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Short Communication

Coccidian infection may explain the differences in the life history of octopus host populations

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ABSTRACT

The prevalence of coccidian parasites in three *Octopus tehuelchus* populations from San Matías Gulf (Patagonia, Argentina) is compared. The prevalence was similar between sexes, but varied between seasons (being highest during cold months) and sites. Islote Lobos had the highest prevalence (42.7–100%) followed by San Antonio Bay (0–66%) and El Fuerte (0–24.5%). Octopuses under 27 mm of dorsal mantle length showed a low prevalence (less than 50%), which increased with size. We hypothesize that the high prevalence of parasites, which affect the three populations differentially, could account for the observed variability in life-span and growth, size–frequency distributions, reproduction and densities of *O. tehuelchus* populations.

1. Introduction

Parasites can influence the population dynamics of their hosts by affecting the life-history strategies and behavior. The impact of parasites on individuals is often severe, though their effects at the population level are dependent on prevalence and intensity of infection (Mouritsen and Poulin, 2002).

In mollusks, parasitism can affect several aspects of host life history, including reproduction (Lafferty, 1993b; Gilardoni et al., 2012), growth (Lafferty, 1993a,b; Miura et al., 2006), survival, declines or fluctuations in abundance (Huxham et al., 1993; Lafferty, 1993a; Sokolova, 1995; Fredensborg et al., 2005), and can even alter the community structure (Mouritsen and Poulin, 2002).

Although numerous ecological studies demonstrate the effect of parasites on mollusks host populations, evidences on its effect on cephalopod populations are poor (Pascual et al., 1997). The coccidian genus *Aggregata* (Protozoa: Apicomplexa) is an intracellular parasite with a two-host life cycle transmitted through the food-web (Gestal et al., 2002a). The sexual stages (gamogony and sporogony) are found in the digestive tract of cephalopods, the definitive host, and the asexual stages (merogony) infect the digestive tract of crustaceans, the intermediate hosts (Hochberg, 1990). Gestal et al. (2002a) described the histopathological effects of *Aggregata octopiana* in the digestive tract of *Octopus vulgaris*, and analyzed the decrease of the enzymes involved in the absorption process with increasing infection. This detrimental effect on the gastrointestinal function may produce a malabsorption syndrome (Gestal et al., 2002b). Moreover, these authors suggest that although coccidiosis is not believed to be a primary cause of death, it is likely that the malabsorption syndrome impairs octopus development and growth, making them more vulnerable to other biotic and abiotic stressors.

In Patagonian waters (Argentina), the small octopus *Octopus tehuelchus* is infected by *Aggregata valdessensis* (Sardella et al., 2000), which has shrimps (*Pleoticus muelleri* and *Artemesia longinaris*) as intermediate hosts (Sardella and Martorelli, 1997). In this octopus, coccidian sporocysts were observed in the crop, proximal intestine, and cecum. All the gamogony and sporogony stages of *Aggregata* sp. were found at high prevalence and intensities in *O. tehuelchus* from Puerto Lobos (south of San Matías Gulf, Patagonia) and were related to the activity (i.e. feeding intensity during spring–summer months) and the chances of parasite–host encounter (Sardella and Ré, 1990; Sardella et al., 2000).

Due to several aspects of the life history of *O. tehuelchus* in San Matías Gulf seem to vary between different intertidal environments (Storero et al., 2010, 2012, 2013a,b) the aim of this contribution is to compare the prevalence of coccidian parasites in three octopus populations from San Matías Gulf. The results are discussed in relation to the effect that parasite infection may have on the life-history traits of its host populations.

2. Materials and methods

Octopuses were collected monthly by an expert fisher in the intertidal zone of San Antonio Bay (SAB, 40°42′S-40°50′S/

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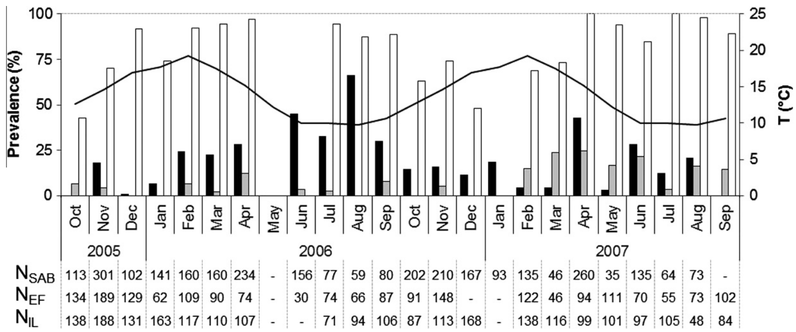

Fig. 1. Monthly prevalence of parasites (columns) and seasonal variation of the water temperature (line). SAB: San Antonio Bay (black), EF: El Fuerte (grey), IL: Islote Lobos (white). N: total number of octopuses (male and female) analyzed by month and site.

64°43′W-65°07′W), El Fuerte (EF, 41°14′S/65°08′W) and Islote Lobos (IL, 41°26′S/65°03′W) from October 2005 to September 2007. Samples were taken to the laboratory and frozen, then defrosted and processed. Dorsal mantle length (DML, in mm) and sex were recorded for each individual. The prevalence of parasites (number of octopus infected from the total of octopus analyzed, Bush et al., 1997) was evaluated macroscopically, recording the presence/absence of spherical white cysts with coccidia (1–2 mm diameter, Sardella and Ré, 1990) in the crop, proximal intestine, and cecum.

The proportion of infected octopus was monthly compared between sexes with the Chi-square test. Also, the proportion of infected octopus was modeled using a generalized linear model (GLM) with a logit link and the binomial family. A GLM with site, season and their interaction as fixed effects was used, using the function glm from library lme4 (Bates et al. 2011) provided by the R package. The statistical software R (R Core Team, 2013) was used for modeling and the Fisher's least-significant difference (LSD) for *a posteriori* comparisons. The frequency distribution of the proportion of infected octopus by size was compared between sites with Kolmogorov–Smirnov test (KS test).

The exact sampling protocol, the characterization of each study site and several characteristics of *O. tehuelchus* populations in San Matías Gulf (population structure, sex-ratios, recruitment, growth and life-span, reproductive traits, density and distribution) are described in Pujals (1986), Iribarne (1991) and Storero et al. (2010, 2012, 2013a, 2013b).

3. Results and discussion

The populations of *O. tehuelchus* in San Matías Gulf have a high prevalence of coccidian parasites. Although not confirmed in this study, the species reported for *O. tehuelchus* in the south of San Matías Gulf is *Aggregata valdessensis* (Sardella et al., 2000).

In the three study sites, the monthly proportion of infected individuals was similar between sexes (test χ^2, $P > 0.05$), but varied between sites (GLM, Deviance = 3129.15, $df = 2$, $P = 0.000001$), seasons (GLM, Deviance = 173.03, $df = 3$, $P = 0.000001$) and their interaction (GLM, Deviance = 33.06, $df = 6$, $P = 0.00001$). Islote Lobos had the highest prevalence (42.7–100%), followed by San Antonio Bay (0–66%), and El Fuerte with the lowest prevalence (0–24.5%). The highest number of infected octopus was observed during cold months (autumn–winter, March to August) (Fig. 1, Table 1).

The prevalence by size was different for the three study sites (KS test, $KS_{SAB-EF} = 0.086$, $P < 0.05$; $KS_{SAB-IL} = 0.046$, $P < 0.05$; $KS_{EF-IL} = 0.079$, $P < 0.05$). In general, juveniles under 27 mm of DML showed a low prevalence (less than 50%) which increased with size. In Islote Lobos, individuals larger than 39 mm of DML had prevalence higher than 75% (Fig. 2).

Table 1
Fisher's least-significant difference (LSD test). Mean prevalence (%) by site and season. SAB: San Antonio Bay, EF: El Fuerte, IL: Islote Lobos. SE: standard error. Different letters indicate significant differences ($P < 0.05$).

Site	Season	Mean prevalence	SE
IL	Winter	92.3	0.184 **A**
IL	Autumn	91.4	0.154 **A**
IL	Summer	73.2	0.084 **B**
IL	Spring	69.7	0.081 **B**
SAB	Winter	34.6	0.088 **C**
SAB	Autumn	29.4	0.081 **C**
SAB	Spring	15.5	0.092 **D**
EF	Autumn	15.4	0.136 **DE**
SAB	Summer	11.4	0.111 **EF**
EF	Winter	8.70	0.185 **FG**
EF	Spring	6.10	0.152 **G**
EF	Summer	5.90	0.206 **G**

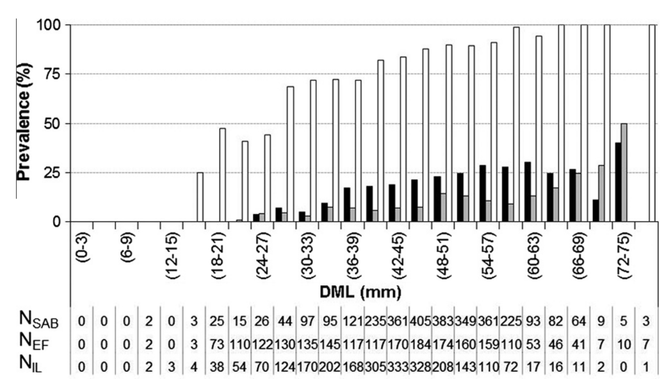

Fig. 2. Prevalence of parasites by host size. SAB: San Antonio Bay (black), EF: El Fuerte (grey), IL: Islote Lobos (white). N: total number of octopuses (male and female) analyzed by size.

In the three study sites the prevalence increased during cold months, which could be related with the presence of adults and mature octopus. At the larger sizes, the percentage of infected individuals reached 100% in Islote Lobos, and between 25% and 50% in El Fuerte and San Antonio Bay. Sardella and Ré (1990) mentioned that infection of *O. tehuelchus* by *Aggregata* sp. increases with age due to the longer time for encounter of parasites and hosts, or due to the increasing feeding rate during summer months.

As reported for *O. tehuelchus* and other octopus (Sardella and Ré, 1990; Gestal et al., 2002b; Ibáñez et al., 2005), the high densities of cysts reduce the absorption area along the digestive tract and, when the infection is generalized, could diminish octopus growth, maximum size, condition and life-span. Although, *Aggregata* spp.

infection does not seems to be the main cause of death in octopus, the coccidiosis could weaken the individuals making them vulnerable to other biotic and abiotic stressors (Gestal et al., 2002a). Moreover, the high prevalence of parasites in *O. tehuelchus* could affect the population characteristics, particularly in Islote Lobos, where 100% of the adults are infected.

Our previous studies suggested that phenotypic plasticity in *O. tehuelchus* due to variable environmental characteristics, could explain some of the observed variability in life-span and growth (Storero et al., 2010), size–frequency distributions (Storero et al., 2013a), reproduction (Storero et al., 2012) and densities (Storero et al., 2013b). In these previous studies, we have hypothesized that the annual cycle of seawater temperature, which has certain differences between sites, could explain some of the growth variations. Also, differences in the abundance and diversity of prey could influence the growth rates and size at maturity between populations. On the other hand, we have suggested that the high predation pressure may be another factor influencing foraging time, and the corresponding growth and survival rates. The mentioned factors and others (e.g. fishing pressure, shelter availability) in the external environment, acting together with the inherent life history of cephalopods, were suggested as drivers of the population dynamics of *O. tehuelchus* in the Patagonian coast.

Another possible hypothesis, not evaluated yet, that could account for the variability in the life history of *O. tehuelchus* is the high coccidian infection, which affects differentially the three populations. In other mollusks, parasites decrease survival and gamete production of the host, the infection slows growth, and is correlated with reduced shell height of some gastropods (Huxham et al., 1993). Thus, parasites could be the main explanation for the smaller size and shorter life-span of octopuses from Islote Lobos (mean size = 27.4 g; 27 months approximately) with respect to El Fuerte and San Antonio Bay (mean size = 35.5 and 44.8 g respectively, and between 27 and 36 months approximately) (Storero et al., 2010, 2013a). Similarly, the size at maturity of females and the number of vitellogenic oocytes in ovary is lower in Islote Lobos (Storero et al., 2012).

Several authors already demonstrated that parasites are capable of influencing different aspects of host population dynamics (e.g. growth, survival, reproduction and density), and can play an important role in the structure of populations (Lafferty, 1993a,b; Fredensborg et al., 2005; Miura et al., 2006). High population densities and aggregated distributions could favor the reinfection and the higher levels of parasitism in the final host. Densities of *O. tehuelchus* are different in the three study sites: Islote Lobos has the highest densities (mean octopus per transect 7.32 ± 1.16) followed by El Fuerte (5.55 ± 0.94) and San Antonio Bay (3.40 ± 0.85). Within each site, octopus densities vary between seasons (Storero et al., 2013b). The highest densities were observed during warm months, when octopuses are actively feeding, growing, and prevalence of parasites is increasing. Moreover, the crustaceans, which are the intermediate host of *Aggregata* sp., are conspicuous and abundant in the intertidal, and one of the main item prey of *O. tehuelchus* during warm months (Pers. Obs.).

The intensity of infection was not evaluated in this study, and we are aware that it may affect our conclusions. A particular location with high prevalence may have a low intensity of infection, thus it may not affect the individuals or the population characteristics of the host. Moreover, not all coccidian infections have a negative impact on molluscan hosts. For instance, heavy infections in abalone kidney have no detectable effect on their host (Friedman et al., 1997). Although a more comprehensive analysis still needs to be done on coccidian prevalence, intensity and its impact on octopus fitness, the patterns presented in this manuscript highlight a novel and exciting outcome that deserves further development: Parasitic infection may both explain and be explained by differences in octopus populations.

Despite the important role that parasite infection plays in host demography, it has been often ignored in ecological studies (Sokolova, 1995). Also, considering that cephalopods play a major role (as prey and predators) in the trophic webs of marine ecosystems, and are valuable fisheries resources, it is necessary to start elucidating the importance of the parasite–host relationship, in order to comprehend their effect in the populations and the structure of community.

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