Seasonality of Parasitic Copepods on Bullseye Puffer, Sphoeroides annulatus (Pisces: Tetraodontidae), From the Northwestern Coast of Mexico

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SEASONALITY OF PARASITIC COPEPODS ON BULLSEYE PUFFER, *SPHOEROIDES ANNULATUS* (PISCES: TETRAODONTIDAE), FROM THE NORTHWESTERN COAST OF MEXICO

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ABSTRACT: Seasonal occurrence of parasitic copepods in wild bullseye puffer, *Sphoeroides annulatus* (Pisces: Tetraodontidae), was analyzed in conjunction with variation of biotic and abiotic factors. Eleven samples were taken between February 2007 and February 2008 in Santa María La Reforma lagoon (northwestern coast of México). In total, 337 fish was examined; 5 parasitic copepod species were observed, including *Acantholochus zairae, Caligus serratus, Lepeophtheirus simplex, Pseudochondracanthus diceraus,* and *Parabrachiella* sp. The most common species were *L. simplex, P. diceraus,* and *C. serratus* (overall prevalence, 59, 53, and 35%, respectively), which significantly varied in prevalence and mean intensity between sampling months. A seasonal pattern was only observed for *L. simplex,* with higher infection levels in the warmest month than in the coldest month. Statistical analyses indicated that the intensity of *L. simplex* was positively correlated with water temperature. There were no significant differences in prevalence and intensity of infection among female and male hosts. At the component community level, species richness ranged between 4 and 5 during most of the study period, and no seasonality was observed in the number of individuals, Shannon diversity index, evenness index, or the Berger–Parker dominance index. At the infracommunity level, 4 descriptors used (mean species richness, mean number of individuals, mean Brillouin's diversity index, and mean Berger–Parker index) varied significantly between sampling months, but no seasonality was observed, except for a slight increase in the number of individuals during the warmest month. A significant positive association was detected between number of individuals and water temperature and between host size and both species richness and number of individuals. This is the first account of the ecology of these 5 parasitic copepods. Although no significant association was detected between fish condition factor and the burden of parasitic copepods, given the high occurrence of the caligid copepod *L. simplex,* we suggest that this copepod could represent a threat for the culture of *S. annulatus.*

The bullseye puffer, *Sphoeroides annulatus* (Pisces: Tetraodontidae), is a coastal fish whose distribution ranges from southern California down to Peru, including the Gulf of California and the Galapagos Islands (Thomson et al., 2000). *Sphoeroides annulatus* is an economically important species, especially in northwestern México, which is one of the most important puffer fish exporters worldwide (Chávez-Sánchez et al., 2008). Furthermore, it has been shown that *S. annulatus* possess a good potential for aquaculture, and pilot project to produce juveniles has been initiated (Álvarez-Lajonchère et al., 2007; Chávez-Sánchez et al., 2008).

The recent use of *S. annulatus* in aquaculture stresses the need for knowledge of the parasite fauna associated with wild fish populations because parasitic organisms are among the main health problems within mariculture facilities. Identification of parasites should facilitate the best treatment and perhaps stimulate more detailed investigation in the future. Although parasitic copepods represent a potential threat both for aquaculture and for wild fish exposed to water effluents from fish farms (Krkošek et al., 2006; Costello, 2009), enteric helminths are the best known metazoan parasites of *S. annulatus* (Moravec and Fajer-Ávila, 2000; Fajer-Ávila et al., 2003, 2004; Álvarez-Borrego and Fajer-Ávila, 2006). However, information regarding parasitic copepods of bullseye puffers is scarce. Only 3 species of parasitic copepods have been reported on *S. annulatus* collected off the northwestern coast of México: *Caligus elongatus, Lepeophtheirus dissimulatus,* and *Lepeophtheirus simplex* (Causey, 1960; Ho et al., 2001). The latter has been associated with skin lesions, anorexia, and mortality of *S. annulatus* juveniles reared in tanks (Fajer-Ávila et al., 2008); nevertheless, knowledge on the ecology of these parasites is poor. This subject needs to be addressed to help prevent economic losses and to decrease the environmental impact of bullseye puffer aquaculture. The study of the seasonal dynamics of populations and communities of parasitic copepods may help to reveal periods during which epizootic outbreaks are likely to occur. In addition, study of the natural infestation levels before fish farms are established might prove useful in reaching conclusions about the potential impact of copepods from farmed fish on wild fish stocks, as shown by Krkošek et al. (2006) and Costello (2009).

The aims of the present study are therefore to (1) analyze the seasonal variation in parasitic copepod community structure and species composition in *S. annulatus* from Santa María La Reforma lagoon (northwestern México), (2) identify possible biotic and abiotic factors responsible for such seasonal variation, and (3) assess the association between parasitic copepod burdens and fish condition factor.

MATERIALS AND METHODS

Fish sampling and parasitological examination

Santa María La Reforma lagoon (25°10′N, 108°20′W and 24°50′N, 107°55′W) is a coastal ecosystem located on the Mexican Pacific coast (Fig. 1). It has a surface area of approximately 583 km² and a mean depth of 3.5 m (maximum depth, 26 m) (Serrano and Ramírez-Félix, 2003). The annual mean temperature is approximately 24 C. The region experiences 2 distinct seasons during the year: a rainy season from June to November, which includes the warmest month (August–October); and a dry season from December to May, which includes the coldest month (January–February).

In total, 337 specimens of *S. annulatus* was collected between February 2007 and February 2008 (February 2007 [n = 51], March [n = 25], April [n
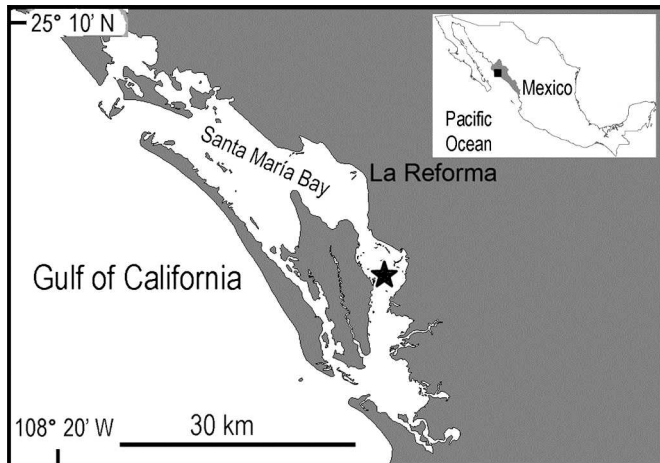
FIGURE 1. Map of Santa María La Reforma lagoon. The star denotes the sampling site. The inset shows the location of the study area in the state of Sinaloa, México.
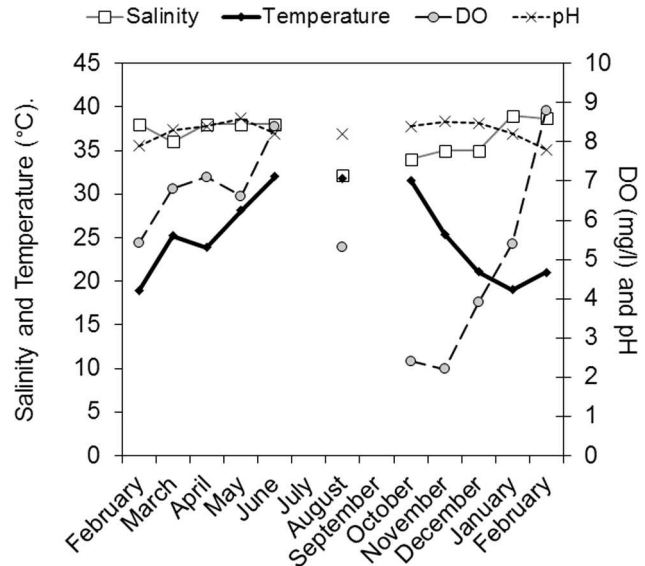

FIGURE 2. Variation in water temperature, salinity, dissolved oxygen (DO), and pH recorded during 1-yr sampling period (from February 2007 to February 2008).

= 43], May [n = 6], June [n = 6], August [n = 46], October [n = 45], November [n = 44], December [n = 43], January [n = 10], and February 2008 [n = 18]). Despite a similar sampling effort throughout the study, monthly sample sizes varied considerably. This could be either due to movements of fish within the large body of water they inhabit or be a consequence of fishing pressure, because artisanal *S. annulatus* fishery takes place in the study area. The sampling site was located in the southern portion of the lagoon, near "Carillero" (24°53.107′N, 108°02.005′W). Fish were collected using hook and line; placed individually in labeled, re-sealable plastic bags; and frozen until inspection in the laboratory. A sample of bottom water was taken at each sampling site by using a horizontal Niskin bottle; bottom-water salinity (parts per thousand), temperature (Celsius), pH, and dissolved oxygen (milligrams per liter) were determined.

Each fish was examined for the presence of copepods on skin, fins, and gills. Examination was performed under good illumination in a tray. Gill arches were removed from each fish and carefully inspected in a Petri dish by using a stereomicroscope with a magnification of ×40. Water contained in each of the plastic bags where the fish were stored was filtered and examined for detached copepods. Parasites found on each fish were preserved in labeled vials with 70% ethanol. Standard body length (centimeters), wet weight (grams), and sex of each fish were recorded. Fulton's condition factor *K* was assessed using the following formula:

$$K = \frac{100 \times W}{L^3},$$

where *W* is total body weight (grams) and *L* is standard length (centimeters).

Data analysis

Differences in standard body length, wet weight, and condition factor *K* of fish between sampling months were contrasted using a Kruskal–Wallis test and Dunn's method as a posteriori test. Differences in the same 3 parameters between male and female fish hosts were compared with Mann–Whitney *U*-tests.

Monthly variations in the numbers of each species of parasitic copepod were analyzed in terms of prevalence (percentage of infected fish) and mean intensity of infection (mean number of parasites per infected fish), calculated according to Bush et al. (1997). Significant differences were detected using chi-square tests (comparison between all samples) and Fisher's exact tests (pairwise sample comparisons) for prevalence and Kruskal–Wallis tests (comparison between all samples) and bootstrap *t*-tests with 2,000 replications (pairwise sample comparisons) for intensity. Ninety-five percent confidence intervals were calculated for prevalence and mean intensity by using Quantitative Parasitology 3.0 software (Rózsa et al., 2000).

Associations between parasites and fish sex were evaluated using Fisher's exact tests for prevalence and using bootstrap *t*-tests with 2,000 replications for intensity. Canonical correspondence analysis (CCA) was used to determine possible associations between intensity of infection and biotic and abiotic factors. Environmental data used in CCA were transformed to $\log_{10}$.

Analyses were made at the component community level (all copepods in all hosts collected per month) and infracommunity level (all copepods in an individual fish) (Holmes and Price, 1986). Component community parameters included total copepod species richness, total number of individual copepods, the Shannon index (*H'*) as a measure of diversity, the Pielou index (*J'*) as a measure of evenness, and the Berger–Parker index as a measure of numerical dominance. Infracommunities were described through the mean copepod species richness per infected fish, mean number of individual copepods per infected fish, mean value of the Brillouin diversity index per infected fish, and the mean value of the Berger–Parker dominance index. These infracommunity descriptors were compared between sampling months by using Kruskal–Wallis tests to detect significant differences. Considering both infected and uninfected fish, Mann–Whitney *U*-test and Spearman's rank correlation test, respectively, were used to determine the influence of fish sex and environmental factors on both richness and number of individuals of the infracommunities Finally, Spearman's rank correlations were performed to determine whether parasitic copepod burdens were associated with fish condition factor *K*.

Kruskal–Wallis tests, Dunn's method, Mann–Whitney *U*-tests, and Spearman's correlations were calculated with the SigmaStat 3.0 software (Systat Software, Inc., San Jose, California). Fisher's exact tests, bootstrap *t*-tests, and confidence limits were calculated with Quantitative Parasitology 3.0 software (Rózsa et al., 2000). CCA was performed in the MultiVariate Statistical Package MVSP 3.13 (Kovach, 2005).

RESULTS

Abiotic factors

Water temperature ranged from 19 (February 2007) to 32 C (June, August, and October) (Fig. 2). Salinity ranged from 32 (August) to 39‰ (January and February 2008) (Fig. 2). Dissolved oxygen ranged from 2.2 mg L^{-1} (November) to 8.8 mg L^{-1} (February 2008) (Fig. 2). Throughout the study period, pH varied slightly (range, 8.2–8.6) (Fig. 2).
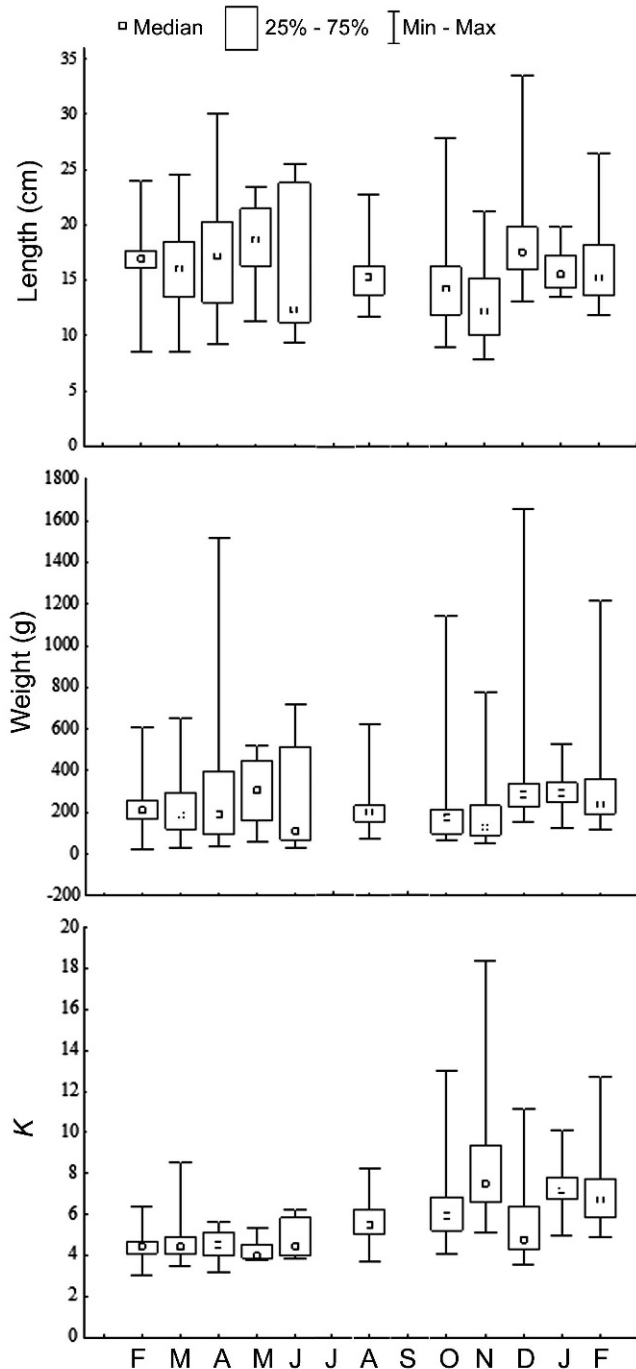
FIGURE 3. Variation in length, wet weight, and condition factor *K* of bullseye puffer (*Sphoeroides annulatus*) during 1-yr sampling period (from February 2007 to February 2008). Box plots show median, percentiles, and minimum and maximum observations.

Host population

The body length of fish ranged between 7.9 and 33.5 cm (n = 337; mean ± SD = 15.9 ± 4.04 cm). Wet weight ranged between 23.5 and 1,653.5 g (n = 337; mean ± SD = 254.2 ± 204.8 g), and condition factor *K* varied between 3 and 18.4 (n = 337; mean ± SD = 5.8 ± 2.1). Data distributions are depicted in Figure 3. Kruskal–Wallis and Dunn multiple comparison tests revealed significant

differences in total body length, wet weight, and condition factor between sampling months (for length: $H = 66.14$, $P < 0.001$; for weight: $H = 43.35$, $P < 0.001$; for condition factor: $H = 169.59$, $P < 0.001$). Length recorded in November was significantly lower than that observed in February 2007, March, April, May, and December (Fig. 3). Wet weight registered in November was significantly lower than that in December (Fig. 3). Condition factor *K* calculated for fish caught in November was significantly higher than the condition factor of all other samplings, except October (Fig. 3).

The sex could be determined for 332 fish: 173 females and 159 males were caught. When all samples were pooled in the same analysis, the Mann–Whitney *U*-test showed that there were no significant differences in body length ($T = 25038.5$, $P > 0.05$) or condition factor *K* ($T = 26991$, $P > 0.05$) between females and males, but wet weight was significantly higher for females (mean ± SD = 280.9 ± 246.4 g) than for males (mean ± SD = 221.9 ± 143.3 g) ($T = 24550.5$, $P < 0.05$).

The sex distribution in the 11 monthly samples was as follows: 23 females, 28 males (February 2007); 13 females, 12 males (March); 25 females, 18 males (April); 4 females, 2 males (May); 3 females, 3 males (June); 18 females, 26 males (August); 19 females, 26 males (October); 25 females, 19 males (November); 27 females, 16 males (December); 5 females, 2 males (January); and 11 females, 7 males (February 2008). There were no significant differences between both sexes within monthly samples in body length, wet weight, and condition factor *K* (data not shown).

Species composition

Five parasitic copepod species were identified from the 1,777 individuals collected. They include the caligids *C. serratus* and *L. simplex* found on the skin, the chondracanthid *Pseudochondracanthus diceraus*, the bomolochid *Acantholochus zairae* found attached to gill filaments, and the lernaeopodid *Parabrachiella* sp. found on gill rakers.

Seasonal changes in prevalence and mean intensity

Overall prevalence and mean intensity levels were as follows for the 5 copepod species: 58.8% and 4.2 parasites per host for *L. simplex*, 52.5% and 3.4 parasites per host for *P. diceraus*, 35% and 2.1 parasites per host for *C. serratus*, 14.0% and 1.3 parasites per host for *A. zairae*, and 6.2% and 2.1 parasites per host for *Parabrachiella* sp. Because of their rare occurrence, the last 2 species were not analyzed further.

The chi-square and Kruskal–Wallis tests showed that prevalence and intensity, respectively, of *L. simplex* ($\chi^2 = 104.4$, $P < 0.01$ and $H = 22.4$, $P < 0.05$), *P. diceraus* ($\chi^2 = 37.3$, $P < 0.01$ and $H = 20.5$, $P < 0.05$), and *C. serratus* ($\chi^2 = 52.9$, $P < 0.01$ and $H = 20.8$, $P < 0.05$) differed significantly between sampling months (Figs. 4, 5). The highest values of prevalence (87 and 93%) and mean intensity (4.1 and 6 parasites/host) of *L. simplex* occurred during the warmest months (August and October) and were significantly higher than those observed in relatively colder months (Figs. 4, 5). Prevalence of *P. diceraus* did not vary much during the 1-yr period (ranging from 50 to 67%), except for a significant decrease (18%) in November (Fig. 4). Also, mean intensity of *P. diceraus* was not significantly different between most sampling months, except for significantly lower values in November and February 2008 (Fig. 5). Prevalence of *C. serratus* showed an irregular pattern, varying from 13.7 (February 2007)
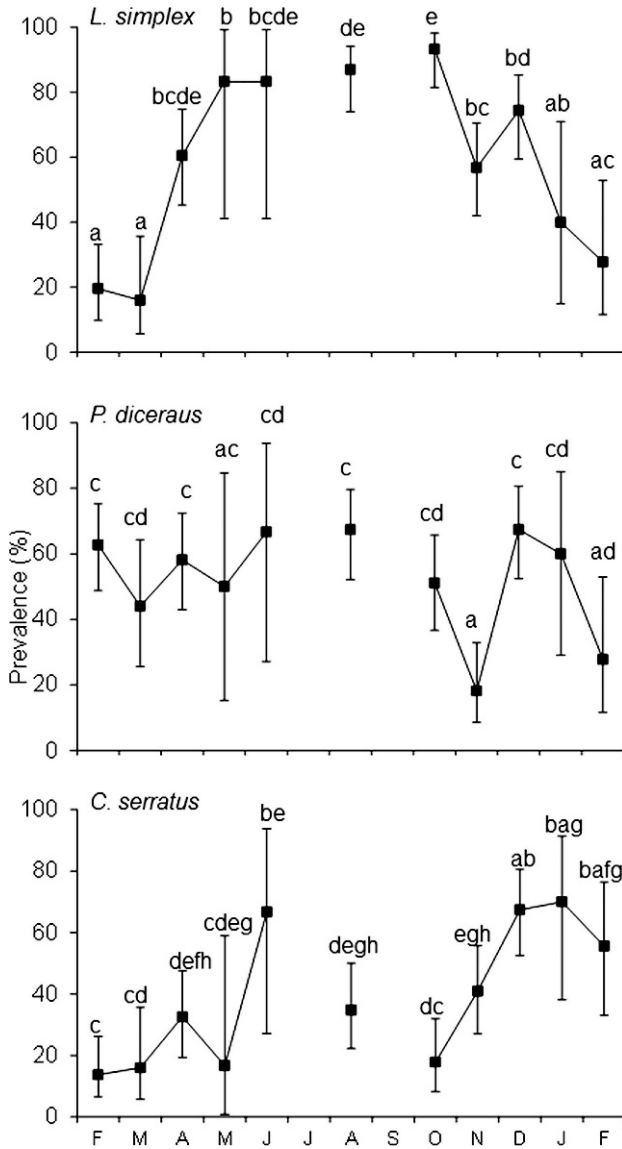
FIGURE 4. Variation in prevalence of infection of *Lepeophtheirus simplex*, *Pseudochondracanthus diceraus*, and *Caligus serratus* on bullseye puffer (*Sphoeroides annulatus*) during 1-yr sampling period (from February 2007 to February 2008). Bars denote 95% confidence intervals. Letters group months with prevalences that do not differ significantly (Fisher's exact test, $P > 0.05$).
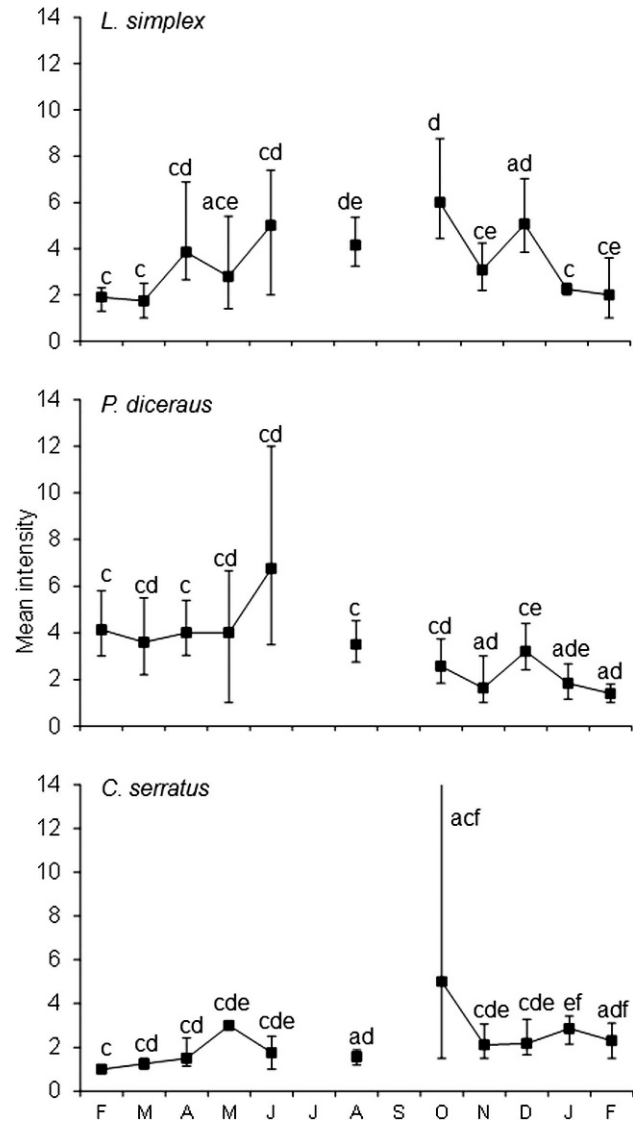

FIGURE 5. Variation in mean intensity of infection of *Lepeophtheirus simplex*, *Pseudochondracanthus diceraus*, and *Caligus serratus* on bullseye puffer (*Sphoeroides annulatus*) during 1-yr sampling period (from February 2007 to February 2008). Bars denote 95% confidence intervals. Letters group month with mean intensities that do not differ significantly (bootstrap *t*-test, $P > 0.05$).

to 67.4% (December), whereas its mean intensity was not significantly different between most sampling months, except when contrasting February 2007 (1.0 parasite/host) with January and February 2008 (2.9 and 2.3 parasites/host, respectively).

There were no significant differences in prevalence and mean intensity of *L. simplex* and *C. serratus* between female and male hosts when all samples were pooled in the same analysis. Also, there were no significant differences in prevalence of *P. diceraus*, but its mean intensity was significantly lower in females (2.9 parasites/host) than in males (3.9 parasites/host) (Fisher's exact test: for *L. simplex*, $P = 0.578$; for *P. diceraus*, $P = 0.379$; and for *C. serratus*, $P = 0.358$; bootstrap *t*-test: for *L. simplex*, $t = 0.02$, $P > 0.05$; for *P. diceraus*, $t = -2.051$, $P < 0.05$; and for *C. serratus*, $t = 0.988$, $P > 0.05$). When samplings were considered separately, there were no

significant differences in prevalence and intensity of the 3 copepod species between female and male hosts, except for February 2007 when prevalence of *P. diceraus* was significantly higher in females (78%) than in males (50%) (Fisher's exact test, $P = 0.047$).

The canonical correspondence analysis explained 49.4% of the relationship between the intensity of copepods and 5 environmental variables (Table I). Water temperature was the most important variable explaining the intensity of *L. simplex*, whereas dissolved oxygen influenced the intensity of *P. diceraus* and salinity that of *C. serratus* (Fig. 6).

Component community

Eighty-two percent of fish sampled were infected: 29% with 1 species, 29% with 2 species, 17% with 3 species, and 7% with 4

TABLE I. Eigenvalues of the canonical correspondence analysis.

	Axis 1	Axis 2
Eigenvalues	0.075	0.015
Percentage	11.361	2.276
Cum. percentage	11.361	13.637
Cum.Constr.Percentage	83.310	100.000
Species–environment correlations	0.494	0.206

species. No host was parasitized by all 5 copepod species simultaneously. Table II shows the descriptors of the parasitic copepod component communities of *S. annulatus*. Species richness in each sampling month varied from 3 to 5. The highest value of diversity index was found in February 2008, where the evenness index showed its second highest value. The Berger–Parker dominance index varied from 0.4 (April, June, and February 2008) to 0.8 (February 2007). *Lepeophtheirus simplex* numerically dominated in most sampling months.

Infracommunities

Mean copepod species richness ranged from 1.3 ± 0.5 (February 2007) to 3.0 ± 1.2 (June), and the mean number of copepod individuals ranged from 3.3 ± 2.7 (February 2008) to 12.6 ± 10.5 (June) (Fig. 7). Brillouin diversity index values varied from 0.1 ± 0.2 (February 2007) to 0.7 ± 0.4 (June) and the Berger–Parker dominance index varied from 0.6 ± 0.2 (June) to 0.9 ± 0.2 (February 2007) (Fig. 7). These 4 infracommunity descriptors varied significantly between sampling months (Kruskal–Wallis test: for species richness, $H = 51.53$, $P < 0.001$; for number of individuals, $H = 33.83$, $P < 0.001$; for Brillouin index, $H = 58.68$, $P < 0.001$; and for Berger–Parker index, $H = 47.06$, $P < 0.001$).

No significant associations were found between host sex and both richness species and number of individuals, neither when all fish were pooled in the same analysis (Mann–Whitney U-test: for species richness, $T = 25726.0$, $P > 0.05$; for number of individuals, $T = 26657.0$, $P > 0.05$) nor when samples were considered separately (data not shown). Host length and wet weight were positively and significantly correlated with species richness and number of individuals (Table III). However, water salinity was negatively correlated with both infracommunity descriptors, whereas water temperature was positively correlated with the number of individuals (Table III). To eliminate the confounding effect of seasonality on the correlation between host length and both infracommunity descriptors, analyses were repeated using data from those sampling months among which there were no significant differences in infracommunity descriptors; even then, positive and significant correlations were observed (for species richness, $r = 0.311$, $P < 0.0001$; for number of individuals, $r = 0.438$, $P < 0.0001$).

Association between burdens of parasitic copepods and fish condition factor

The analysis was done considering the intensity of *L. simplex*, *P. diceraus*, and *C. serratus* and the number of individuals of the infracommunities. When data from all sampling months were included in the same analysis, a positive and significant correlation between the condition factor K and the intensity of
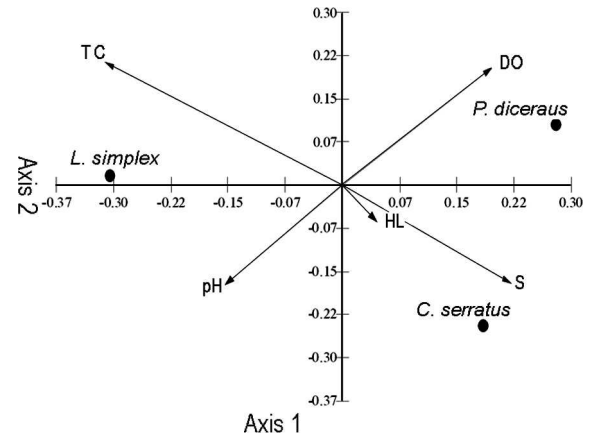

FIGURE 6. Canonical correspondence analysis ordination showing 3 parasitic copepods (*Caligus serratus*, *Lepeophtheirus simplex*, and *Pseudochondracanthus diceraus*) with respect to host length (HL) and water temperature (T C), salinity (S), pH, and dissolved oxygen (DO), relative to the first two canonical axes.

both *L. simplex* ($r = 0.156$, $P < 0.05$) and *C. serratus* ($r = 0.125$, $P < 0.05$) was observed. However, those correlations were not observed when the effect of seasonality was eliminated. Neither intensity of *P. diceraus* nor number of individuals was correlated with the condition factor K.

DISCUSSION

Seasonal changes in prevalence and mean intensity

To date, nothing is known about the ecology of the 5 parasitic copepods found in this survey. *Acantholochus zairae* was recently described from the same fish species examined here (Morales-Serna and Gómez, 2010). *Lepeophtheirus simplex* was described 10 yr ago from *S. annulatus* off the southern coast of Sinaloa, México (Ho et al., 2001). Recently, this copepod was reported to cause health problems for *S. annulatus* reared in the laboratory (Fajer-Ávila et al., 2008). *Caligus serratus* was described by Shiino (1965) on *Atherinopsis californiensis* caught near La Jolla, California; to our knowledge, this copepod has not been recorded since. *Pseudochondracanthus diceraus* has been reported to infect species of *Sphoeroides* from both the north Atlantic and north Pacific, although information regarding this species has mainly focused on its taxonomy (Wilson, 1908; Bere, 1936; Pearse, 1947; Ho, 1970). *Parabrachiella* sp. probably represents an unknown species; however, its identification must be considered with caution because, according to Piasecki et al. (2010), many of the existing species have been inadequately described and illustrated. In the present study, new geographical records and new host species records are given for *P. diceraus* and for *C. serratus*.

Acantholochus zairae and *Parabrachiella* sp. occurred rarely. Probably, *S. annulatus* is not the most suitable host, or the environmental conditions in Santa María La Reforma lagoon are not favorable for these parasites. In contrast, *L. simplex*, *P. diceraus*, and *C. serratus* exhibited high values of prevalence and intensity of infestation, but only *L. simplex* showed a seasonal pattern throughout the year. Its prevalence and mean intensity was significantly higher in August and October (months with the highest water temperature) compared with February–March 2007 and January–February 2008 (months with the lowest water

TABLE II. Characteristics of the parasitic copepods component communities on the bullseye puffer (*Sphoeroides annulatus*) during a 1-yr period (from February 2007 to February 2008). *J′*, evenness; *H′*, Shannon diversity index; B-P, Berger–Parker dominance index. Pse, *Pseudochondracanthus diceraus*; Leo, *Lepeophtheirus simplex*; Cse, *Caligus serratus*.

Sampling month	No. of hosts	No. of species	Mean no. of parasites	*J′*	*H′*	B-P	Dominant species
February 2007	51	5	3.2	0.44	0.71	0.80	Pse
March	25	4	2.2	0.64	0.88	0.72	Pse
April	43	5	5.5	0.71	1.15	0.43	Pse-Leo
May	6	4	5.0	0.77	1.07	0.47	Leo
June	6	4	10.5	0.83	1.15	0.43	Pse
July							
August	46	4	6.8	0.74	1.03	0.53	Leo
September							
October	45	5	7.9	0.53	0.86	0.71	Leo
November	44	4	3.1	0.76	1.06	0.57	Leo
December	43	5	7.8	0.75	1.21	0.48	Leo
January	10	3	4.0	0.94	1.04	0.50	Cse
February 2008	18	5	2.9	0.90	1.45	0.43	Cse

temperature). This result is supported by CCA, which indicated that the intensity of *L. simplex* was influenced by water temperature. Seasonality also has been observed in 2 other species of *Lepeophtheirus* (*L. salmonis* and *L. pectoralis*) from higher latitudes; both reached high infection levels in summer (Schram et al., 1998; Cavaleiro and Santos, 2009).

The rate of development of *L. simplex* seems to decrease in cold water, as observed in *L. salmonis* (Tully and Nolan, 2002). Adult females of *L. salmonis* from winter generations are significantly larger, produce longer egg strings, and a greater number of smaller eggs than females in summer generations. However, the

proportion of non-viable eggs is higher at low temperatures. Moreover, smaller eggs with lower nutritional reserves are produced and larval survival is probably lower at low temperatures (Ritchie et al., 1993; Heuch et al., 2000). In contrast, egg length is greater and the production of the egg strings is faster in warmer waters (Heuch et al., 2000; Tully and Nolan, 2002). In addition, it has been shown that settlement and survival of *L. salmonis* copepodids is higher in warmer waters at a constant salinity (Tucker et al., 2000). Thus, it is probable that the development of *L. simplex* is temperature-dependent, and strong epizootics could be expected in farms of *S. annulatus* during the
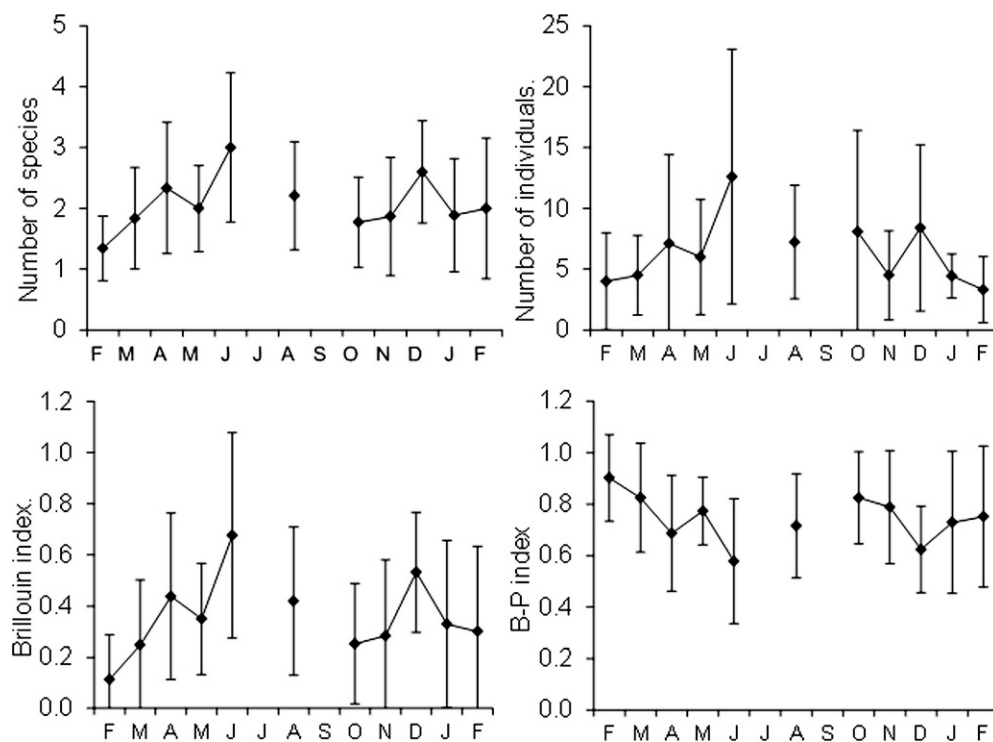

FIGURE 7.   Variation in mean number of species, mean number of individuals, mean Brillouin's diversity index, and mean Berger–Parker (B-P) dominance index of parasitic copepod infracommunities on the bullseye puffer (*Sphoeroides annulatus*) during 1-yr-period (from February 2007 to February 2008).

TABLE III. Spearman's rank correlation coefficient between biotic and abiotic factors and number of species and number of individuals from parasitic copepods infracommunities on the bullseye puffer (*Sphoeroides annulatus*) during a 1-yr period (from February 2007 to February 2008).

Biotic and abiotic factors	No. of species		No. of individuals	
	r	P	r	P
Host length	0.373	0.000	0.430	0.000
Host weight	0.469	0.000	0.510	0.000
Water temperature	0.091	0.094	0.153	0.004
Water salinity	−0.183	0.000	−0.255	0.000
Water oxygen	−0.017	0.750	−0.082	0.129
Water pH	0.069	0.203	0.052	0.337

warmest months. In view of the potential threat posed by *L. simplex*, more detailed information regarding its biology is required.

There was no significant variation in *P. diceraus* infestation levels between most of the sampling months. This suggests that *P. diceraus* is tolerant of physical and chemical environmental changes, which would also allow a wider distribution. The most evident difference was observed during November when prevalence and mean intensity were significantly lower. CCA analyses indicated that dissolved oxygen was the main factor influencing the intensity of *P. diceraus*; in fact, the lowest concentration of oxygen was observed in October and November. So far, there is limited knowledge regarding the effects of this variable on parasitic copepods. Other gill parasites, such as monogeneans, are negatively correlated with dissolved oxygen, reaching high infestation levels under hypoxic conditions (Raymond et al., 2006). It would therefore seem that parasitic copepods, as is the case with their free-living relatives, are rather sensitive to oxygen depletion. Raymond et al. (2006) observed that a parasitic copepod was most prevalent in sites with higher dissolved oxygen levels. Also, it is possible that the lower prevalence and mean intensity of *P. diceraus* observed in November was due to the effect of host-size, which was low during this month. Although it is not a recurrent pattern, the occurrence of fish parasites is positively associated with host size because larger bodies conceivably provide more space and other resources for parasites (Poulin, 2007). Particularly, large-bodied fishes are more likely to be colonized by ectoparasites because they possess a larger external surface area for attachment by infective stages.

The prevalence of *C. serratus* varied significantly between sampling months, but it did not show a regular pattern. This could suggest that the occurrence of *C. serratus* on *S. annulatus* is not affected by environmental factors. However, the mean intensity of this copepod was almost constant throughout the 1-yr-period of study, except for a significantly lower value observed in February 2007. CCA indicated that the intensity of *C. serratus* was positively influenced by water salinity and, to some extent, by host size. Experimental studies by Bricknell et al. (2006) on the caligid *L. salmonis* indicate that both survival and host infectivity are severely compromised by short-term exposure to reduced salinity levels. Also, water temperature has been shown to be positively associated with the development of other *Caligus* species such as *C. elongatus* and *C. rogercresseyi* (Pike et al., 1993; González and Carvajal, 2003; Costello, 2006). If *C. serratus* is equally affected by water temperature, higher infection levels

could have been expected during warm months, i.e., June–October, but this was not the case. The increase in water temperature might have led to an increase in larval production of *C. serratus*. However, the recruitment of the larvae might have taken place in other host species, which might have been facilitated given the low host specificity by species of *Caligus* (Costello, 2009).

The prevalence of all 3 parasitic copepod species (*L. simplex*, *P. diceraus*, and *C. serratus*) was more variable than their mean intensity. This supports the hypothesis that intensity of infection is a species characteristic and that the biological features of parasitic species can potentially override local environmental conditions in driving parasite population dynamics. According to Poulin (2006), this is possible because prevalence is determined by encounter rates between parasites and hosts, which are influenced by processes external to the fish, e.g., survival of free-living parasite stages, probably determined by local factors, whereas intensity of infection is determined to a large extent by processes acting within the fish.

In this survey, host sex was not associated with variations in both prevalence and intensity between sampling months. Only the prevalence of *P. diceraus* was significantly higher in female than in male hosts during February 2007, but the significance was marginal and the difference was not repeated in the remaining months. Some studies have noted that host sex is associated with levels of parasitic infection, and this has been explained by the energetic trade-off hypothesis, i.e., a cost in reproduction associated with an investment in immune function (Skarstein et al., 2001; Šimková et al., 2005). For example, spawning males of the Arctic charr (*Salvelinus alpinus*) have a smaller spleen, which is an important lymphocyte-producing organ, and they were found to have higher intensities of macroparasitic infections than resting males (Skarstein et al., 2001). Sánchez-Cárdenas et al. (2007) found that *S. annulatus* from the northwestern coast of México has 2 reproductive periods throughout the year, the first and most important one takes place during spring–summer (from April to August), and the second takes place during October–November. Considering this, as well as the infection data presented here, it is reasonable to suggest that the occurrence of parasitic copepods on both sexes of *S. annulatus* is random, even during reproductive periods. However, additional research must be undertaken to test such a hypothesis, i.e., discriminating between spawning and resting fish.

Component community and infracommunities

Overall, at the component community level, the number of copepod species ranged from 4 to 5. This low variability could be attributed to both the continuous reproduction (gravid females were found during the whole study period) and high longevity of the copepods (e.g., the estimated lifetime for *L. salmonis* is approximately 7 mo; Costello, 2006). Along the same lines, Cavaleiro and Santos (2009) observed that the reproduction cycle of parasitic copepods runs throughout the year. The number of copepod species observed here is not surprisingly low because ectoparasite communities are generally impoverished with respect to species diversity; however, the number of parasitic copepod species in this report is higher than that found by Fajer-Ávila et al. (2006) (4 species) on white mullet (*Mugil curema*) from other lagoons of the region (northwestern México) and by Violante-

González et al. (2008) (1 species) on threespot cichlid (*Cichlasoma trimaculatum*) from a brackish system of the Mexican south Pacific. Unfortunately, information regarding parasitic copepod communities of other host species is not abundant.

At the infracommunity level, there were significant differences in number of species, Brillouin diversity index, number of individuals, and Berger–Parker dominance index between sampling months. However, a clear seasonal pattern was not seen, suggesting that these differences could be spurious. Because temperature seems to be an important factor in influencing biodiversity, a seasonal pattern in biodiversity variation was expected, with the highest values during the warmest months. Nonetheless, one of the highest mean values in number of species, number of individuals, and Brillouin index was observed in December (a comparatively cold month), when the largest fish were caught; but, as suggested, large-bodied hosts also are more likely to be colonized by ectoparasites, thereby increasing species richness (Lo et al., 1998; Šimková, Morand et al., 2001). In addition, statistical analyses revealed a positive correlation between both number of species and number of individuals, and host size. Therefore, species richness of parasitic copepods of *S. annulatus* could well be host size-dependent, as shown for ectoparasitic species richness of other fish species (Šimková, Morand et al., 2001, and references therein). Also, the number of individuals was positively correlated with water temperature, making apparent a slight seasonality, mainly due to the increase of abundance of *L. simplex* during warm months (August and October). This supports the work of Šimková, Sasal et al. (2001), who found that despite the different effect of temperature on the different parasitic species, the total abundance of ectoparasites increases with rising temperatures.

Parasitic burdens and host body condition

Finally, no significant association was detected in this study between the burden of parasitic copepods and fish condition factor *K*. Similarly, other studies failed to indicate that parasites affect the fish condition in natural systems (Mo and Heuch, 1998; Olivero-Vervel et al., 2005; Jones et al., 2006). In contrast, Lemly and Esch (1984) provided a clear example of mortality due to the direct effects of parasitism in a natural population of fish. Evidence of damage produced by parasitic copepods is better documented from aquaculture studies. In a southern bluefin tuna (*Thunnus maccoyii*) farm, e.g., Hayward et al (2009) found that the sea louse (*Caligus chiatos*) was strongly associated with both fish condition and severity of eye damage. It is possible that the health of *S. annulatus* was already reduced by copepod infection because these crustaceans damage their hosts directly through their attachment mechanisms and through their feeding activities; however, severity of damage probably was low, and the method that we used was unable to detect any significant effect of copepod parasitism on *S. annulatus*.

ACKNOWLEDGMENTS

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