all 7 of our male specimens of *C. olsoni* from El Golfo de Santa Clara, Mexico, in all 8 male specimens of *C. serratus* we had examined from the collection of Morales-Serna *et al.* (2011), and in both male specimens of *C. serratus* examined by Morales-Serna et al. (2013). In the light of these similarities, we propose to treat *C. serratus* as a junior subjective synonym of *C. olsoni*.

Wilson (1905) established *C. teres* based on specimens of both sexes removed from an unidentified species of *Callorhinchus* Lacepède, 1798 (as *Callorhynchus*) (Chimaeriformes; Callorhinchidae) and a ray captured off Lota, Chile and subsequently accessioned at the U.S. National Museum (now the Smithsonian National Museum of Natural History). Wilson (1905) noted that it was possible the copepods may have transferred from one host to the other since specimens of the two host taxa were found in the same tub at the U.S. National Museum. Fagetti and Stuardo (1961) redescribed *C. teres* based on specimens of both sexes collected from Plownose Chimaera, *Callorhinchus callorhynchus* (Linnaeus, 1758) (as *Callorhynchus*

callorhynchus), caught in the Gulf of Arauco and off Valparaíso, Chile. They noted differences between their observations and the original description of the armature of the female maxilliped, legs 1 to 3, and the caudal rami. *Caligus teres* was subsequently reported on: (a) Peruvian hake, *Merluccius gayi peruanus* Ginsburg, 1954 (Gadiformes; Merluccidae), from Peru (Durán 1980); and (b) farmed Coho salmon, *Oncorhynchus kisutch* (Walbaum, 1792) (Salmoniformes; Salmonidae), and rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792) (Salmoniformes; Salmonidae), and on wild Patagonian blennie, *Eleginops maclovinus* (Perciformes; Eleginospidae) and Chilean silverside, *Odontesthes regia* (Humboldt, 1821) (Atheriniformes; Atherinopsidae), in Chilean waters (Carvajal *et al.* 1998; Bravo 2003; Sepúlveda *et al.* 2004; De los Ríos 2019). *Caligus teres* can be distinguished from *C. olsoni* by having a small process next to the outer distal spine on the first exopodal segment of leg 1 and more denticles on the male corpus maxillipedis. In addition, *C. teres* lacks the proximomedial seta and medial ridges on the female corpus maxillipedis, as well as the accessory process on the middle and inner apical spines on the distal exopodal segment of leg 1. It is possible, however, that *C. olsoni* is a junior synonym of *C. teres*, as the original description and redescription of *C. teres* are inadequate by modern standards. Thus, these two species are maintained as separate here pending examination of type material of *C. teres*.

The host specificity of caligids is generally high but some species have very low host-specificity, involving both teleost and elasmobranch hosts from different families and genera (Dojiri and Ho 2013). The same is observed within the *C. pseudorhombi* species-group; some species have relatively low host specificity (e.g. *C. acanthopagri*, *C. hobsoni*, *C. ligatus*, and *C. xystercus*) but other species may be more host-specific (Ohtsuka and Boxshall 2019). Based on previous reports, *C. olsoni* historically appeared to be highly host-specific, infecting only two fish hosts in the genus *Leuresthes* (Atherinopsidae, reported as Atherinidae in Ohtsuka and Boxshall 2019), its type host *L. tenuis* in California, U.S.A. and Baja California, Mexico (Pearse 1953; Olson 1955; Olson 1972), and the type host's sister species *L. sardina*, in the Gulf of California, Mexico (Olson 1979). However, with the proposed synonymy of *C. olsoni* and *C. serratus*, *C. olsoni* has, in fact, low host specificity, with 16 fish host species currently reported from 12 families (Table 2.4). This includes fish hosts previously reported for *C. serratus* (Shiino 1965; Hobson 1971; Morales-Serna *et al.* 2013, 2014) and a new host record, *A. nobilis*, collected in southern California (this study).

Species of *Caligus* with low host specificity could pose a risk for finfish aquaculture (Morales-Serna *et al.* 2013). Future studies need to focus on aspects of the biology and taxonomy of *C. olsoni* and its relationship to other species known to pose a risk to finfish aquaculture. The new host record for *C. olsoni*, the white seabass *A. nobilis*, was obtained from aquaculture pens in southern California. Details of the pathology of *C. olsoni* on *A. nobilis* are currently unknown and merit further investigation to determine if *C. olsoni* could pose a risk for the aquaculture of finfish. Out of the 6 species of *Caligus* reported to infect farmed salmonids around the world (Hemmingsen *et al.* 2020), two belong to the *C. pseudorhombi* species-group: *C. clemensi* and *C. teres*. As previously mentioned in this study, we obtained and compared specimens of *C. clemensi* to our specimens of *C. olsoni*. While these two species share some similarities, many of which attributed to species in the *C. pseudorhombi* species-group, our observations confirm that *C. clemensi* and *C. olsoni* are two distinct species. However, the description of *C. teres* suggests that this species is morphologically very similar to *C. olsoni*. We plan to obtain specimens of *C. teres* and compare them to *C. olsoni* to verify if they are, in fact, separate species.

ACKNOWLEDGMENTS

We thank Dr. Donald Buth (University of California, Los Angeles), Dr. Ralph Appy (Cabrillo Marine Aquarium), Dr. David Jacobs (University of California, Los Angeles), Dr. Karen Martin (Pepperdine University), and Dr. Michael Shin (University of California, Los Angeles) for their comments on an earlier draft of this manuscript. We also thank Geoff Keel and William Moser (Smithsonian Institution) for arranging the loan of copepod type material, Samuel Gómez (Universidad Nacional Autónoma de México) for kindly providing samples of *Caligus serratus* from Mexico, Mark S. Okihiro (California Department of Fish and Wildlife) for providing samples of *Caligus olsoni* infecting *Atractoscion nobilis* in aquaculture, and Simon Jones (Pacific Biological Station) for providing the specimens of *Caligus clemensi* from Canada.

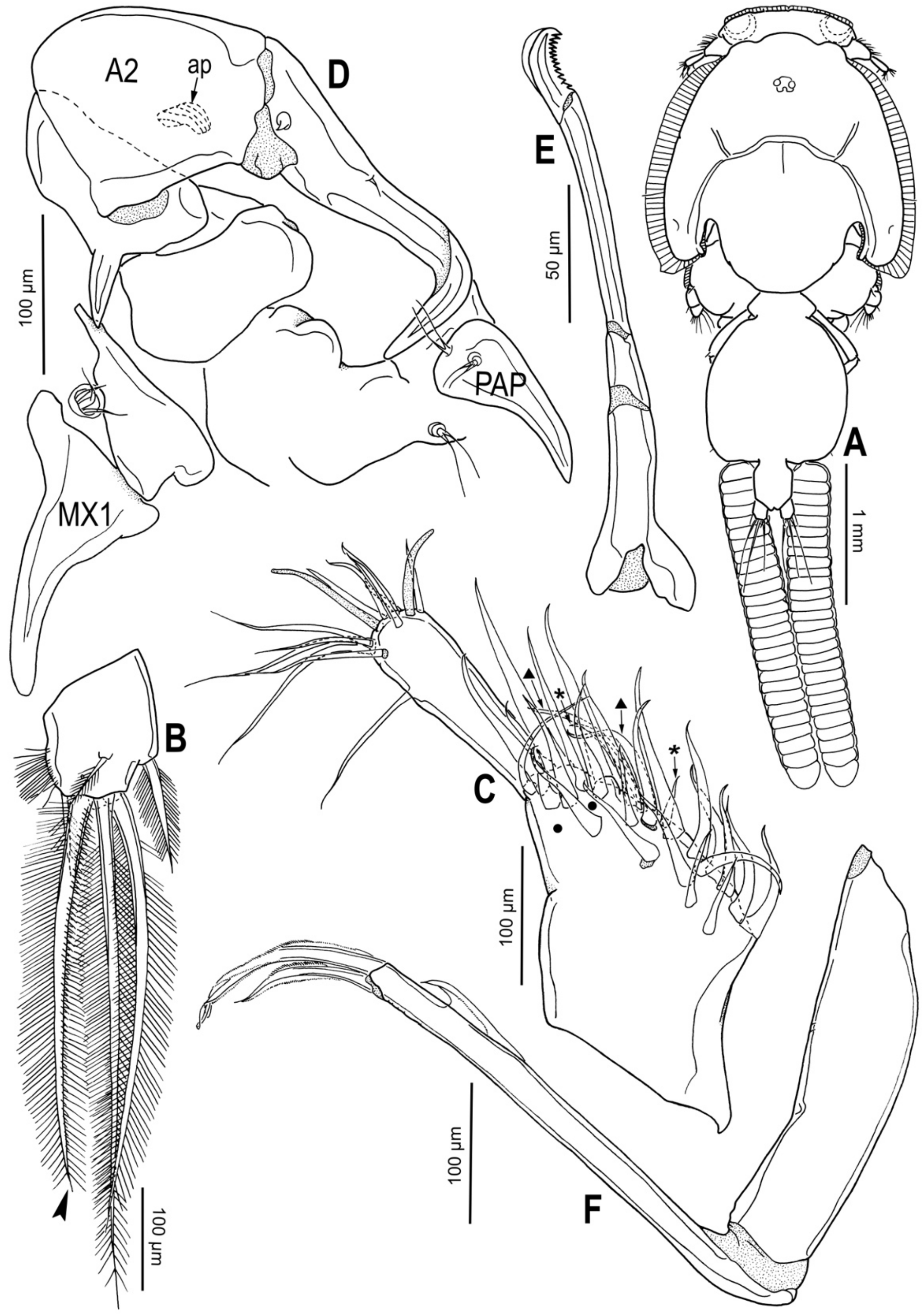

FIGURE 2.1. *Caligus olsoni* Pearse, 1953, adult female. (**A**) Habitus, dorsal. (**B**) Left caudal ramus (arrowhead indicates seta VI), ventral. (**C**) Right antennule (star symbol indicates plumose seta; black triangle indicates naked seta; black circle indicates position of additional seta on adult male antennule), ventral. (**D**) Left antenna, postantennal process and maxillule, ventral. (**E**) Right mandible, posterior. (**F**) Left maxilla, anterior. Abbreviations: adhesion pad, ap; antenna, A2; maxillule, MX1, postantennal process, PAP.

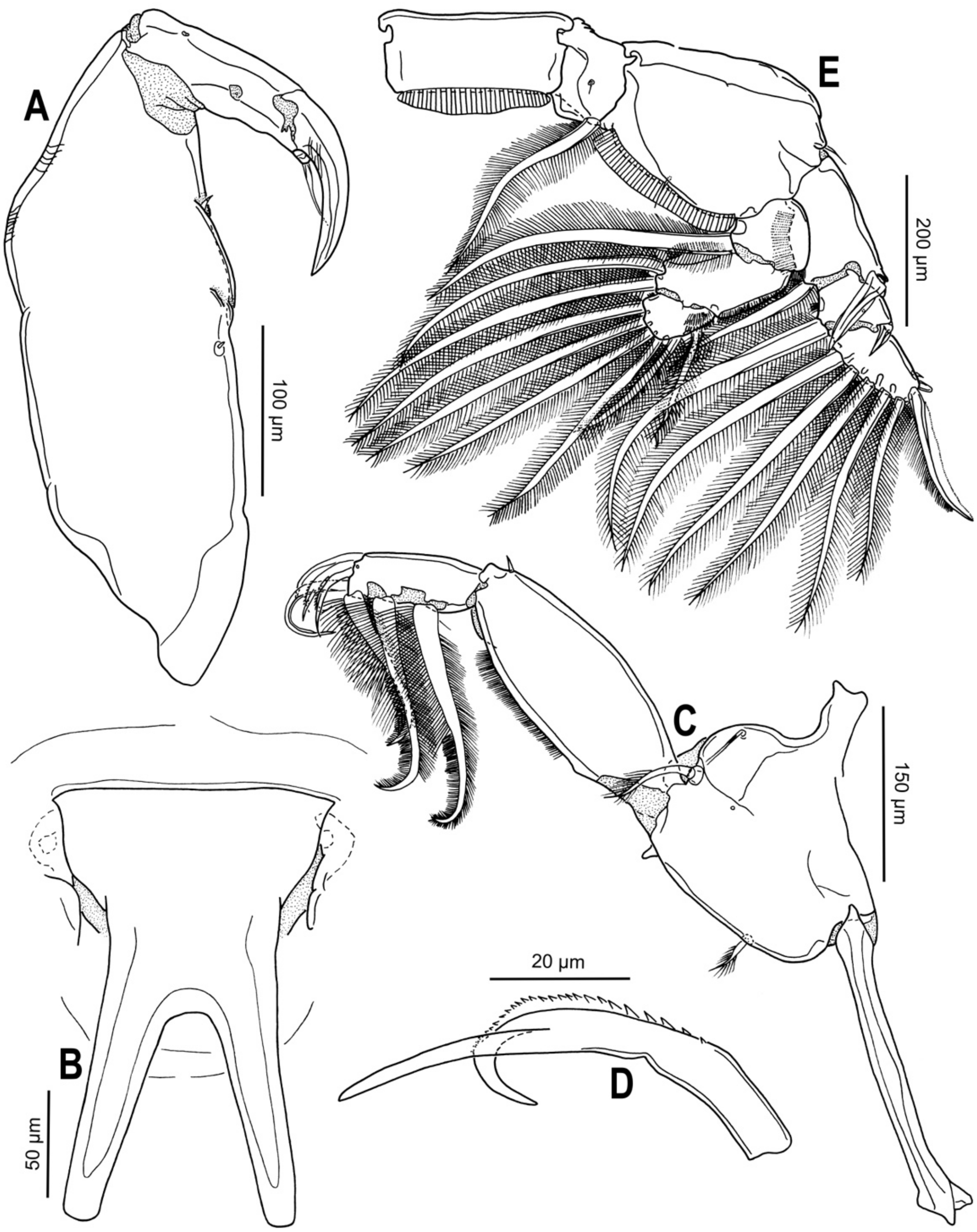

FIGURE 2.2. *Caligus olsoni* Pearse, 1953, adult female. (**A**) Right maxilliped, posterior. (**B**) Sternal furca, anterior. (**C**) Right leg 1, anterior. (**D**) Inner apical spine on second exopodal segment of right leg 1, anterior. (**E**) Left leg 2, anterior.

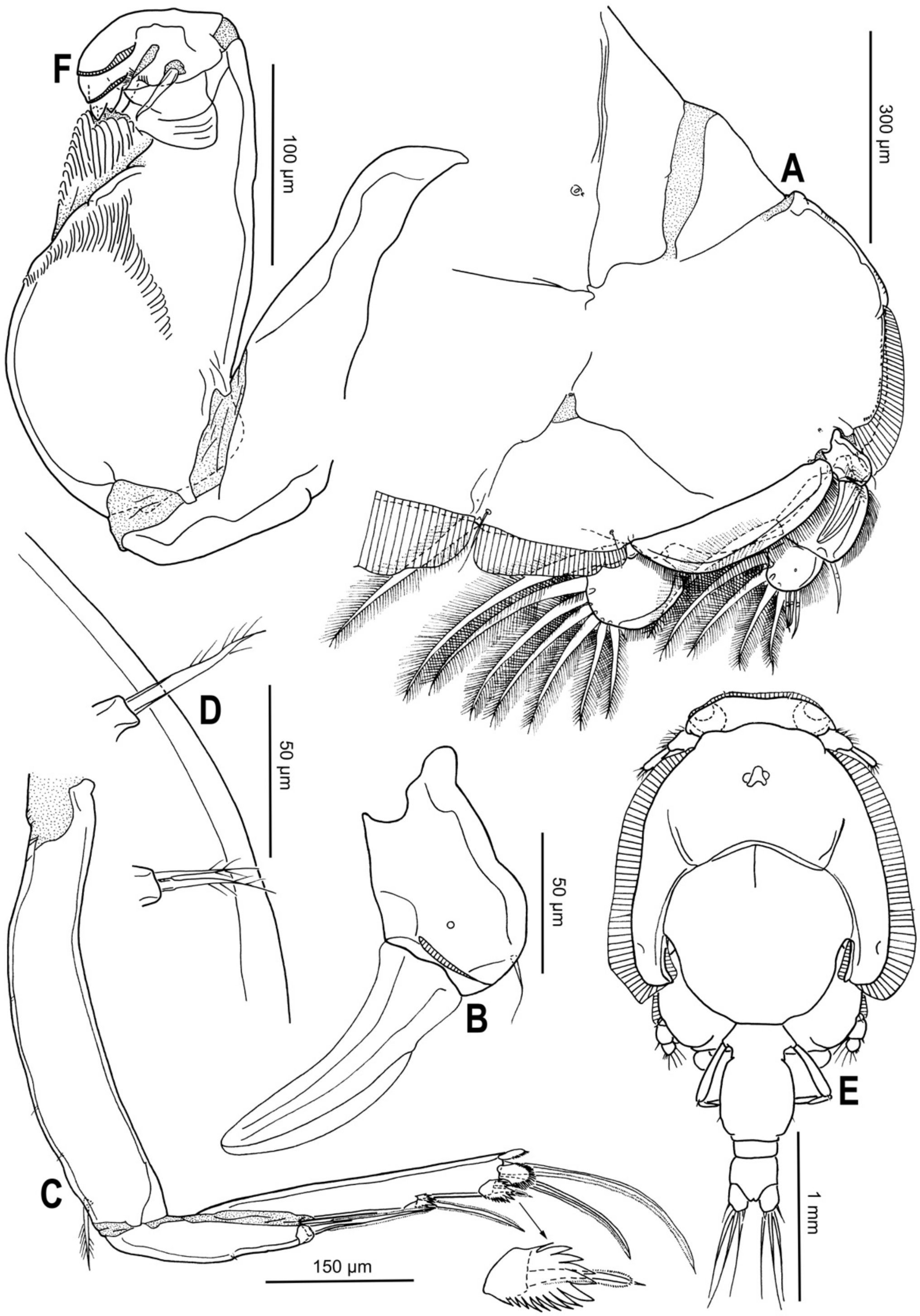

FIGURE 2.3. *Caligus olsoni* Pearse, 1953, adult female (A–D) and adult male (E–F). (**A**) Left leg 3, ventral. (**B**) First exopodal segment of left leg 3, ventral. (**C**) Right leg 4 with detail of outer apical spine on second exopodal segment, ventral. (**D**) Left leg 5, ventral. (**E**) Habitus, dorsal. (**F**) Left antenna, posterior.

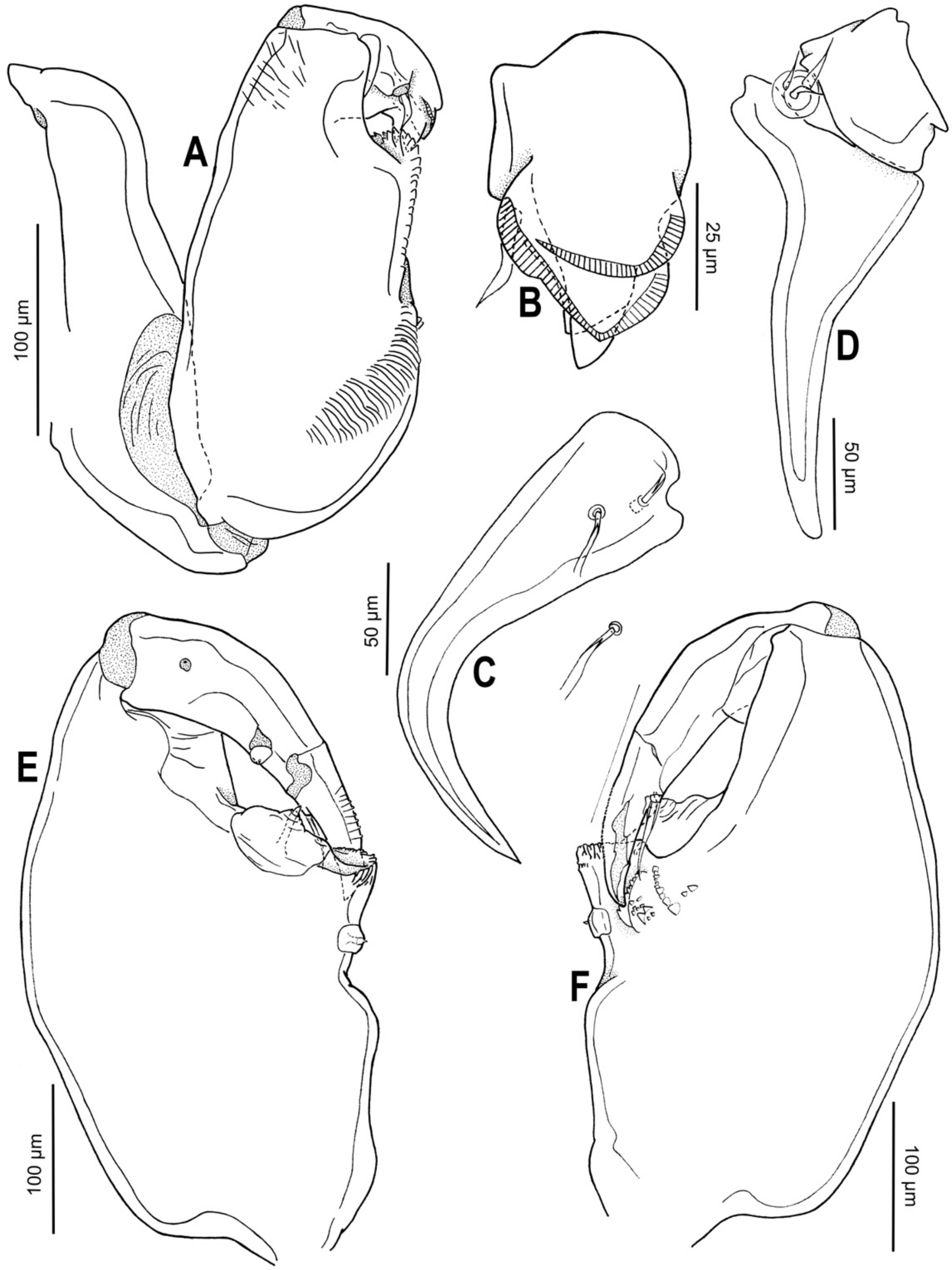

FIGURE 2.4. *Caligus olsoni* Pearse, 1953, adult male. (**A**) Left antenna, anterior. (**B**) Third segment of left antenna, medial. (**C**) Right postantennal process, ventral. (**D**) Left maxillule, ventral. (**E**) Right maxilliped, posterior. (**F**) Right maxilliped, anterior.

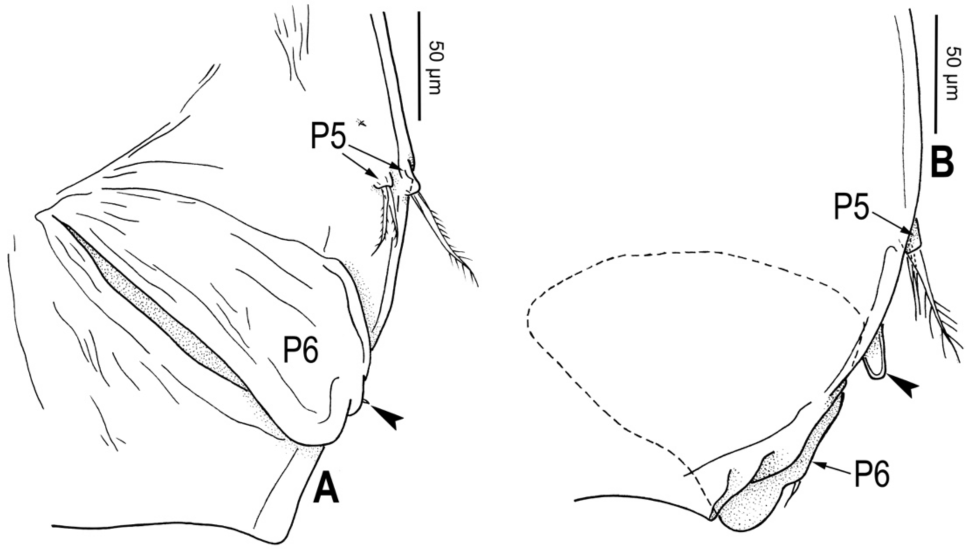

FIGURE 2.5. *Caligus olsoni* Pearse, 1953, adult male. (**A**) Left legs 5 and 6 (arrowhead indicates tiny element on leg 6), ventral. (**B**) Posterolateral corner of genital complex (arrowhead indicates digitiform process), dorsal. Abbreviations: leg 5, P5; leg 6, P6.

Table 2.1. Fish hosts and locality records for species of *Caligus* reported from California, U.S.A. Species of *Caligus* are listed alphabetically, then by host family alphabetically.

Species of *Caligus*	Host family	Host species	Locality	Reference
Caligus sp.	Paralichthyidae	*Citharichthys stigmaeus* Jordan & Gilbert, 1882	southern California	Kalman (2006)
C. bonito Wilson, 1905	Scombridae	*Sarda chiliensis* (Cuvier, 1832)	San Diego, California	Shiino (1960)
C. bonito (reported as *C. kuroshio*)	Engraulidae	*Engraulis mordax* Girard, 1854	southern California	Love and Moser (1983)
C. gurnardi	Chimaeridae	*Hydrolagus colliei* (Lay & Bennett, 1839)	La Jolla, California	Wilson (1908)
	Salmonidae	*Oncorhynchus tshawytscha* (Walbaum, 1792)	Monterey, California	Wilson (1908)
C. hobsoni Cressey, 1969	Embiotocidae	*Phanerodon atripes* (Jordan & Gilbert, 1880)	southern California	Hobson (1971)
		Damalichthys vacca (Girard, 1855)	southern California	Hobson (1971)
		Rhacochilus toxotes Agassiz, 1854	southern California	Cressey (1969)
	Kyphosidae	*Girella nigricans* (Ayres, 1860)	southern California	Hobson (1971)
	Labridae	*Semicossyphus pulcher* (Ayres, 1854)	southern California	Hobson (1971)
		Oxyjulis californica (Günther, 1861)	southern California	Hobson (1971)
	Pomacentridae	*Chromis punctipinnis* (Cooper, 1863)	southern California	Cressey (1969)
		Hypsypops rubicundus (Girard, 1854)	southern California	Cressey (1969), Hobson (1971)
	Scorpaenidae	*Scorpaenichthys marmoratus* (Ayres, 1854)	southern California	Hobson (1971)
		Sebastes mystinus (Jordan & Gilbert, 1881)	southern California	Hobson (1971)
		Sebastes serranoides (Eigenmann & Eigenmann, 1890)	southern California	Hobson (1971)
	Synodontidae	*Synodus lucioceps* (Ayres, 1855)	southern California	Love and Moser (1983)
C. klawei Shiino, 1959	Engraulidae	*Engraulis mordax* Girard, 1854	San Diego, California	Shiino (1959)
C. macarovi Gusev, 1951	Atherinopsidae	*Leuresthes tenuis* (Ayres, 1860)	southern California	this study
C. olsoni Pearse, 1953	Atherinopsidae	*Atherinopsis californiensis* Girard, 1854	Long Beach, California	this study
		Leuresthes tenuis (Ayres, 1860)	southern California	Pearse (1953), Olson (1955), Olson (1972), Olson (1979), this study
C. olsoni (reported as *C. serratus*)	Scianidae	*Atractoscion nobilis* (Ayres, 1860)	southern California	this study
	Atherinopsidae	*Atherinops affinis* (Ayres, 1860)	southern California	Hobson (1971)
		Atherinopsis californiensis Girard, 1854	La Jolla, California	Shiino (1965)
	Labridae	*Oxyjulis californica* (Günther, 1861)	southern California	Hobson (1971)
C. pectinatus Shiino, 1965	Paralichthyidae	*Citharichthys stigmaeus* Jordan & Gilbert, 1882	southern California	Kalman (2006)
		Hippoglossina stomata Eigenmann & Eigenmann, 1890	southern California	Kalman (2006)
		Paralichthys californicus (Ayres, 1859)	southern California	Kalman (2006)
	Scorpaenidae	*Eopsetta jordani* (Lockington, 1879)	San Diego, California	Shiino (1965)
		Sebastes saxicola (Gilbert, 1890)	southern California	Kalman (2006)
C. pelamydis Krøyer, 1863	Carangidae	*Trachurus symmetricus* (Ayres, 1855)	southern California	Shiino (1965)
C. quadratus Shiino, 1954	Embiotocidae	*Cymatogaster aggregata* Gibbons, 1854	southern California	Love and Moser (1983)
C. rotundogenitalis Yü, 1933	Atherinopsidae	*Leuresthes tenuis* (Ayres, 1860)	southern California	this study

Table 2.2. Fish host species, locality, and collection dates of specimens of *Caligus olsoni* examined in this study. Fish host species are listed alphabetically by scientific name. Collection of *Leuresthes tenuis* is listed by locality from north to south and chronologically within localities.

Host	Locality	Collection Date	*C. olsoni*
Atherinopsis californiensis	Belmont Shore Beach, California, U.S.A. (33°45'17.2"N, 118°08'20.6"W)	11/18/2017	1 female
Atractoscion nobilis	Channel Islands Harbor, California, U.S.A. (34°09'55.4"N, 119°13'28.6"W)	6/4/2017	10 females, 15 males
Leuresthes sardina	El Golfo de Santa Clara, Sonora, Mexico (31°40'33.5"N, 114°29'28.4"W)	4/8/2019	16 females, 7 males
Leuresthes tenuis	Goleta Beach, California, U.S.A. (34°25'00.3"N, 119°49'47.3"W)	4/28/2017	1 male
		6/11/2017	2 males
	Malibu Beach, California, U.S.A. (34°02'00.5"N, 118°40'45.0"W)	5/22/2016	2 females, 3 males
		3/29/2017	1 female, 2 males
		5/16/2018	2 females, 4 males
	Cabrillo Beach, California, U.S.A. (33°42'32.6"N, 118°17'00.1"W)	3/21/2015	1 female, 1 male
		3/25/2016	1 female, 1 male
		4/23/2016	1 female, 1 male
		5/22/2016	6 females, 1 male
		6/22/2016	11 females, 4 males
		5/12/2017	1 female
		4/2/2018	1 male
		6/16/2018	4 females, 2 males
	Seal Beach, California, U.S.A. (33°44'24.6"N, 118°06'51.9"W)	4/12/2017	1 female, 3 males
		5/12/2017	2 females, 2 males
		6/10/2017	3 females, 1 male
		5/31/2018	6 females, 2 males
	Pacific Beach, California, U.S.A. (32°47'32.0"N, 117°15'20.1"W)	4/25/2016	1 female
		5/23/2016	3 females
		3/30/2017	4 females
		4/27/2017	9 females, 2 males
		5/27/2017	4 females, 1 male
		6/10/2017	14 females, 1 male
		5/1/2018	17 females, 7 males

Table 2.3. Details of the armature on the legs 1-4 of *Caligus olsoni*.

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

Table 2.4. Fish hosts reported for *Caligus olsoni*.

Host species	Host family	Locality	Reference(s)
Atherinopsis californiensis Girard, 1854	Atherinopsidae	Long Beach, California, U.S.A.	this study
Atractoscion nobilis (Ayres, 1860)	Scianidae	Oxnard, California, U.S.A.	this study
Leuresthes sardina (Jenkins and Evermann, 1889)	Atherinopsidae	Gulf of California, Sonora, Mexico	Olson (1979), this study
Leuresthes tenuis (Ayres, 1860)	Atherinopsidae	Southern California*, U.S.A.	Pearse (1953), Olson (1955), Olson (1972), Olson (1979), this study
		Estero Beach, Baja California, Mexico	Olson (1955), Olson (1972)
***Atherinops affinis* (Ayres, 1860)	Atherinopsidae	La Jolla, California, U.S.A.	Hobson (1971)
***Atherinopsis californiensis* Girard, 1854	Atherinopsidae	La Jolla, California, U.S.A.	Shiino (1965)
***Calamus brachysomus* (Lockington, 1880)	Sparidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Caranx caballus* Günther, 1868	Carangidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Caranx caninus* Günther, 1867	Carangidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Cynoscion xanthulus* Jordan and Gilbert, 1882	Scianidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Elops affinis* Regan, 1909	Elopidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Haemulon steindachneri* (Jordan and Gilbert, 1882)	Haemulidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Kyphosus elegans* (Peters, 1869)	Kyphosidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Lutjanus argentiventris* (Peters, 1869)	Lutjanidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Microlepidotus brevipinnis* (Steindachner, 1869)	Haemulidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Oxyjulis californiaca* (Günther, 1861)	Labridae	La Jolla, California, U.S.A.	Hobson (1971)
***Scomberomorus sierra* Jordan and Starks, 1895	Scombridae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013, 2014)
***Sphoeroides annulatus* (Jenyns, 1842)	Tetraodontidae	Santa María La Reforma lagoon, Sinaloa, Mexico	Morales-Serna *et al.* (2013, 2014)
***Tylosurus pacificus* (Steindachner, 1876)	Belonidae	Chamela Bay, Jalisco, Mexico	Morales-Serna *et al.* (2013)

* San Clemente, Coronado Strand, Del Mar, Mission Beach, Pacific Beach, and San Diego Bay, California, U.S.A. (Pearse, 1953; Olson, 1955; Olson, 1972, Olson 1979); Goleta Beach, Malibu Beach, Cabrillo Beach, Seal Beach, and Pacific Beach (this study)

** for these hosts, the copepod species was reported as *Caligus serratus*

REFERENCES

Arthur, J. R. and Arai, H. P. 1980. Studies on the parasites of Pacific herring (*Clupea harengus* pallasi Valenciennes): Survey results. *Canadian Journal of Zoology* 58: 64–70.

Boxshall, G. 2018. The sea lice (Copepoda: Caligidae) of Moreton Bay (Queensland, Australia), with descriptions of thirteen new species. *Zootaxa* 4398: 1–172.

Boxshall, G. A. and El-Rashidy, H. H. 2009. A review of the *Caligus productus* species group, with the description of a new species, new synonymies and supplementary descriptions. *Zootaxa* 2271: 1–26.

Bravo, S. 2003. Sea lice in Chilean salmon farms. *Bulletin of the European Association of Fish Pathologists* 23: 197–200.

Carvajal, J., González, L. and George-Nascimento, M. 1998. Native sea lice (Copepoda: Caligidae) infestation of salmonids reared in netpen systems in southern Chile. *Aquaculture* 166: 241–246.

Costello, M. J. 2009. The global economic cost of sea lice to the salmonid farming industry. *Journal of Fish Diseases* 32: 115–118.

Cressey, R. F. 1969. *Caligus hobsoni*, a new species of parasitic copepod from California. *The Journal of Parasitology* 55: 431.

De los Ríos, P. 2019. A checklist of marine parasite copepods of the genus *Caligus* (O.F. Müller, 1785) and their respective marine fish hosts in Chile. *Proceedings of the Biological Society of Washington* 132: 65-72.

Dojiri, M. and Ho, J.-S. 2013. Systematics of the Caligidae, copepods parasitic on marine fishes. *Crustaceana Monographs* 18: 1–448.

Durán, L. E. 1980. Copépodos parásitos en peces del Peru: genero *Caligus* Müller, 1785, *Caligus callaoensis* n. sp. y tres nuevos registros (Crustacea, Copepoda). *Boletín del Museo Nacional de Historia Naturale, Santiago, Chile* 37: 309–316.

Fagetti, E. and Stuardo, J. 1961. Copépodos parásitos chilenos III. Redescripción de *Caligus teres* Wilson y nueva localidade para la especie japonesa *Trebius akajeii* Shiino. *Zoología* 5–12.

Hemmingsen, W., MacKenzie, K., Sagerup, K., Remen, M., Bloch-Hansen, K. and Imsland, A. K. D. 2020. *Caligus elongatus* and other sea lice of the genus *Caligus* as parasites of farmed salmonids: A review. *Aquaculture* 522: 735160.

Hobson, E. 1971. Cleaning symbiosis among California inshore fishes. *Fishery Bulletin* 69: 491–523.

Humes, A. G. and Gooding, R. U. 1964. A method for studying the external anatomy of copepods. *Crustaceana* 6: 238–240.

Huys, R. and Boxshall, G. A. 1991. *Copepod Evolution*. The Ray Society, London, 468 p.

Kabata, Z. 1972. Developmental Stages of *Caligus clemensi* (Copepoda: Caligidae). *Journal of the Fisheries Board of Canada* 29: 1571–1593.

Kabata, Z. 1988. Copepoda and Branchiura. In Guide to the Parasites of Fishes of Canada. Part II – Crustacea. Kabata, Z. and Margolis, L.(eds.). Canadian Special Publication in Fisheries and Aquatic Sciences 101: 3–127, Ottawa, Canada.

Kalman, J. E. 2006. Parasites of marine fishes associated with wastewater discharge in the Southern California Bight. Ph.D. Dissertation. University of California Los Angeles, Los Angeles, California.

Love, M. S. and Moser, M. 1984. A Checklist of Parasites of California, Oregon, and Washington Marine and Estuarine Fishes. NOAA Technical Report NMFS SSRF-777, 576 pp.

Love, M. S. and Passarelli, J. K. 2020. Miller and Lea's Guide to the Coastal Marine Fishes of California, 2nd Edn. UC Agriculture and Natural Resources Publications, Davis, CA.

Morales-Serna, F. N., Rubio-Godoy, M. and Gomez, S. 2011. Seasonality of parasitic copepods on bullseye puffer, *Sphoeroides annulatus* (Pisces: Tetraodontidae), from the Northwestern coast of Mexico. *The Journal of Parasitology* 97: 565–573.

Morales-Serna, F., Hernández-Inda, Z., Gomez, S. and León, G. 2013. Redescription of *Caligus serratus* Shiino, 1965 (Copepoda: Caligidae) parasitic on eleven fish species from Chamela Bay in the Mexican Pacific. *Acta Parasitologica* 58: 367–375.

Morales-Serna, F. N., Pinacho-Pinacho, C. D., Gomez, S. and León, G. P.-P. de 2014. Diversity of sea lice (Copepoda: Caligidae) parasitic on marine fishes with commercial and aquaculture importance in Chamela Bay, Pacific coast of Mexico by using morphology and DNA barcoding, with description of a new species of *Caligus*. *Parasitology International* 63: 69–79.

Ohtsuka, S. and Boxshall, G. A. 2019. Two new species of the genus *Caligus* (Crustacea, Copepoda, Siphonostomatoida) from the Sea of Japan, with a note on the establishment of a new species group. *ZooKeys* 893: 91–113.

Olson, A. C. 1955. Parasites of the Grunion, *Leuresthes tenuis* (Ayres). Ph.D. Dissertation. Oregon State College, Corvallis, Oregon.

Olson, A. C. 1972. *Argulus melanostictus* and other parasitic crustaceans on the California grunion, *Leuresthes tenuis* (Osteichthyes: Atherinidae). *The Journal of Parasitology* 58: 1201.

Olson, L. J. 1979. Host-parasite associations of the grunions *Leuresthes sardina* and *Leuresthes tenuis* from the Gulf of California and California. Ph.D. Dissertation. The University of Arizona. Tucson, Arizona.

Page, L.M., H. Espinosa-Perez, L. T. Findley, C. R. Gilbert, R. N. Lea, N. E. Mandrak, R. L. Mayden, and J. S. Nelson. 2013. Common and Scientific Names of Fishes from the United States, Canada, and Mexico. 7th Edition. American Fisheries Society Special Publication 34. Bethesda, MD.

Parker, R. R. and Margolis, L. 1964. A new species of parasitic copepod, *Caligus clemensi* sp. nov. (Caligoida: Caligidae), from pelagic fishes in the coastal waters of British Columbia. *Journal of the Fisheries Board of Canada* 21: 873–889.

Pearse, A. S. 1953. A new copepod parasite from the grunion. *The Journal of Parasitology* 39: 332.

Sepúlveda, F., Marín, S. L. and Carvajal, J. 2004. Metazoan parasites in wild fish and farmed salmon from aquaculture sites in southern Chile. *Aquaculture* 235, 89–100.

Shiino, S. M. 1959. On a new species of *Caligus* (Copepoda Parasitica) from the coast of California. *Pacific Science* 8: 351–356.

Shiino, S. M. 1960. Parasitic copepods of fishes from the Eastern Pacific. *Report of Faculty of Fisheries, Prefectural University of Mie* 3 (3): 527–541.

Shiino, S. M. 1965. Parasitic Copepods of the Eastern Pacific Fishes. *Report of Faculty of Fisheries, Prefectural University of Mie* 5: 391–420.

Shinn, A. P., Pratoomyot, J., Bron, J. E., Paladini, G., Brooker, E. E. and Brooker, A. J. 2015. Economic costs of protistan and metazoan parasites to global mariculture. *Parasitology* 142: 196–270.

Walter, T.C., Boxshall, G. 2021. World of Copepods Database. Accessed at http://www.marinespecies.org/copepoda on 2021-06-30. doi:10.14284/356

Wilson, C. B. 1905. North American parasitic copepods belonging to the family Caligidae, Part I. The Caliginae. *Proceedings of the United States National Museum* 479–672.

Wilson, C. B. 1908. North American parasitic copepods: A list of those found upon the fishes of the Pacific coast, with descriptors of new genera and species. *Proceedings of the United States National Museum* 35 (1653): 431–481.

Chapter 3

Comparison of parasite communities of California grunion *Leuresthes tenuis* with three other species of New World silversides (Atherinopsidae) in southern California, U.S.A., and in the Gulf of California, Mexico

Bruno Passarelli[1]

[1]Department of Ecology and Evolutionary Biology, University of California Los Angeles, California, 90095-7246, U.S.A.

ABSTRACT: In this study, the parasite communities of four host species of New World silversides (Atherinopsidae) were analyzed and compared. Samples of *Atherinops affinis* (Ayres, 1860), *Atherinopsis californiensis* Girard, 1854, and *Leuresthes tenuis* (Ayres, 1860) were collected in southern California, U.S.A., and samples of *Leuresthes sardina* (Jenkins and Evermann, 1889) were collected in the Gulf of California, Mexico. Fishes were dissected and inspected for ectoparasites and endoparasites. A total of 5,677 parasites from 25 taxa were recovered from the four host species. The most abundant parasite taxa were *Contracaecum (rudolphii)* (Nematoda), *Galactosomum* sp. (Digenea), and larval trypanorhynchs (Cestoda). Nine parasite taxa are new host records for *A. affinis* and eleven parasite taxa are new host records for *As. californiensis*. No new host records were found for *L. sardina* or *L. tenuis*. Non-Metric Multidimensional Scaling (nMDS) analysis indicated that the parasite communities were different among the four host species at the infracommunity level. A multivariate analysis of abundance (*mvabund*) showed significant differences in parasite communities in relation to host species. Species indicator analysis (*IndVal*) showed that the three most abundant parasite taxa found in this study, which combined accounted for more than 78% of the total number of parasites recovered, were associated with two host species, *A. affinis* and *As. californiensis*. Differences in diet and feeding strategies among the hosts species suggest that this may be an important factor explaining differences in parasite communities among the four host species of New World silversides studied.

INTRODUCTION

Parasite assemblages are a set of parasite species that infect a host species within specific spatial and temporal limits (Poulin 2015). The diversity of parasites found in such assemblages can be determined by both ecological and evolutionary factors (Vickery and Poulin 1998; Munoz *et al*. 2005). For example, species richness, the number of parasite species infecting a host, varies among host individuals, host populations, and host species (Poulin 1995). This variation may be explained by factors such as host body size, diet, and habitat temperature (Kuris *et al.* 1980; Poulin *et al.* 2011). On an ecological scale, environmental variables influence the distribution of hosts and their parasites (Poulin 1995; Poulin and Rohde 1997). However, because of coevolution between hosts and parasites, host phylogeny is just as important a factor to consider when studying parasite communities (Poulin 1995; Munoz *et al.* 2005). Host species that are more closely related phylogenetically are likely to share combined characteristics (e.g. diet, body size, habitat use) that are good predictors of the composition of parasite assemblages (Poulin *et al*. 2011).

The California grunion *Leuresthes tenuis* (Ayres, 1860) and other species of New World silversides (Atherinopsidae) provide an interesting context in which parasite communities can be studied. The closest relative to *L. tenuis* is its sister species, the Gulf grunion *Leuresthes sardina* (Jenkins and Evermann, 1889), which is endemic to the Gulf of California, Mexico. Speciation between *L. tenuis* and *L. sardina* likely occurred between 0.4 and 3 million years ago (Bernardi *et al.* 2003) when the two species were separated by the uplifting of the Baja California Peninsula. Although *L. sardina* and *L. tenuis* are more closely related to each other than to any other species in the family Atherinopsidae, the environmental conditions (e.g. salinity, temperature, tidal regimes) in the Gulf of California, where *L. sardina* is found, and the Pacific

Ocean, where *L. tenuis* is found, are very different. Two other species of fishes in the family Atherinopsidae, topsmelt *Atherinops affinis* (Ayres, 1860), and jacksmelt *Atherinopsis californiensis* Girard, 1854, are native to southern California, and therefore, are exposed to similar environmental conditions as *L. tenuis*. Although *A. affinis* and *As. californiensis* share the same geographic area as *L. tenuis*, speciation likely occurred more than 20 million years ago (Campanella *et al.* 2015).

The parasite assemblages of *A. affinis*, *As. californiensis*, *L. sardina* and *L. tenuis* share a few of the same species of parasites in common (Olson 1979; Love and Moser 1983) but a direct comparison of the parasite assemblages of these four hosts has never been done. The goal of this study was to document the parasites of two species of New World silversides found in southern California, *A. affinis* and *As. californiensis*, and the parasites of the Gulf grunion, *L. sardina*, found in the Gulf of California, and to compare them to the parasites of the California grunion, *L. tenuis*. Comparisons of assemblages of metazoan parasites were made using multivariate analysis (nMDS, *mvabund*) to assess similarity at the infracommunity level (i.e. all individuals of all species of parasites infecting a single host specimen) among the host species. Indicator species analysis (*IndVal*) was used to determine the relationship between occurrence and abundance of parasite species in relation to a host species or a combination of host species.

MATERIALS AND METHODS

Study area and examination of fish

Samples of *A. affinis*, *As. californiensis* and *L. tenuis* were collected by the Vantuna Research Group, Occidental College, in North San Diego Bay, California, U.S.A., on 3 April, 2016. This sample was unique because specimens of all three species, *A. affinis* (n = 10), *As.*

californiensis (n = 7), and *L. tenuis* (n = 20) were collected in the same net haul. Fishes were collected by purse seine, placed in individual plastic bags and frozen until inspection for parasites. Samples of *L. sardina* (n = 30) were collected during a spawning run in El Golfo de Santa Clara, Sonora, Mexico, on 8 April, 2019. Fish were collected by hand, placed in individual plastic bags and frozen until inspected for parasites. To obtain a similar sample size for all host species, additional samples of *A. affinis* (n = 7 and n = 10, respectively) were collected by beach seine at Cabrillo Beach, California, U.S.A., on 10 November 2019 and in San Diego Bay, California, U.S.A., on 16 November 2020. Additional samples of *As. californiensis* (n = 20) were collected by beach seine at Belmont Shore Beach, California, U.S.A., on 23 November 2019 (Fig. 3.1, Table 3.1).

For comparisons of parasite communities among host species, 30 specimens of *L. tenuis* were randomly selected from a database of specimens previously collected at Cabrillo Beach, Seal Beach, and Pacific Beach (Chapter 1) using the function random_n in R Software. The 20 specimens of *L. tenuis* from San Diego Bay were included in the database from which the 30 specimens were randomly selected.

All fishes examined were thawed, then each fish and plastic bag were rinsed under running water to remove excess sand or other debris and the double-netting method (Madinabeitia and Nagasawa 2013) was used to collect parasites that may have been dislodged during sampling. The standard length (SL) of each fish was measured to the nearest mm. A one-way ANOVA was used to compare SL of the four host species. Parasitological examination included body, fins, oral cavity, gill cavity, gills, heart, liver, spleen, gonads, body cavity, mesenteries, and digestive tract. Examination for parasites and identification were made using stereoscopic and compound microscopes. After fishes were visually inspected, the double netting method (Madinabeitia and Nagasawa 2013) was used again with the remains of the body and head to maximize collection of parasites. Parasites were identified to the lowest taxonomical level possible and preserved in either 75% or 90% ethanol. Quantitative descriptors (prevalence, mean intensity, and mean abundance) were calculated for each species of parasite following Bush *et al*. (1997). Vouchers of parasite specimens recovered were deposited at Cabrillo Marine Aquarium (CMA), San Pedro, California, U.S.A. (CMA 2021.01.0011 through CMA 2021.01.0019).

Multivariate analyses of infracommunities and Indicator Species Analysis

Non-Metric Multidimensional Scaling (nMDS) was used to visualize similarity among infracommunities among host species. Zero-adjusted Bray-Curtis (Clarke *et al.* 2006) similarity indices were calculated among all samples and with samples from all possible pairs of host species. Abundance data were transformed log (x+1) prior to analysis. nMDS plots were generated with the similarity matrices to visualize the groupings of samples using parasite abundance data (total number of individuals of a species of parasite in a single host). The fit of the nMDS ordination was quantified by a value of stress. A model-based analysis of multivariate abundance data was performed using the *mvabund* package (Wang *et al.* 2012) to evaluate the similarity of parasite infracommunities among host species. A permutational test, Indicator Species Analysis (*IndVal*) (Dufrêne and Legendre 1997; De Cáceres *et al.* 2010), was performed to determine the relationship between occurrence and abundance of parasite species in relation to a host species or a combination of host species. All calculations of quantitative descriptors, visual, and statistical analyses were done using R software (R Development Core Team; www.r-project.org).

RESULTS

Overall parasite data

A total of 5,677 parasites from 25 taxa were recovered from the four host species, *A. affinis*, *As. californiensis*, *L. sardina*, and *L. tenuis* (Figure 3.2). From *A. affinis* (n = 27), 1,982 parasites belonging to 15 taxa were recovered, 100% of the specimens were infected with at least one species of parasite, and the mean intensity was 76.4 parasites per infected fish. From *As. californiensis* (n = 27), a total of 2,872 parasites belonging to 16 taxa were recovered, 100% of the specimens of were infected with at least one species of parasite, and the mean intensity was 106.0 parasites per infected fish. From specimens of *L. tenuis* (n = 30, previously collected in Cabrillo Beach, Seal Beach, and Pacific Beach for Chapter 1), a total of 91 parasites belonging to 11 taxa were recovered, 76.7% of the specimens of *L. tenuis* were infected with at least one species of parasite, and the mean intensity was 3.9 parasites per fish. From *L. sardina* (n = 30) collected in the upper Gulf of California, Mexico, a total of 732 parasites belonging to 7 taxa were recovered. Overall, 100% of the specimens of *L. sardina* were infected with at least one species of parasite with a mean intensity of 24.4 parasites per infected fish.

Mean SL varied significantly among host species (ANOVA, $F_{3,110} = 333.1$, df = 3, $P < 0.001$). The host species in decreasing order of mean SL were *As. californiensis* (n = 27, mean SL = 248.5 mm ± 26.8 SD), *L. sardina* (n = 30, mean SL = 159.3 mm ± 26.8 SD), *L. tenuis* (n = 30, mean SL = 134.9 mm ± 9.95 SD), *A. affinis* (n = 27, mean SL = 124.2 mm ± 12.2 SD). A post-hoc Tukey test comparison showed a significant difference in mean SL for all host pairs, except for *A. affinis* and *L. tenuis* (P=0.065).

The most abundant parasite taxa were *Contracaecum (rudolphii)* (Nematoda), *Galactosomum* sp. (Digenea), and larval trypanorhynchs (Cestoda) (Figure 3.2). Combined, these three parasite taxa accounted for more than 78% (4,474 out of 5,677) of the total number of individual parasites recovered in this study. A summary of all parasite taxa and abundance of parasites infecting *A. affinis*, *As. californiensis*, *L. sardina*, and *L. tenuis* is given in Table 3.2 and a summary with the three most abundant ectoparasites and endoparasites is given in Table 3.3.

The following nine parasite taxa are new host records for *A. affinis*: *Argulus melanostictus* (Branchiura), *Leuresthicola olsoni* (Monogenea), *Lacistorhynchus* sp. (Cestoda), Trypanorhyncha gen. sp. (Cestoda), *Lepocreadium manteri* (Digenea), Acuariidae gen. sp. (Nematoda), *Anisakis* sp. (Nematoda), *Cucullanus* sp. (Nematoda), and *Hysterothylacium* sp. (Nematoda).

The following eleven parasite taxa are new host records for *As. californiensis*: *Argulus melanostictus* (Branchiura), *Bomolochus* sp. (Copepoda), *Clavellotis* sp. (Copepoda), *Leuresthicola olsoni* (Monogenea), *Corynosoma* sp. B (Acanthocephala), *Lacistorhynchus* sp. (Cestoda), Didymozoidae type Pseudotorticaecum (Digenea), *Galactosomum* sp. (Digenea), *Phyllostomum* sp. (Digenea), *Hysterothylacium* sp. (Nematoda), and *Pseudoterranova* sp. (Nematoda).

No new host records were found for *L. sardina* or *L. tenuis*.

Multivariate analyses of parasite communities

Non-metric multidimensional scaling (nMDS) analysis was used to obtain a visual representation of the similarity of parasite communities among different host species at the infracommunity level. The first nMDS plot shows that the parasite communities of the three host species (*A. affinis*, *As. californiensis*, and *L. tenuis*) collected in the same net haul in San Diego Bay were different (Figure 3.3). The second nMDS plot also shows differences in parasite communities among the three host species (*A. affinis*, *As. californiensis*, and *L. tenuis*) collected in southern California and the host species (*L. sardina*) collected in the Gulf of California (Figure 3.4). Shepard diagrams showing the distances of the nMDS against the dissimilarities in the Bray-Curtis matrices are given in Chapter 3 – Supplemental Materials (Figures 1.S3 and 2.S3). The stress scores for the nMDS analyses were 0.064 and 0.134, respectively. Based on the nMDS plot (Figure 3.4), the metazoan parasites of the four host species appeared to differ at the infracommunity level, even though some parasite species were found in more than one host species and many species of parasites were shared between *A. affinis* and *As. californiensis*. Parasite infracommunities of *A. affinis* and *As. californiensis* were associated with high abundance of many different species of parasites, especially the most abundant parasites found in this study, *Contracaecum (rudolphii)* (Nematoda), *Galactosomum* sp. (Digenea), and larval trypanorhynchs (Cestoda). The parasite infracommunities of *L. tenuis* were associated with high abundance of *Bomolochus* sp. (Copepoda), and *Leuresthicola olsoni* (Monogenea). The parasite infracommunities of *L. sardina*, the only species collected in the Gulf of California, were associated with high abundance of *Aponurus* sp. (Digenea), *Diplostomulum* sp. (Digenea), and larval tetraphyllideans (Cestoda) (Figure 3.4). Overall, there was a significant difference in parasite communities among the four host species at the infracommunity level (Dev = 968.3, $p < 0.001$). Separate results for each species of parasite with significant differences are given in Table 3.4.

Species Indicator Analysis

Among the 26 parasite taxa found in this study, 17 showed a significant association in the indicator value analysis in relation to host species. Among the 17 parasite taxa showing significant associations, four were associated to a combination of two host species and 13 were associated to a single host species (Table 3.5). The three most abundant parasites found in this study, *C. (rudolphii)* (Nematoda), *Galactosomum* sp. (Digenea), and larval trypanorhynchs (Cestoda) were associated to a combination of two host species, *A. affinis* and *As. californiensis*. *Leuresthicola olsoni* (Monogenea) were associated to a different combination of two host species, *As. californiensis* and *L. tenuis*. Among the parasite associated to a single host species, *Spirocamallanus pereirai* (Nematoda) was associated to *A. affinis*. *Lacistorhynchus* sp. (Cestoda), *Asymphylodora atherinopsidis* (Digenea), didymozoid type Pseudotorticaecum (Digenea), *Anisakis* sp. (Nematoda), *Hysterothylacium* sp. (Nematoda), *Pseudoterranova* sp. (Nematoda), Learnopodidae gen. sp. (Copepoda) were associated to *As. californiensis*. *Caligus olsoni* (Copepoda)*, Aponurus* sp. (Digenea), *Diplostomulum* sp. (Digenea), and tetraphyllidean larvae (Cestoda) were associated to *L. sardina* and *Bomolochus* sp. (Copepoda) were associated to *L. tenuis*.

DISCUSSION

The parasite burden of *A. affinis* and *As. californiensis* was high in relation to *L. sardina* and *L. tenuis*. The total number of parasites recovered from *A. affinis* and *As. californiensis* represent approximately 85% (4,854 out of 5,677) of the total number of parasites. The three most abundant parasite taxa found in this study, *C. (rudolphii)*, *Galactosomum* sp., and larval trypanorhynchs, were major contributors to the difference in total number of parasites among host species. The unequal distribution of the most abundant parasites suggest that differences in parasite communities among host species may not occur randomly. Many of the parasite taxa recovered from *A. affinis* (eight out of 14) and *As. californiensis* (nine out of 14) are new host records (Love and Moser 1983). These new records add to the knowledge on fish parasites in the family Atherinopsidae and are useful to show differences in parasite communities among the four host species in this study. However, further research is needed to investigate many aspects related to these parasite taxa including their taxonomy, geographic range, life-cycles, temporal and spatial variation. These future investigations are beyond the scope of this study.

The nMDS analyses suggested that parasite communities were different among host species at the infracommunity level (Figures 3.3 and 3.4). The nMDS plot of *A. affinis*, *As. californiensis*, and *L. tenuis* collected in the same net haul (Figure 3.3) showed that the parasite communities of *A. affinis* and *As. californiensis* appeared more similar between these two hosts in relation to the parasite communities of *L. tenuis*. The parasite communities used in this analysis (Figure 3.3) were recovered from *A. affinis*, *As. californiensis*, and *L. tenuis* caught in the same net haul, indicating that differences in parasite communities are more likely related to differences in host species rather than to differences in environmental conditions. The second nMDS plot of *A. affinis*, *As. californiensis*, *L. sardina*, and *L. tenuis* also showed differences in parasite communties among the host species (Figure 3.4). As indicated by abundance and other quantitative descriptors (Figure 3.2, Table 3.3), the most abundant parasite taxa, *C. (rudolphii)*, *Galactosomum* sp., and larval trypanorhynchs, contributed greatly to the differences observed in parasite communities among the host species, which was confirmed by the multivariate analysis of abundance. This analysis showed a significant difference in parasite communities among *A. affinis*, *As. californiensis*, *L. sardina*, and *L. tenuis*.

The Species Indicator Analysis (*IndVal*) showed that 17 out of 26 parasite taxa were significantly associated to a single hosts species or a combination of two host species. It is important to note that this analysis provides a qualitative assessment of the association of species (parasite species) and their niches (hosts species) only in the spatial, temporal, and environmental context of a particular study (De Cáceres *et al.* 2008; Willner *et al*. 2009). In this study, *IndVal* was useful to show differences in parasite communities only considering the four host species collected in southern California and the Gulf of California. While *IndVal* was useful to detect patterns of association between parasite and host species, the analysis does not indicate an explanation for the patterns observed (De Cáceres *et al.* 2010). Nevertheless, the associations shown in the *IndVal* were not random and the three most abundant parasite taxa, *C. (rudolphii)*, *Galactosomum* sp., and larval trypanorhynchs, were significantly associated to two host species, *A. affinis* and *As. californiensis*.

Contracaecum (rudolphii) was the most abundant (dominant) species of parasite found in this study and the only species recovered from all four hosts that showed significant differences in abundance. Typically, species in the genus *Contracaecum* have a global distribution and low host-specificity (Ángeles-Hernández *et al.* 2020). The general life cycle for the genus *Contracaecum* involves first intermediate hosts that include a broad range of planktonic invertebrates (such as gastropods, copepods, mysids, and amphipods). Second intermediate hosts include a great variety of teleost fishes. The definitive hosts are various species of piscivorous birds, such as cormorants and pelicans (Bartlett 1996; Moravec 2009; Shamsi 2019). The fish hosts investigated in this study are secondary intermediate hosts to *C. (rudolphii)* (found at the third larval (L3) stage). Morphological features and measurements of specimens of *Contracaecum (rudolphii)* found in *A. affinis*, *As. californiensis*, *L. sardina*, and *L. tenuis* were similar, suggesting that these nematodes belong to the same species, *C. (rudolphii)*, although genetic studies may reveal that different sibling species may be present (Li *et al.* 2005; Ralph Appy, pers. comm.). The low host-specificity and wide-spread geographic range of *C.*

(rudolphii) was confirmed in this study, as this parasite was recovered from all four hosts, three of them, *A. affinis*, *As. californiensis*, and *L. tenuis*, collected in southern California, U.S.A., and one host, *L. sardina* collected in the Gulf of California, Mexico. However, differences in abundance, overall prevalence and mean intensity (Table 3.2) suggest that the association of *C. (rudolphii)* is not equal among the four hosts species. Many factors such as host size, host diet, host sample size, habitat, and latitude are likely to contribute to differences in parasite communities among different host species, affecting, for example, parasite species richness and mean number of parasites per host (Poulin 1995).

Host body size may influence characteristics of parasite assemblages, such as parasite abundance and species richness (Timi and Poulin 2003; Poulin 2007). However, some studies on parasite communities of marine fishes have found little correlation between host size and parasite abundance or species richness (Henríquez *et al.* 2011; Henríquez and González 2012). In this study, host body size was variable among *A. affinis*, *As. californiensis*, *L. sardina*, and *L. tenuis*. However, in this case, differences in host body size did not appear to explain parasite abundance among host species. For example, the dominant parasite taxa, *C. (rudolphii)*, was significantly associated with *A. affinis* and *As. californiensis* (Table 3.5) but these host species were, respectively, the smallest (mean SL = 124.2 mm ± 12.2 SD) and largest (mean SL = 248.5 mm ± 26.8 SD) host species in this study. *Atherinops affinis* and *L. tenuis* (mean SL = 134.9 mm ± 9.95 SD) were similar in size but overall abundance and prevalence of *C. (rudolphii)* was much higher in *A. affinis* in relation to and *L. tenuis* (Table 3.2).

Host diet and feeding strategy is another important factor explaining differences in parasite infracommunities among different host species (Poulin 1995; Chen *et al.* 2008; Timi *et al.* 2011). The dietary breadth of *A. affinis* and *As. californiensis* is much broader in relation to the dietary breadth of *L. sardina* and *L. tenuis* (Horn *et al.* 2006; Higgins and Horn 2014). While *A. affinis* and *As. californiensis* have an omnivorous diet, *L. sardina* and *L. tenuis* are strictly carnivorous, feeding primarily on highly evasive prey items such as mysid crustaceans (Higgins and Horn 2014). The narrow diet of *L. sardina* and *L. tenuis* may be an adaptation related to their beach-spawning behavior, where the evolution of suction feeding allows for efficient feeding on prey commonly found near spawning sites (Higgins and Horn 2014). In this study, many different species of invertebrates and algae were observed in the intestines of *A. affinis* and *As. californiensis*. Small fishes, such as anchovies, are also known to be a part of the diet of *As. californiensis* (Ralph Appy, pers. comm.). No food items were not found in the intestines of *L. sardina* and *L. tenuis* collected during spawning runs. A single food item, mysid crustaceans, was found in the intestines of some of the *L. tenuis* collected by purse seine. The difference in diet between the omnivorous *A. affinis* and *As. californiensis* and the carnivorous *L. sardina* and *L. tenuis* may be explained by the feeding strategies of the four host species. When feeding, *A. affinis* and *As. californiensis* thrust their jaws straightforward or upwards to feed on a variety of food items while *L. tenuis* and *L. sardina* open their jaws on a more oblique, downward direction. In fact, the jaw orientation and feeding habits of *L. sardina* and *L. tenuis* differ in relation to the other three genera of atherinopsids (Higgins and Horn 2014). The narrower diet of *L. sardina* and *L. tenuis* likely means that these species would consume fewer prey species that may serve as intermediate hosts to different species of endoparasites. Because endoparasites are trophically transmitted, this narrow diet would result in a less diverse endoparasitic fauna for *L. sardina* and *L. tenuis* in relation to *A. affinis* and *As. californiensis*. Such a trend was observed in this study. Differences in diet and feeding strategies among the four hosts species suggest that this may be an important factor explaining differences in parasites among host species.

The distribution range of parasites may also be influenced by environmental conditions (Poulin 1995). Two out of the three most abundant parasite taxa, *Aponurus* sp. and larval tetraphyllideans, recovered from *L. sardina* collected in the Gulf of California were not recovered from any of the other three hosts collected in southern California. The only survey of parasites of *L. sardina* prior to this study reported 26 parasite taxa (Olson 1979). Eighteen of those parasite taxa were reported as being found in "low frequency" (i.e. low prevalence) and eight taxa were reported as "common parasites" (Olson 1979). The six parasite taxa reported from *L. sardina* in this study, are the same as six out of the eight common parasites reported in Olson (1979). The most common parasite reported in Olson (1979) *Diplostomulum* sp. (Digenea) was also found at 100% prevalence in this study. *Argulus melanostictus* (Branchiura), *Caligus olsoni* (Copepoda), larval tetraphyllideans larva type VI (Cestoda), *Contracaecum (rudolphii)* (Nematoda), and *Aponurus* sp. (Digenea), were also recovered from *L. sardina* in both studies. Two species of parasites previously reported from *L. sardina*, *Gyrodactylus* sp. and *Spirocamallanus* sp. (Olson 1979) were not found in this study. The difference in parasite richness between the previous study (Olson 1979) (18 taxa) and this study (6 taxa) may be explained by the difference in the sample sizes of *L. sardina* examined in the two studies. Olson (1979) examined 346 specimens while 30 specimens were examined in this study. Rare species of parasites are more likely to be found in large host sample sizes (Poulin 1998). Considering the difference in sample size and the time (40 years) between the two studies, the parasite infracommunities of *L. sardina* were similar between Olson (1979) and this study.

This study showed the first direct comparison of the parasite communities of three host species *A. affinis*, *As. californiensis*, and *L. tenuis*, in southern California, U.S.A. and one host species, *L. sardina*, in the Gulf of California, Mexico. Many parasite taxa reported are new host records for *A. affinis* and *As. californiensis*. The parasite communities were different among the four host species at the infracommunity level. The most abundant parasite taxa, *C. (rudolphii)*, *Galactosomum* sp., and larval trypanorhynchs were associated with two host species, *A. affinis* and *As. californiensis*. Host diet and feeding strategy may be an important variable affecting the composition of parasite communities among the four host species studied mainly because these parasites are trophically transmitted and the dietary breadth of *A. affinis* and *As. californiensis* is much broader in relation to *L. sardina* and *L. tenuis*.

ACKNOWLEDGMENTS

I thank Dr. Donald Buth (University of California, Los Angeles), Dr. Ralph Appy (Cabrillo Marine Aquarium), Dr. David Jacobs (University of California, Los Angeles), Dr. Karen Martin (Pepperdine University), and Dr. Michael Shin (University of California, Los Angeles) for their comments on an earlier draft of this manuscript. Dr. Ralph Appy, Dr. Ian Beveridge (University of Melbourne), Dr. Julianne Passarelli (Cabrillo Marine Aquarium), and Dr. Danny Tang (Orange County Sanitation District) provided invaluable help with identification of parasites. I would extend a special thanks to Dr. Ralph Appy, Dr. Kimo Morris (Santa Ana College), Dr. Jeff Watanabe (Ohlone College), Adriana Hernández-Álvarez (Universidad Autónoma de Baja California Sur) and Bayne Westrick-Snapp (Cabrillo Marine Aquarium) for invaluable assistance with fish collections in Mexico. Thanks to Dr. Ralph Appy, Chelsea Williams (Occidental College), and Johnathan Williams (Occidental College) for samples of *A. affinis*, *As. californiensis*, and *L. tenuis* from San Diego Bay and Dr. Julianne Passarelli for samples of *A. affinis* from Cabrillo Beach.

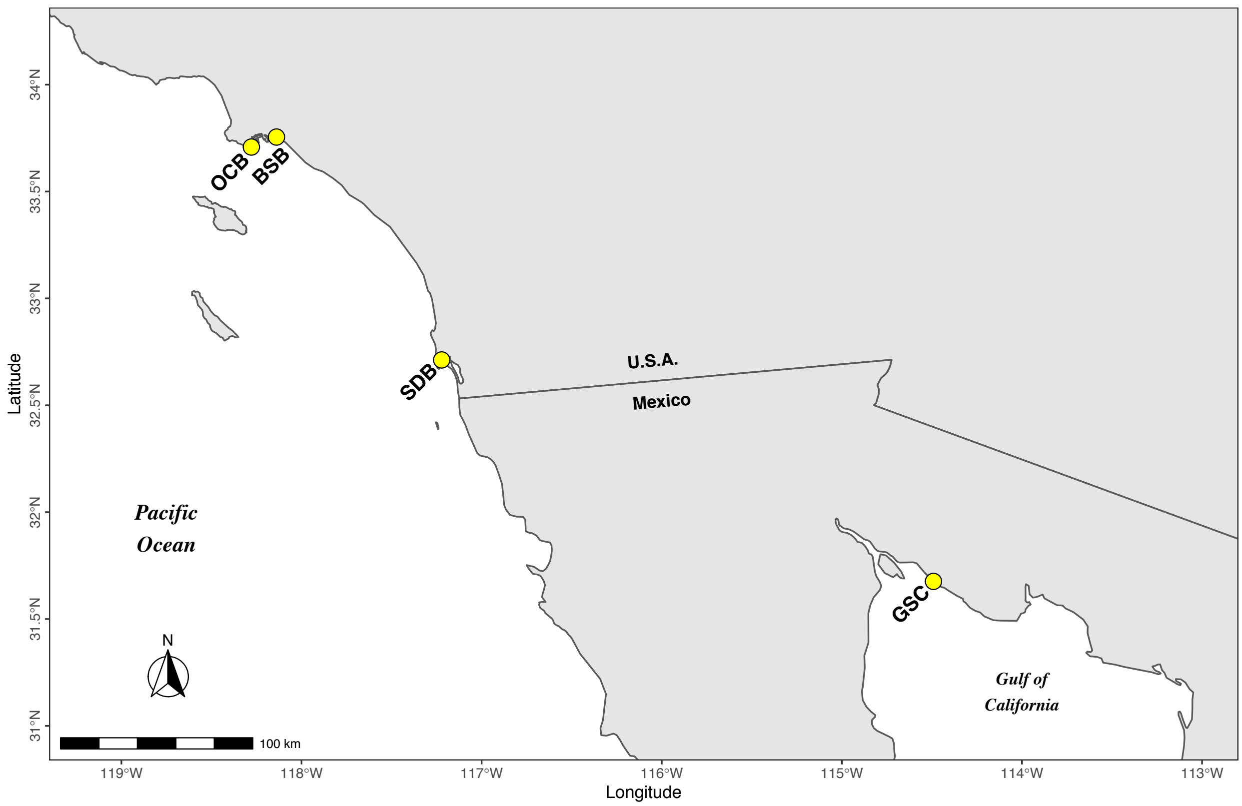

Figure 3.1. Map of the sampling localities of *Atherinops affinis* (OCB, SDB), *Atherinopsis californiensis* (BSB, SDB), and *Leuresthes tenuis* (SDB) in southern California, U.S.A. and the sampling locality of *Leuresthes sardina* (GSC), in Sonora, Mexico. Localities: OCB = Outer Cabrillo Beach, BSB = Belmont Shore Beach, SDB = San Diego Bay, GSC = El Golfo de Santa Clara.

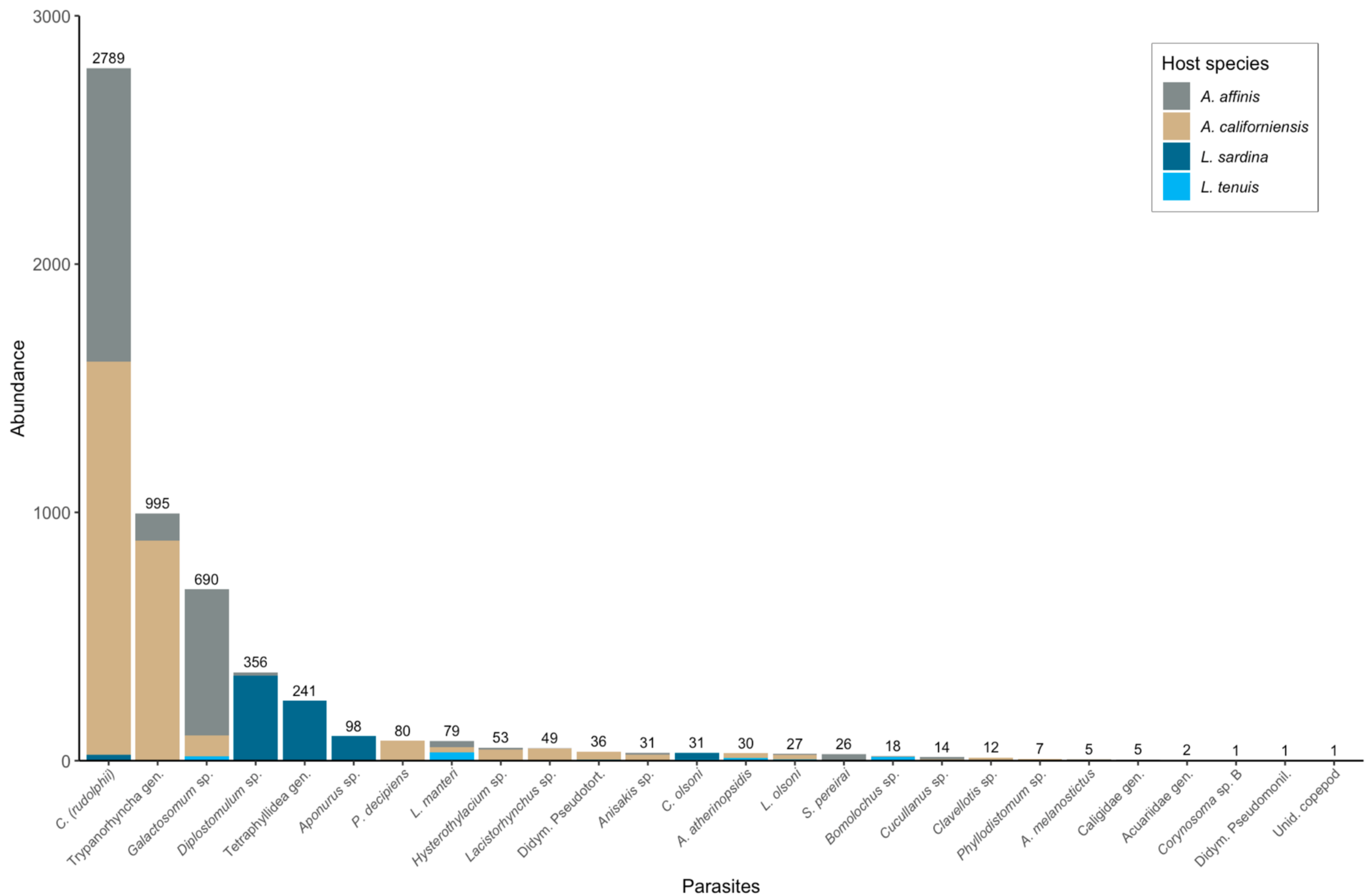

Figure 3.2. Rank abundance of metazoan parasites of recovered from *Atherinops affinis*, *Atherinopsis californiensis*, and *Leuresthes tenuis* collected in southern California, U.S.A., and *Leuresthes sardina* collected in the Gulf of California, Mexico.

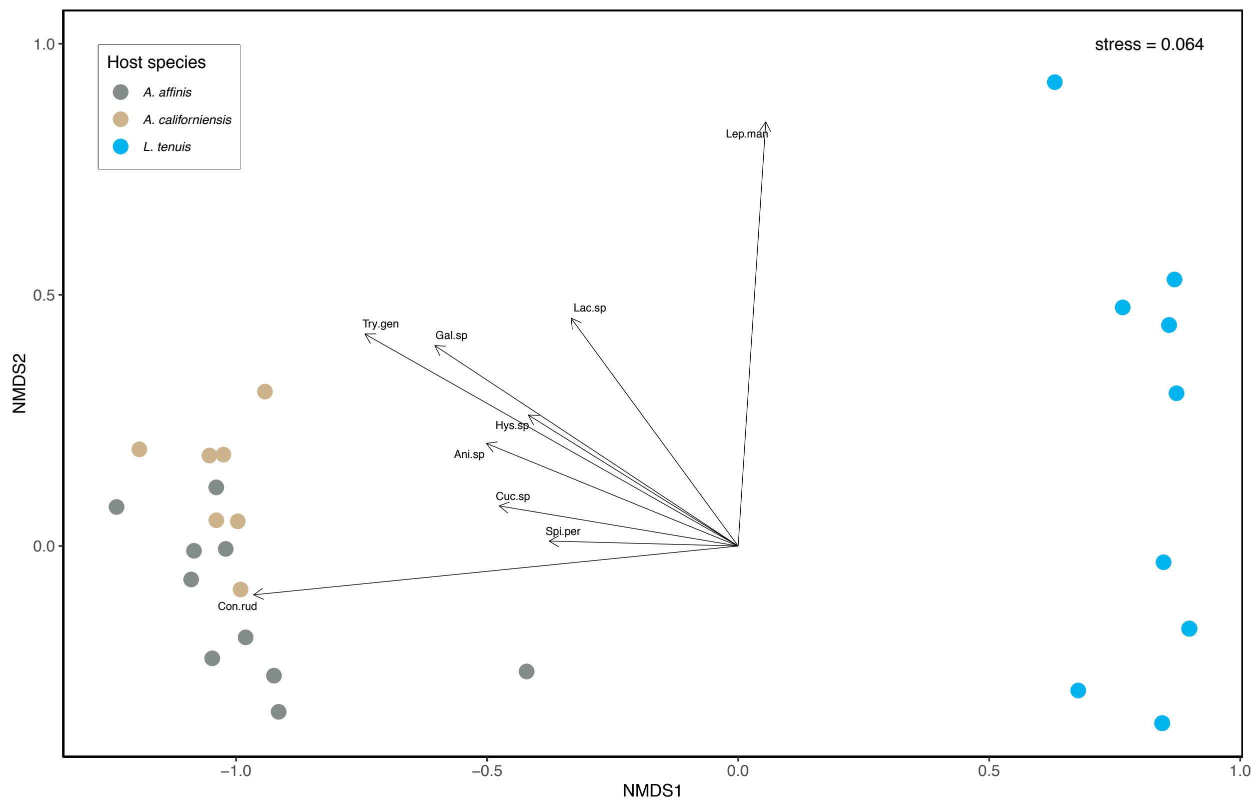

Figure 3.3. Nonmetric multidimensional scaling (nMDS) plot based on abundance of metazoan parasites of *Atherinops affinis*, *Atherinopsis californiensis*, and *Leuresthes tenuis*. The plot shows similarity among parasite infracommunities recovered from specimens of the three host species collected in the same net haul in San Diego Bay, California, U.S.A. on 3 April 2016.

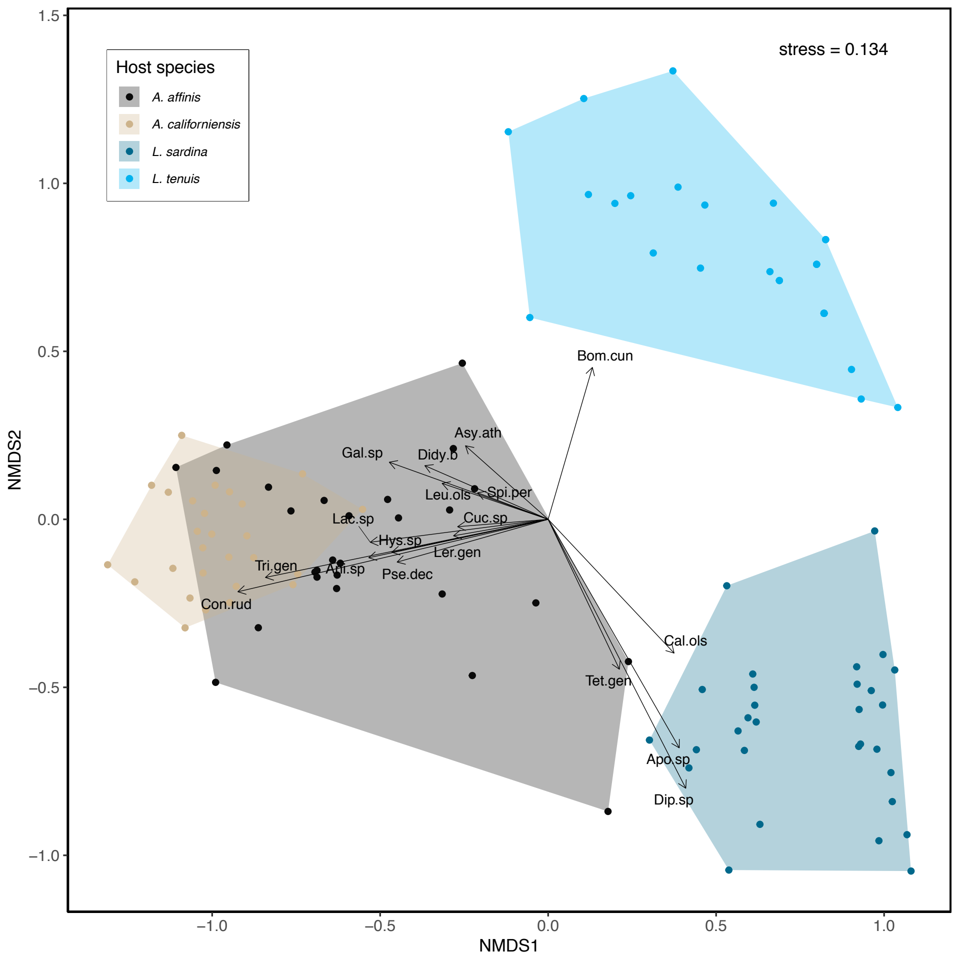

Figure 3.4. Nonmetric multidimensional scaling (nMDS) plot based on abundance of metazoan parasites recovered from *Atherinops affinis*, *Atherinopsis californiensis*, *Leuresthes sardina* and *Leuresthes tenuis*. The plot shows similarity among parasite infracommunities. Specimens of *Atherinops affinis*, *Atherinopsis californiensis*, and *Leuresthes tenuis* were collected in southern California, U.S.A., and specimens of *Leuresthes sardina* were collected in the Gulf of California, Mexico.

Table 3.1. GPS coordinates of the sampling localities of *Atherinops affinis* (ICB, SDB), *Atherinopsis californiensis* (BSB, SDB), and *Leuresthes tenuis* (SDB) in southern California, U.S.A. and the sampling locality of *Leuresthes sardina* (GSC), in Sonora, Mexico.

Locality	Locality Code	State/Country	Latitude	Longitude
Outer Cabrillo Beach	OCB	California, U.S.A	33°42'29.0"N	118°16'42.6"W
Belmont Shore Beach	BSB	California, U.S.A	33°45'17.2"N	118°08'20.6"W
San Diego Bay	SDB	California, U.S.A	32°42'43.1"N	117°13'19.2"W
El Golfo de Santa Clara	GSC	Sonora, Mexico	31°40'33.5"N	114°29'28.4"W

Table 3.2. Overall prevalence (P%), mean intensity (I), and mean abundance (A) of metazoan parasites recovered from *Atherinops affinis*, *Atherinopsis californiensis*, and *Leuresthes tenuis* collected in southern California, U.S.A., and specimens of *Leuresthes sardina* collected in the Gulf of California, Mexico.

	Host Species											
	A. affinis			***As. californiensis***			***L. sardina***			***L. tenuis***		
Parasite species	P (%)	I	A	P (%)	I	A	P (%)	I	A	P (%)	I	A
BRANCHIURA												
Argulus melanostictus	3.70	1.0	0.04	7.41	1.0	0.07	3.33	1.0	0.03	3.33	1.0	0.03
COPEPODA												
Bomolochus sp.	7.41	1.0	0.07	3.70	1.0	0.03	---	---	---	33.3	1.5	0.5
Caligus olsoni	---	---	---	---	---	---	60.0	1.5	0.9	13.3	1.0	0.13
Lernaeopodidae gen. sp.	---	---	---	22.2	1.83	0.41	---	---	---	---	---	---
Caligidae (chalimus) gen. sp.	3.70	3.0	0.11	---	---	---	---	---	---	---	---	---
MONOGENEA												
Leuresthicola olsoni	7.41	1.5	0.11	29.6	2.0	0.59	---	---	---	10.0	1.33	0.13
ACANTHOCEPHALA												
Corynosoma sp. B	---	---	---	3.7	1.0	0.04	---	---	---	---	---	---
CESTODA												
Lacistorhyncus sp.	3.70	1.0	0.04	66.7	2.61	1.74	---	---	---	3.33	1.0	0.03
Tetraphyllidean gen. sp.	---	---	---	---	---	---	23.3	34.4	8.03	---	---	---
Trypanorhyncha gen. sp.*	77.8	5.24	4.07	100	32.5	32.5	---	---	---	---	---	---
DIGENEA												
Aponurus sp.	---	---	---	---	---	---	83.3	3.92	3.27	---	---	---
Asymphylodora atherinopisidis	---	---	---	44.4	1.67	0.741	---	---	---	23.3	1.43	0.33
Didymozoidae Pseudomonilicaecum	---	---	---	---	---	---	---	---	---	3.33	1.0	0.03
Didymozoidae Pseudotorticaecum	---	---	---	40.7	2.91	1.19	---	---	---	6.67	2.0	0.13
Diplostomulum sp.	22.2	2.33	0.52	---	---	---	100	11.4	11.4	---	---	---
Galactosomum sp.	29.6	73.5	21.8	66.7	4.72	3.15	---	---	---	26.7	2.12	0.57
Lepocreadium manteri	14.8	6.25	0.93	11.1	7.0	0.78	---	---	---	10.0	11.0	1.1
Phyllodistomum sp.	7.41	3.5	0.26	---	---	---	---	---	---	---	---	---
NEMATODA												
Acuariidae gen. sp.	3.70	2.0	0.07	---	---	---	---	---	---	---	---	---
Anisakis sp.	7.41	1.5	0.11	29.6	0.519	1.75	---	---	---	---	---	---
Contracaecum (rudolphii)	96.3	45.5	43.8	100	58.7	58.7	46.7	1.57	0.73	3.33	1.0	0.03
Cucullanus sp.	7.41	3.0	0.22	---	---	---	---	---	---	---	---	---
Hysterothylacium sp.	7.41	1.5	0.11	33.3	3.67	1.22	---	---	---	---	---	---
Pseudoterranova sp.	---	---	---	55.6	5.53	3.07	---	---	---	---	---	---
Spirocamallanus pereirai	25.9	3.71	0.96	---	---	---	---	---	---	---	---	---

* Recently, Trypanoryncha gen. sp. was identified as *Grillotia (Christianella) carvajalregorum* by Dr. Ian Beveridge

Table 3.3. Most abundant species of ectoparasites and endoparasites recovered from *Atherinops affinis*, *Atherinopsis californiensis*, and *Leuresthes tenuis* collected in southern California, U.S.A., and from *Leuresthes sardina* collected in the Gulf of California, Mexico.

Parasite species	**Total**	***A. affinis***	***As. californiensis***	***L. sardina***	***L. tenuis***
Ectoparasites					
Contracaecum (rudolphii)	**2789**	1182	1584	22	1
Trypanorhyncha gen. sp.	**995**	110	885	0	0
Galactosomum sp.	**690**	588	85	0	17
Endoparasites					
Caligus olsoni	**31**	0	0	27	4
Leuresthicola olsoni	**27**	3	20	0	4
Bomolochus sp.	**18**	2	1	0	15

Table 3.4. Species of parasites showing significant difference in abundance in relation to host species.

Parasite species	**Dev**	***P* value**
Bomolochus sp.	22.053	0.001
Caligus olsoni	47.46	0.001
Lernaeopodidae gen. sp.	18.223	0.001
Leuresthicola olsoni	17.561	0.004
Lacistorhyncus sp.	57.607	0.001
Tetraphyllidean gen. sp.	20.555	0.002
Trypanorhyncha gen. sp.	163.297	0.001
Aponurus sp.	96.304	0.001
Asymphylodora atherinopisidis	33.746	0.001
Didymozoidae Pseudotorticaecum	28.258	0.001
Diplostomulum sp.	122.363	0.001
Galactosomum sp.	43.304	0.001
Anisakis sp.	39.146	0.001
Contracaecum sp.	164.111	0.001
Hysterothylacium sp.	31.36	0.001
Pseudoterranova sp.	50.652	0.001
Spirocamallanus pereirai	21.419	0.001

Analysis of Deviance (Dev) was used to estimate differences in abundance in relation to host species

Table 3.5. Results of indicator species analysis (*IndVal*) with parasite data. For each host or host combination (Host species), the species of parasites with the highest correlation (Parasite species), the value of the correlation (r_{pb}), the statistical significance of the association (p-value), the Specificity, and Fidelity are indicated.

Host species	Parasite species	r_{pb}	p	Specificity	Fidelity
A. affinis + As. californiensis	*Contracaecum (rudolphi)*	0.987	< 0.001	0.993	0.973
	Tripanorhyncha gen. sp.	0.943	< 0.001	1.000	0.889
	Galactosomum sp.	0.699	< 0.001	0.978	0.500
As. californiensis + L. tenuis	*Asymphylodora atherinospsidis*	0.546	< 0.001	1.000	0.298
A. affinis	*Spirocamallanus* sp.	0.509	< 0.001	1.00	0.259
As. californiensis	*Lacistorhynchus* sp.	0.800	< 0.001	0.961	0.667
	Pseudoterranova sp.	0.745	< 0.001	1.000	0.556
	Didymozoidae Pseudotorticaecum	0.605	< 0.001	0.899	0.407
	Hysterothylacium sp.	0.553	< 0.001	0.917	0.333
	Anisakis sp.	0.494	< 0.001	0.824	0.296
	Lernaeopodidae gen. sp.	0.471	< 0.001	1.000	0.222
	Leuresthicola olsoni	0.458	0.004	0.708	0.296
L. sardina	*Diplostomulum* sp.	0.978	< 0.001	0.957	1.000
	Aponurus sp.	0.913	< 0.001	1.000	0.833
	Caligus olsoni	0.723	< 0.001	0.871	0.600
	Tetraphyllidean larva type VI	0.483	< 0.001	1.000	2.333
L. tenuis	*Bomolochus* sp.	0.522	< 0.001	0.818	0.333

CHAPTER 3 – SUPPLEMENTAL MATERIALS

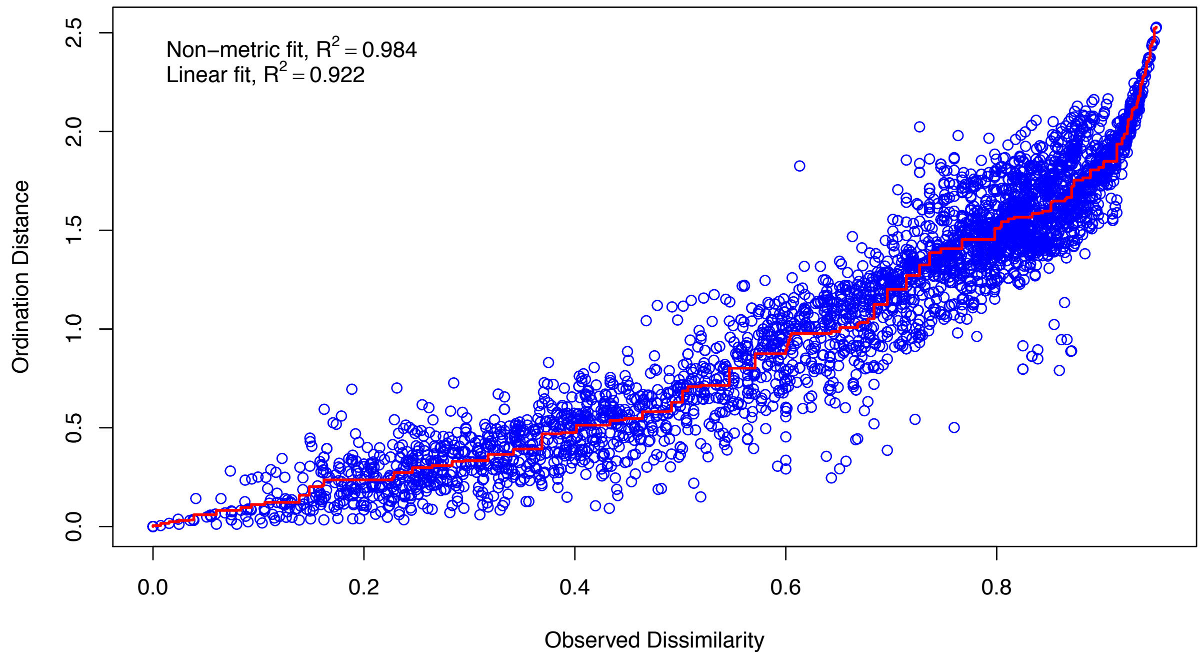

Figure 1.S3. Shepard diagram of the distances in the nMDS plot (Figure 3.3) against the dissimilarities in the Bray-Curtis matrix. The red line represents the fitted non-parametric regression.

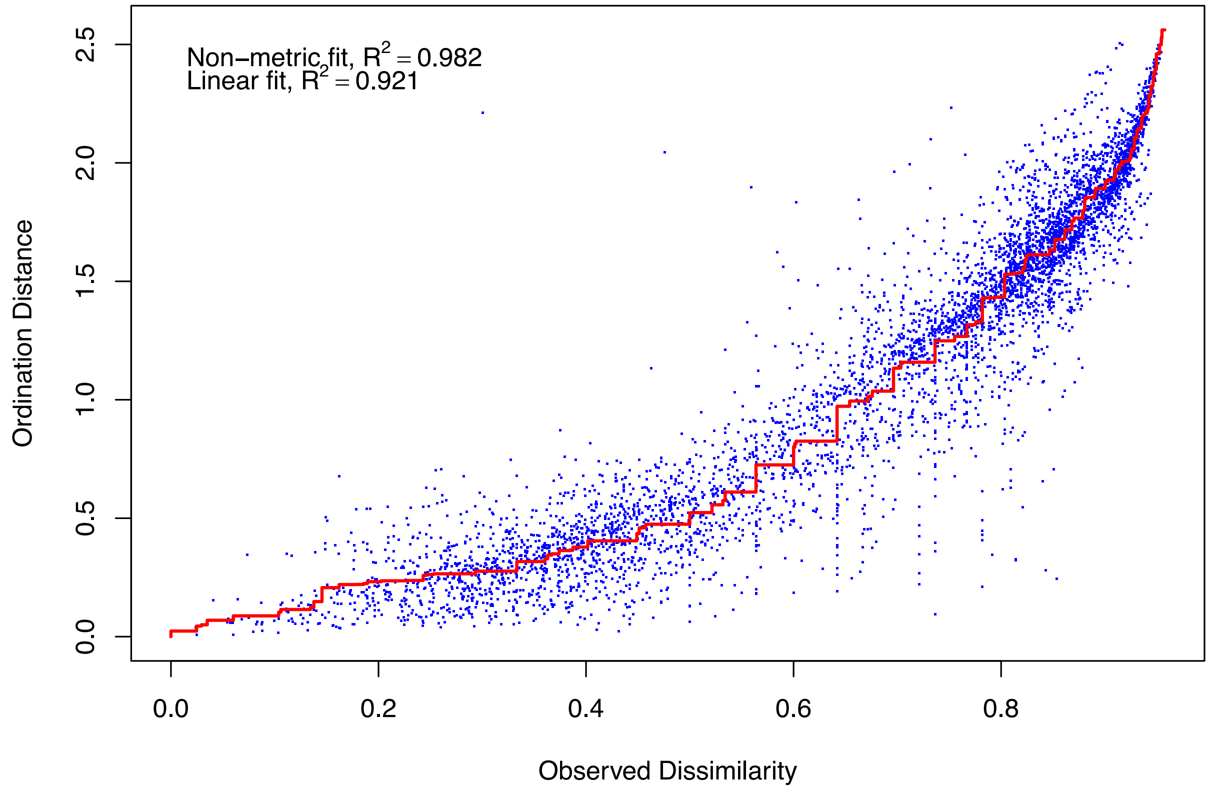

Figure 2.S3. Shepard diagram of the distances in the nMDS plot (Figure 3.4) against the dissimilarities in the Bray-Curtis matrix. The red line represents the fitted non-parametric regression.

REFERENCES

Ángeles-Hernández, J. C., Gómez-de Anda, F. R., Reyes-Rodríguez, N. E., Vega-Sánchez, V., García-Reyna, P. B., Campos-Montiel, R. G., Calderón-Apodaca, N. L., Salgado-Miranda, C., & Zepeda-Velázquez, A. P. 2020. Genera and species of the Anisakidae family and their geographical distribution. *Animals* 10: 2374.

Bartlett, C. M. 1996. Morphogenesis of *Contracaecum rudolphii* (Nematoda: Ascaridoidea), a parasite of fish-eating birds, in its copepod precursor and fish intermediate hosts. *Parasite* 4: 367-376

Bernardi, G., Findley, L. and Rocha-Olivares, A. 2003. Vicariance and dispersal across Baja California in disjunct marine fish populations. *Evolution* 57: 1599–1609.

Bush, A. O., Lafferty, K. D., Lotz, J. M., and Shostak, A. W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *The Journal of Parasitology* 83: 575–583.

Campanella, D., Hughes, L. C., Unmack, P. J., Bloom, D. D., Piller, K. R. and Ortí, G. 2015. Multi-locus fossil-calibrated phylogeny of Atheriniformes (Teleostei, Ovalentaria). *Molecular Phylogenetics and Evolution* 86: 8–23.

Chen, H-W., Liu, W-C., Davis, A. J., Jordán, F., Hwang, M-J., and Shao, K-T. 2008. Network position of hosts in food webs and their parasite diversity. *Oikos* 117: 1847–1855.

Clarke, K. R., Somerfield, P.J., and Chapman, M.G. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* 330: 55–80.

De Cáceres, M., Font, X., and Oliva, F. 2008. Assessing species diagnostic value in large data sets: A comparison between phi-coefficient and Ochiai index. *Journal of Vegetation Science*, 19: 779-788.

De Cáceres, M., Legendre, P., and Moretti, M. 2010. Improving indicator species analysis by combining groups of sites. *Oikos* 119: 1674-1684.

Dufrêne, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Henriquez, V. P., Gonzalez, M. T., Licandeo, R., and Carvajal, J. 2011. Metazoan parasite communities of rock cod *Eleginops maclovinus* along southern Chilean coast and their use as biological tags at a local spatial scale. *Journal of Fish Biology* 79: 1851–1865.

Henríquez, V., and González, M. T. 2012. Patterns of variation in parasite component communities and infracommunities of a littoral fish species from the northern coast of Chile. *Journal of helminthology* 88: 89–96.

Higgins, B. A., and Horn, M. H. 2014. Suction among pickers: jaw mechanics, dietary breadth and feeding behaviour in beach-spawning *Leuresthes* spp. compared with their relatives. *Journal of Fish Biology* 84: 1689–1707.

Horn, M.H., Gawlicka, A.K., German, D.P., Logothetis, E., Cavanagh, J.W., and Boyle, K.S. 2006. Structure and function of the stomachless digestive system in three related species of New World silverside fishes (Atherinopsidae) representing herbivory, omnivory, and carnivory. *Marine Biology* 149, 1237-1245.

Kuris, A. M., Blaustein, A. R. and Alio, J. J. 1980. Hosts as islands. *American Naturalist* 116: 570–586.

Li, A.-X., D'Amelio, S., Paggi, L., He, F., Gasser, R. B., Lun, Z.-R., Abollo, E., Turchetto, M., Zhu, X.-Q. 2005. Genetic evidence for the existence of sibling species within *Contracaecum rudolphii* (Hartwich, 1964) and the validity of *Contracaecum septentrionale* (Kreis, 1955) (Nematoda: Anisakidae). *Parasitology Research* 96, 361–366.

Love, M.S. and Moser, M. 1983. A checklist of parasites of California, Oregon, and Washington marine and estuarine fishes.: NOAA Technical Report NMFS SSRF, U.S. Department of Commerce, Rockville, Maryland. 777:1-576.

Madinabeitia, I., and Nagasawa, K. 2013. Double-netting: an alternative approach for the recovery of parasitic copepods from finfishes. *Journal of Natural History* 47: 529–541.

Moravec F. 2009. Experimental studies on the development of *Contracaecum rudolphii* (Nematoda: Anisakidae) in copepod and fish paratenic hosts. *Folia Parasitol (Praha)*: 56(3):185-93.

Munoz, G., Grutter, A. S. and Cribb, T. H. 2005. Endoparasite communities of five fish species (Labridae: Cheilininae) from Lizard Island: how important is the ecology and phylogeny of the hosts? *Parasitology* 132: 363–13.

Olson, L. J. 1979. Host-parasite associations of the grunions *Leuresthes sardina* and *Leuresthes tenuis* from the Gulf of California and California. Ph.D. Dissertation. The University of Arizona. Tucson, Arizona.

Poulin, R. 1995. Phylogeny, Ecology, and the Richness of Parasite Communities in Vertebrates. *Ecological Monographs* 65: 283–302.

Poulin, R. 1998. Comparison of three estimators of species richness in parasite component communities. *The Journal of Parasitology* 84: 485–490.

Poulin, R. 2007. Evolutionary Ecology of Parasites. Princeton, NJ: Princeton University Press.

Poulin, R. 2015. Quantifying parasite diversity. In S. Morand, B. Krasnov, and D. Littlewood (Eds.), Parasite Diversity and Diversification: Evolutionary Ecology Meets Phylogenetics (pp. 9-26). Cambridge: Cambridge University Press.

Poulin, R., and Rohde, K. 1997. Comparing the richness of metazoan ectoparasite communities of marine fishes: controlling for host phylogeny. *Oecologia* 110: 278–283.

Poulin, R., Guilhaumon, F., Randhawa, H. S., Luque, J. L. and Mouillot, D. 2011. Identifying hotspots of parasite diversity from species–area relationships: host phylogeny versus host ecology. *Oikos* 120: 740–747.

R Core Team 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Shamsi, S. 2019. Parasite loss or parasite gain? Story of *Contracaecum* nematodes in antipodean waters. Parasite Epidemiology and Control 4: e00087.

Timi, J. T., and Poulin, R. 2003. Parasite community structure within and across host populations of a marine pelagic fish: how repeatable is it? *International Journal for Parasitology* 33: 1353–1362.

Timi, J. T., Rossin, M.A., Alarcos, A.J., Braicovich, P.E., Cantatore, D.M.P., Lanfranchi, A.L. 2011. Fish trophic level and the similarity of non-specific larval parasite assemblages. *International Journal for Parasitology* 41: 309–316.

Vickery, W. L., and Poulin, R. 1998. Parasite extinction and colonisation and the evolution of parasite communities: a simulation study. *International Journal for Parasitology* 28: 727–737.

Wang, Y., Naumann, U., Wright, S.T., Warton, D.I. 2012. mvabund– an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution* 3: 471–474.

Willner, W., Tichý, L. and Chytrý, M. 2009. Effects of different fidelity measures and contexts on the determination of diagnostic species. *Journal of Vegetation Science* 20: 130-137.