

## Short Communication

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# Missing link: California rock crabs serve as intermediate hosts for the parasite *Helicometrina nimia*

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## Abstract

Parasites can have strong effects on invertebrate host behaviour, fecundity and survival in marine ecosystems. However, parasites are often poorly documented and still rarely integrated into marine ecological modelling; comprehensive surveys of infection in marine invertebrates are sporadic at best. For example, rock crabs are an important part of Californian coastal ecosystems, both as regulators of mussel populations and non-native species, and as prey items for predators like sea otters, but their parasite communities and potential effects on crab population dynamics are seldom studied or understood. Here, we present the first report of infection by the trematode *Helicometrina nimia* in the economically and ecologically important red rock crab (*Cancer productus*) and Pacific rock crab (*Romaleon antennarium*). As intermediate hosts, they are a missing link for infection by *H. nimia* in Californian fish that was unreported until now. Based on these findings, we advocate for further research into parasite diversity and their potential effects on ecologically and commercially important species.

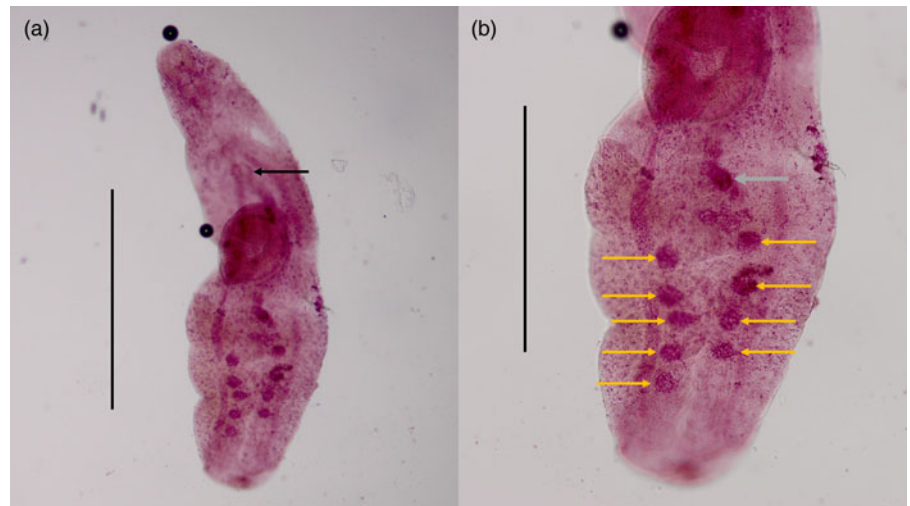
## Introduction

Digenean trematodes comprise one of the most common parasite groups in marine invertebrates, often infecting multiple host species due to their complex lifecycle stages, and affecting host survival, physiology or behaviour (Mouritsen & Poulin, 2002; Lefèvre *et al.*, 2009; Leiva *et al.*, 2017; Dairain *et al.*, 2019). In recent years, parasites have increasingly been recognized as critical components of marine food webs; they can influence biodiversity and ecosystem functioning (Mouritsen & Poulin, 2005; Lafferty *et al.*, 2008; Frainer *et al.*, 2018; Dairain *et al.*, 2019). The effects of parasitism may be particularly important in marine ecosystems for species that alter the physical structure and flow of nutrients in benthic communities (bioturbators) such as rock crabs (Fanjul *et al.*, 2011; Dairain *et al.*, 2019).

Rock crab commercial fishing has been rapidly expanding in California while research into their population dynamics is limited. Proper management will require accurate ecological information (Fitzgerald *et al.*, 2018). Commercial fishing takes vary between 450 and 900 metric tons of crab annually and is a growing market (CDFW, 2019; Fitzgerald *et al.*, 2019). Recent reports have raised concern about a decline in the population of red (*Cancer productus*), yellow (*Metacarcinus anthonyi*) and brown rock crabs (*Romaleon antennarium*), although these trends could not be attributed specifically to either environmental factors or overfishing (Fitzgerald *et al.*, 2019). Beyond their economic importance, rock crabs also fulfil key ecosystem roles as controllers of non-native species like the European green crab (*Carcinus maenas*) (Jensen *et al.*, 2007) or tunicates (Epelbaum *et al.*, 2009). *Cancer productus* and *R. antennarium* may also be important controllers of mussel populations, which, left unchecked, can become dominant in lower intertidal communities (Hull & Bourdeau, 2017). With the loss of keystone predators due to sea star wasting disease, researchers have suggested that rock crabs may be essential in compensating for sea star population decline (Hull & Bourdeau, 2017). They are also important prey items of the southern sea otter (*Enhydra lutris nereis*) (Fujii *et al.*, 2017), as well as benthic fishes, octopus and bottom-foraging sharks (Carroll & Winn, 1989). Here, we outline the discovery of a digenean parasite in these ecologically and environmentally important species, highlighting a significant gap in knowledge of our understanding of cancrid crab populations in the Eastern North Pacific.

## Materials and methods

We surveyed various crab species in central California as part of a broader study investigating the prey of sea otters to discover the intermediate host(s) of their intestinal parasites. Crabs were collected via hand nets and traps in Santa Cruz, Monterey and San Luis Obispo counties from municipal wharfs (Santa Cruz Warf, Monterey Bay Municipal Warf 2, Cayucas Pier and Port San Luis Pier) during the summer of 2019. Specimens were frozen to euthanize, and then



**Fig. 1.** Metacercaria of *Helicometrina* sp. ex *Cancer productus* stained: (a) whole worm, with the genital pore highlighted (arrow); (b) posterior body showing immature testes (yellow) and ovary (grey). Scale bars: (a) 1 mm; (b) 500  $\mu$ m.

dissected at the California Department of Fish and Wildlife office in Santa Cruz, California. Species investigated included *Metacarcinus gracilis* ( $n = 149$ ), *Metacarcinus magister* ( $n = 4$ ), *C. productus* ( $n = 64$ ) and *R. antennarium* ( $n = 63$ ). During these investigations, dissections of *C. productus* and *R. antennarium* from the Monterey Bay revealed infections by metacercarial cysts of an unknown trematode. The cysts had a thin brown melanized capsule, were spherical in shape and found within the haemocoel (just inside the carapace and body wall) and joints of the crabs. Metacercariae were manually extracted from their cysts and were examined morphologically and molecularly to determine the species.

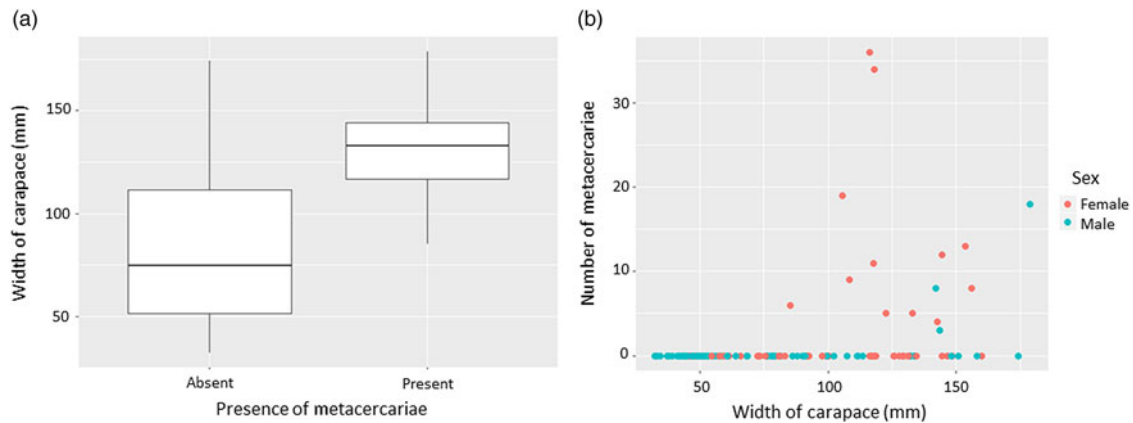
For light microscopy, metacercariae were stained with acetic acid carmine, cleared in clove oil and mounted permanently in Canada balsam (fig. 1). Molecular characterization of the 28 s ribosomal RNA (rRNA) large ribosomal subunit gene was conducted with universal primers T16 (5' GAG ACC GAT AGC GAA ACA AGT AC 3') and T30 (5' TGT TAG ACT CCT TGG TCC GTG 3') (Harper & Saunders, 2001), sequenced via the Sanger method at the University of Otago, New Zealand. Characterization of the 18 s rRNA small ribosomal subunit gene used primers SB3a (5' GGA GGG CAA GTC TGG TGC 3') and A27a (CCA TAC AAA TGC CCC CGT CTG) and was sequenced via the Sanger method at the University of Alberta, Canada. Resulting sequences were identified with a nucleotide-sequence BLASTn search via the National Center for Biotechnology Information website (Altschu *et al.*, 1990; Madden, 2002). The 18 s sequences were edited with the software Mega X, and fragments aligned by MUSCLE with the program's default parameters (Kumar *et al.*, 2018). For the two species infected (*C. productus* and *R. antennarium*), we investigated the effect of host size (width of carapace), location of capture, sex and species on infection prevalence (binomial distribution, 'logit' function) and intensity (quasi-Poisson distribution, 'log' function) of the trematode, through Rstudio ( $n = 127$ ) (Rstudio Team, 2015). *Metacarcinus gracilis* was not included in the model as they were not observed to be infected and would have led to zero inflation of the model.

## Results and discussion

Morphological examination of the metacercariae identified the specimens as members of the genus *Helicometrina* due to the

presence of nine testes and the genital pore located below the caecal bifurcation (fig. 1) (Cribb, 2005). Metacercariae were, on average, 2190  $\mu$ m long and 590  $\mu$ m wide (see supplementary material), and the cysts were, on average, 731  $\mu$ m in diameter. The 28S sequence from metacercariae retrieved from *C. productus* returned a closest match to *Helicometrina nimia* (ex *Haemulon falvolineatum*, French grunt, Mexico) with 97.97% identity (MK648305; see Pérez-Ponce de León & Hernández-Mena, 2019). The 18S sequence from metacercariae retrieved from *C. productus* returned a closest match with *H. nimia*, with 98.93% (KJ995999, ex *Acanthistius pictus*, brick sea bass, Chile; see Gonzalez, 2016). The 18 s sequence from *R. antennarium* also returned a closest match with *H. nimia*, with 98.64% (KY614306, ex *Semicossyphus darwini*, Galapagos sheephead wrasse, Chile; see Ñacari *et al.*, 2018). In three partial 18 s sequences (two ex *C. productus* and one ex *R. antennarium*) with coverage at 307 bp, there were four haplotypes shared by the metacercarial sequences that were different from three exemplar sequences from South America (KJ995995, González *et al.*, 2013; KY614306, Ñacari *et al.*, 2018; KF938641, Oliva *et al.*, 2015). Previous reporting of 18 specimens of *H. nimia* from three different host species found nine variable sites in the 18 s region from a partial sequence of 372 bp, with an average pairwise difference of three (Oliva *et al.*, 2015). We conclude our finding to likely be *H. nimia* based upon comparison to available sequences and morphological similarities. The sequences had some relation to *Helicometrina labrisomi*, but the specimens did not correspond to this species' morphological description (Linton, 1910).

Infection prevalence was 14% in *C. productus* with an average intensity of  $11.7 \pm 3.2$  per infected crab, and 9.5% in *R. antennarium* with an average intensity of  $14.3 \pm 4.9$  parasites per infected crab. Statistical analysis revealed a significant effect of carapace width on prevalence ( $P < 0.01$ ) and intensity ( $P < 0.01$ ), and sex ( $P = 0.01$ ) on intensity, with females having greater intensity of infections (fig. 2). Location of capture, crab species and their interaction had no significant effect in the models and were sequentially removed to create a minimum adequate model. This is interesting as no crabs in San Luis Obispo were infected. The lack of significant effect of location on prevalence may be due to low prevalence and our limited sample size. Future research should expand into broader sampling to determine if infection does occur further south, and if there is a significant difference in infection prevalence.



**Fig. 2.** Effect of carapace width in *Cancer productus* and *Romaleon antennarium* on infection. The two species are pooled as the model showed no significant difference between them. (a) Boxplot of the effect of carapace width on prevalence (presence/absence) of *Helicometrina* sp., median and quartiles. (b) Scatterplot of the interaction of carapace width on intensity of infection (total parasites) by sex of the crab host (male, blue; female, red).

No metacercariae were discovered in any of the Dungeness (*M. magister*) or graceful rock crabs (*M. gracilis*) collected. The lack of infection in *M. gracilis* may be due to differences in habitat and behaviour; *M. gracilis* are much smaller than *C. productus* and *R. antennarium*, and while they co-occur in some habitat, they are also found in shallower, open sandy habitats or eelgrass beds and feed on different prey species (Orensanz & Gallucci, 1988; Orensanz *et al.*, 1995). Since *H. nimia* is not host specific in their decapod hosts in South America (Leiva *et al.*, 2015, 2017), this lack of infection may be due to differences in habitat selection. It should be noted that only four Dungeness crabs were collected, possibly due to the time of year or the difficulty of collection via hand net/trap. Therefore, we cannot comment on whether this species is host for this parasite. Future sampling should target *M. magister* as they are of great economic significance (CDFW, 2019).

Species of *Helicometrina* have previously been reported to utilize various decapod crustaceans as intermediate hosts. In South America, host families include Epialtidae, Porcellanidae and Xanthidae (Leiva *et al.*, 2015, 2017). There exists one report of *Helicometrina* cf. *nimia* infection in a species of Cancridae (*Romaleon polyodon*) in Chile, although this report was from a single crab (Leiva *et al.*, 2015). The definitive hosts of *Helicometrina* spp. are teleost fish. Studies have reported *Helicometrina* spp. in central and South America from fish species in the families Merlucciidae, Serranidae, Pingipedidae, Labrisomidae, Cheilodactylidae, Ophidiinae and Gobiesocidae (Gonzalez *et al.*, 2006; Muñoz & Olmos, 2008; Morales-Serna *et al.*, 2017). In North America, a study found *H. nimia* tended to be a fish generalist (Holmes, 1990). *Helicometrina nimia* has been reported in shiner perch (*Cymatogaster aggregata*) (Arai *et al.*, 1988), and (as *Helicometrina elongata*) in perch (Embiotocidae), Hubbs (Blenniidae) and scorpionfish (Scorpaenidae) in Southern California (Montgomery, 1957). There is one report of *H. nimia* in Monterey California, where our study was conducted, in various species of fish (Chapa, 1969).

This is the first report of a *Helicometrina* species in crabs of the family Cancridae, from Pacific North America. The last report of this parasite in Californian fish was over 30 years ago (Holmes, 1990). Nonetheless, *H. nimia* is a generalist in terms of its definitive host use (Holmes, 1990; Gonzalez *et al.*, 2006; Muñoz & Olmos, 2008; Morales-Serna *et al.*, 2017) so it is likely that the parasite has remained unreported in the fish fauna until now.

For a first intermediate host, other species of *Helicometrina* use gastropod molluscs (Leiva *et al.*, 2015, 2017). In the Mediterranean, species of Opecoelidae were identified in marine snails and abalone, and the authors noted that the parasites, unlike other trematodes, can infect multiple gastropod intermediate host species (Jousson *et al.*, 1999; Leiva *et al.*, 2017). Other trematodes of the order Plagiorchiida have been seen to use mussels of the family Mytilidae (*Perumytilus purpuratus*) (Muñoz *et al.*, 2012) and scallops (*Argopecten purpuratus*) (Oliva & Sanchez, 2005) as their first intermediate hosts in South America. If *H. nimia* also utilizes mussels as their first intermediate host like their relatives in South America this could be significant, considering the possible importance of crab predation on controlling mussel populations (Hull & Bourdeau, 2017). However, the first intermediate host remains unknown (Leiva *et al.*, 2017). Future research should seek this last missing link in order to complete our knowledge of the life cycle of this parasite in California and gain a better understanding of its potential role and effects in the ecosystem, and on crab populations.

Decapod crabs tend to be prey items to teleost fish early in their development and before they attain a size large enough to avoid predation (except during moulting) (Carroll & Winn, 1989). We would expect that infection then increases in prevalence and intensity with size and age (e.g. over time), due to continued exposure to parasite larvae as well as reduced predation. Our analysis showed a significantly positive relationship between carapace width and both infection prevalence and intensity (fig. 2). Interestingly, infection was not seen in any crab with a carapace width smaller than 85 mm. There are a few possible explanations for this (it may be due to higher rates of predation on smaller crabs as a direct result of infection). Digenean trematodes commonly alter the behaviour of their gastropod intermediate hosts (Mouritsen & Poulin, 2002), and their crustacean intermediate hosts (McCurdy *et al.*, 1999; Hansen & Poulin, 2005; Lagrue *et al.*, 2007; Lefèvre *et al.*, 2009). *Paragonimus* cf. *westermanni* alters the behaviour of its decapod host (*Eriocheir japonica*) (Kotsyuba, 2018), *Microphallus turgidus* alters the swimming behaviour of Grass shrimp (*Palaemonetes pugio*) (Gonzalez, 2016) and co-infection by the trematode *Maritrema* sp. and acanthocephalans in the body cavity of shore crabs has been correlated with altered serotonin levels (Poulin *et al.*, 2003). The lack of infection in crabs with a carapace smaller than around 85 mm

may, thus, be indicative of high predation rates in small individuals that are infected. Alternatively, gill physiology and respiration behaviours can affect exposure to trematodes in crabs, which may explain the lack of observed infection in smaller crabs (Smith *et al.*, 2007). Though not all trematodes enter their crab host via the gills, some entering through percutaneous penetration at the leg (Gyoten, 2000). As some of the metacercariae were found in the leg joints of some crabs, percutaneous penetration may be more likely. Differences in habitat selection by juvenile and adults of *C. productus* may also explain the lack of infection in smaller crabs, as adults are more likely to be found in open areas and migrate at night to shallower waters (Orensanz & Gallucci, 1988). The full life cycle of *H. nimia* and how it is transmitted to crabs is unknown. Future investigations of the life cycle and effects of *H. nimia* are essential for our further understanding of the importance of this parasite in marine ecosystems.

Cancer crabs are an important part of marine benthic communities from intertidal to deep water through consumptive and non-consumptive effects (Fanjul *et al.*, 2011; Boudreau & Worm, 2012; Dairain *et al.*, 2019), as prey items for sea otters and fish species (Carroll & Winn, 1989; Fujii *et al.*, 2017), as secondary controllers of mussel populations (Hull & Bourdeau, 2017) and as non-native species control agents (Jensen *et al.*, 2007; Epelbaum *et al.*, 2009). Due to their increasing socio-economic importance, it is essential that research be conducted to investigate not only their little-known population dynamics but also their parasite communities as well (Fitzgerald *et al.*, 2018, 2019). We suggest specific research investigating the possible behavioural effects of infection, and how this might be affecting the role of cancer species in Californian marine food webs.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/S0022149X20000218>

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**Conflicts of interest.** None.

**Ethical standards.** The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals.

## References

- Altschu SF, Gish W, Miller W, Myers EW and Lipman DJ (1990) Basic local alignment search tool. *Journal of Molecular Biology* **215**, 403–410.
- Arai HP, Kabata Z and Noakes D (1988) Studies on seasonal changes and latitudinal differences in the metazoan fauna of the shiner perch, *Cymatogaster aggregata*, along the west coast of North America. *Canadian Journal of Zoology* **66**, 1514–1517.
- Boudreau S and Worm B (2012) Ecological role of large benthic decapods in marine ecosystems: a review. *Marine Ecology Progress Series* **469**, 195–213.
- California Department of Fish and Wildlife (CDFW) (2019) *Final California commercial landings*. Available at <https://www.wildlife.ca.gov/Fishing/Commercial/Landings>
- Carroll JC and Winn RN (1989) *Species profiles. Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest)—brown rock crab, red rock crab, and yellow crab*. US Fish and Wildlife Service Biological Report 82 (11.117). US Army Corps of Engineers, TR EL-82-4. 16 pp.
- Chapa E (1969) *Studies in digenetic trematodes of marine fishes from Monterey and Tomales Bays, California*. Thesis. University of the Pacific, Stockton CA, USA.
- Cribb TH (2005) Family Opecoelidae Ozaki, 1925. pp. 443–532 in Jones A, Bray RA and Gibson DI (Eds) *Keys to the trematoda*. Vol. 2. Cambridge, UK, CAB International.
- Dairain A, Legeay A and de Montaudouin X (2019) Influence of parasitism on bioturbation: from host to ecosystem functioning. *Marine Ecology Progressive Series* **619**, 201–214.
- Epelbaum A, Pearce CM, Barker DJ, Paulson A and Therriault TW (2009) Susceptibility of non-indigenous ascidian species in British Columbia (Canada) to invertebrate predation. *Marine Biology* **156**, 1311–1320.
- Fanjul E, Bazterrica MC, Escapa M, Grela MA and Iribarne O (2011) Impact of crab bioturbation on benthic flux and nitrogen dynamics of Southwest Atlantic intertidal marshes and mudflats. *Estuarine, Coastal and Shelf Science* **92**, 629–638.
- Fitzgerald SP, Wilson JR and Lenihan HS (2018) Detecting a need for improved management in a data-limited crab fishery. *Fisheries Research* **208**, 133–144.
- Fitzgerald SP, Lenihan HS, Wilson JR, Culver CS and Potoski M (2019) Collaborative research reveals cryptic declines within the multispecies California rock crab fishery. *Fisheries Research* **220**, 105340.
- Frainer A, McKie BG, Amundsen P-A, Knudsen R and Lafferty KD (2018) Parasitism and the biodiversity-functioning relationship. *Trends in Ecology & Evolution* **33**, 260–268.
- Fujii JA, Ralls K and Tinker MT (2017) Food abundance, prey morphology, and diet specialization influence individual sea otter tool use. *Behavioral Ecology* **28**, 1206–1216.
- Gonzalez ST (2016) Influence of a trematode parasite (*Microphallus trugidus*) on grass shrimp (*Palaemonetes Pugio*) response to refuge and predator presence. *Journal of Parasitology* **102**, 646–649.
- Gonzalez MT, Barrientos C and Moreno CA (2006) Biogeographical patterns in endoparasite communities of a marine fish (*Sebastes capensis* Gmelin) with extended range in the Southern Hemisphere. *Journal of Biogeography* **33**, 1086–1095.
- González MT, Henríquez V and López Z (2013) Variations in the fecundity and body size of digenetic (Opecoelidae) species parasitizing fishes from Northern Chile. *Revista de Biología Marina y Oceanografía* **48**, 421–429.
- Gyoten J (2000) Infection by *Paragonimus miyazakii* Cercariae of Their Crab Hosts, *Geothelphusa dehaani*, by Percutaneous Penetration. *Journal of Parasitology* **86**, 1342–1345.
- Hansen EK and Poulin R (2005) Impact of a microphallid trematode on the behaviour and survival of its isopod intermediate host: phylogenetic inheritance? *Parasitology Research* **97**, 242–246.
- Harper JT and Saunders GW (2001) The application of sequences of the ribosomal cistron to the systematics and classification of the Rhodophyta. *Cahiers Biologie Marine* **42**, 25–38.
- Holmes JC (1990) Helminth communities in marine fishes. pp. 101–130 in Esch GW, Bush AO and Aho JM (Eds) *Parasite communities: patterns and processes*. Dordrecht, Netherlands, Springer.
- Hull WW and Bourdeau PE (2017) Can crabs kill like a keystone predator? A field-test of the effects of crab predation on mussel mortality on a northeast Pacific rocky shore. *PLoS ONE* **12**, e0183064.
- Jensen GC, McDonald PS and Armstrong DA (2007) Biotic resistance to green crab, *Carcinus maenas*, in California bays. *Marine Biology* **151**, 2231–2243.
- Jousson O, Bartoli P and Pawlowski J (1999) Molecular identification of developmental stages in Opecoelidae (Digenea). *International Journal for Parasitology* **29**, 1853–1858.
- Kotsyuba EP (2018) The influence of the trematode *Paragonimus* cf. *westermani* on NO- and HIF-1 $\alpha$ -containing structures in the brain of the crab *Eriocheir japonica* (De Haan, 1835) Decapoda: Varunidae. *Russian Journal of Marine Biology* **44**, 383–389.

- Kumar S, Stecher G, Li M, Knyaz C and Tamura K** (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* **35**, 1547–1549.
- Lafferty KD, Allesina S, Arim M, et al.** (2008) Parasites in food webs: the ultimate missing links: parasites in food webs. *Ecology Letters* **11**, 533–546.
- Lagroe C, Kaldonski N, Perrot-Minnot MJ, Montreuil S and Bollache L** (2007) Modification of host's behavior by a parasite: field evidence for adaptive manipulation. *Ecology* **88**, 2839–2847.
- Lefèvre T, Adamo SA, Biron DG, Missé D, Hughes D and Thomas F** (2009) Invasion of the body snatchers: The Diversity and Evolution of Manipulative Strategies in Host–Parasite Interactions. pp. 45–83 in Rollinson D, Hay S and Webster JP (Eds) *Advances in Parasitology*. London, Academic Press.
- Leiva N, George-Nascimento M and Muñoz G** (2015) Parasite burden in decapod crustaceans from central coast of Chile: is there any association with the relationship with definitive host abundances? *Latin American Journal of Aquatic Research* **13**, 726–738.
- Leiva NV, López Z, González MT and Muñoz G** (2017) Determining intermediate hosts for Opecoelidae and Microphallidae species (Platyhelminthes: Trematoda) in the southeastern Pacific Coast, using molecular markers. *Journal of Parasitology* **103**, 132–137.
- Linton E** (1910) Helminth fauna of the Dry Tortugas II. Trematodes. Carnegie Institution Washington. Publication No. 133. *Papers Tortugas Laboratory* **4**, 11–98.
- Madden T** (2002) The BLAST sequence analysis tool (updated 13 August 2003) in McEntyre J and Ostell J (Eds) *The NCBI handbook*. Bethesda, MD, National Center for Biotechnology Information (US). Available at <http://www.ncbi.nlm.nih.gov/books/NBK21097/>
- McCurdy DG, Forbes MR and Boates JS** (1999) Testing alternative hypotheses for variation in amphipod behaviour and life history in relation to parasitism. *International Journal for Parasitology* **29**, 1001–1009.
- Montgomery WR** (1957) Studies on digenetic trematodes from marine fishes of La Jolla, California. *Transactions of the American Microscopical Society* **76**, 13.
- Morales-Serna FN, García-Vargas F, Medina-Guerrero RM and Fajer-Ávila EJ** (2017) Helminth parasite communities of spotted rose snapper *Lutjanus guttatus* from the Mexican Pacific. *Helminthologia* **54**, 240–249.
- Mouritsen KN and Poulin R** (2002) Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology* **124**, 101–107.
- Mouritsen KN and Poulin R** (2005) Parasites boosts biodiversity and changes animal community structure by trait-mediated indirect effects. *Oikos* **108**, 344–350.
- Muñoz G and Olmos V** (2008) Bibliographic revision of endoparasite and host species from aquatic systems of Chile. *Revista de biología marina y oceanografía* **43**, 173–245.
- Munoz G, Lopez Z and Cardenas L** (2012) Morphological and molecular analyses of larval trematodes in the intertidal bivalve *Perumytilus purpuratus* from central Chile. *Journal of Helminthology* **87**, 356–363.
- Ñacari LA, Sepulveda FA, Escribano R, Bray RA and Oliva ME** (2018) Morphological and molecular characterisation of digenean parasites of the Galápagos sheephead *Semicossyphus darwini* (Jenyns) with the re-description of *Labrifer secundus* Manter, 1940 (Lepidapedidae) from the Humboldt current large marine ecosystem. *Systematic Parasitology* **95**, 391–401.
- Oliva ME and Sanchez M** (2005) Metazoan parasites and commensals of the northern Chilean scallop *Argopecten purpuratus* (Lamarck, 1819) as tools for stock identification. *Fisheries Research* **71**, 71–77.
- Oliva ME, Valdivia IM, Chavez RA, Molina H and Cárdenas L** (2015) Molecular and Morphological Evidence Demonstrating Two Species of Helicometrina Linton 1910 (Digenea: Opecoelidae) in Northern Chile. *Journal of Parasitology* **101**, 694–700.
- Orensanz JM and Gallucci VF** (1988) Comparative study of postlarval life-history schedules in four sympatric species of cancer (Decapoda: Brachyura: Cancridae). *Journal of Crustacean Biology* **8**, 187–220.
- Orensanz JM, Parma AM, Armstrong DA, Armstrong J and Wardrup P** (1995) The breeding ecology of *Cancer gracilis* (Crustacea: Decapoda: Cancridae) and the mating systems of cancrid crabs. *Journal of Zoology* **235**, 411–437.
- Pérez-Ponce de León G and Hernández-Mena DI** (2019) Testing the higher-level phylogenetic classification of Digenea (Platyhelminthes, Trematoda) based on nuclear rDNA sequences before entering the age of the 'next-generation' Tree of Life. *Journal of Helminthology* **93**, 260–276.
- Poulin R, Nichol K and Latham ADM** (2003) Host sharing and host manipulation by larval helminths in shore crabs: cooperation or conflict? *International Journal for Parasitology* **33**, 425–433.
- RStudio Team** (2015) *RStudio: integrated development for R*. Boston, MA, RStudio, Inc. Available at <http://www.rstudio.com/>.
- Smith NF, Ruiz GM and Reed SA** (2007) Habitat and host specificity of trematode metacercariae in fiddler crabs from mangrove habitats in Florida. *Journal of Parasitology* **93**, 999–1005.