

Temporal variation of *Mexiconema cichlasomae* (Nematoda: Daniconematidae) in the Mayan cichlid fish *Cichlasoma urophthalmus* and its intermediate host *Argulus yucatanus* from a tropical coastal lagoon

A. L. MAY-TEC^{1*}, D. PECH², M. L. AGUIRRE-MACEDO¹, J. W. LEWIS³
and V. M. VIDAL-MARTÍNEZ¹

¹Departamento de Recursos del Mar, Cinvestav-IPN Unidad Mérida, Carretera antigua a Progreso km 6, Apdo. Postal 73–Cordemex, 97310 Mérida, Yucatán, México

²Instituto EPOMEX, Universidad Autónoma de Campeche, A. Agustín Melgar S/N Col. Buena Vista, 24039 Campeche, Campeche, México

³School of Biological Sciences, Royal Holloway University of London, UK

(Received 16 July 2012; revised 12 September 2012; accepted 17 September 2012; first published online 6 November 2012)

SUMMARY

The aim of the present investigation was to determine whether temporal variation in environmental factors such as rainfall or temperature influence long-term fluctuations in the prevalence and mean abundance of the nematode *Mexiconema cichlasomae* in the cichlid fish *Cichlasoma urophthalmus* and its crustacean intermediate host, *Argulus yucatanus*. The study was undertaken in a tropical coastal lagoon in the Yucatan Peninsula (south-eastern Mexico) over an 8-year period. Variations in temperature, rainfall and monthly infection levels for both hosts were analysed using time series and cross-correlations to detect possible recurrent patterns. Infections of *M. cichlasomae* in *A. yucatanus* showed annual peaks, while in *C. urophthalmus* peaks were bi-annual. The latter appear to be related to the accumulation of several generations of this nematode in *C. urophthalmus*. Rainfall and temperature appear to be key environmental factors in influencing temporal variation in the infection of *M. cichlasomae* over periods longer than a year together with the accumulation of larval stages throughout time.

Key words: temporal variation, parasitic nematodes, tropics, seasonality, long-term studies, Global Climate Change.

INTRODUCTION

Understanding variation in the infection levels of parasites in hosts through time, relative to biotic and abiotic factors, has become a critical issue due to the potential effect of Global Climate Change (GCC) (Benedetti-Cecchi *et al.* 2000; Zander, 2003, 2004, 2005; Abell *et al.* 2006). There is no clear proof that climate change will increase climate variability and there are also some disputes on the increase of extreme climate events. However, there is evidence that climate variability (such as El Niño Southern Oscillation, ENSO) (Oliva *et al.* 2007; Soniat *et al.* 2009), extreme weather events (Easterling *et al.* 2000; Martínez and Merino, 2011) (such as hurricanes) (Lafferty, 2009; Aguirre-Macedo *et al.* 2011), and seasonality (Kennedy, 1993; Simková, 2005; Kerans *et al.* 2005; Poulin and Mouritsen, 2006; Krasnov *et al.* 2008; Luque and Poulin, 2008; Knipes and Janovy, 2009) can influence the life cycles of human and animal parasites in both terrestrial and aquatic

environments producing phenological or physiological as well as distributional changes (Githeko *et al.* 2000; Parmesan and Galbraith, 2004; Patz *et al.* 2005; Poulin and Mouritsen, 2006; Marcogliese, 2008; Mas-Coma *et al.* 2009; Ujvari *et al.* 2010).

For temperate latitudes, the majority of studies on temporal variation of parasites in aquatic hosts has been undertaken over the short term or annually, due to seasonality of temperature being a key variable causing fluctuations ranging from annual cycles (Kennedy, 1993; Simková, 2005; Kerans *et al.* 2005; Poulin and Mouritsen, 2006; Krasnov *et al.* 2008; Luque and Poulin, 2008; Knipes and Janovy, 2009). For notifiable human diseases, few long-term studies have shown the lack of temporal variability associated to large-scale weather changes as described by the North Atlantic Oscillation (NAO) (Húbalek *et al.* 2003; Húbalek, 2005).

For tropical latitudes, most studies on the temporal variability of the infection parameters of parasites of aquatic organisms have been carried out over the short term (e.g. Leong, 1986; Coley and Aide, 1991; Fiorillo and Font, 1999; Steinauer and Font, 2003; Vincent and Font, 2003; Martin *et al.* 2004; Violante-Gonzalez *et al.* 2008). A further complication in the tropics for the study of the temporal dynamics of the

* Corresponding author: Laboratorio de Parasitología, Departamento de Recursos del Mar, Cinvestav, Carretera antigua a Progreso km 6, Apdo. Postal 73–Cordemex, 97310 Mérida, Yucatán, Mexico. Tel.: +52 999 942 9400. Fax: +52 999 981 23 34. E-mail: amayt@mda.cinvestav.mx

infection parameters of aquatic parasites is its climate variability due to the presence of phenomena that occur at time scales longer than a year such as El Niño 3–5 years (Ghil, 2002), and hence long-term observations are necessary. Recently, Pech *et al.* (2010) and Aguirre-Macedo *et al.* (2011) have shown over a relatively long term of 9 years that rainfall and hurricanes rather than temperature are key variables in driving the proportion of snails and fish hosts infected in the Peninsula of Yucatan (tropical Mexico). In both cases, these authors combined the data of several trematode species into a single index called the ‘percentage of infected hosts’ (PIH). This strategy is useful to address general patterns of infection over the long term, but without determining the effect of rainfall or other environmental variables on the infrapopulations of specific parasite species. Apart from the work of Jiménez-García and Vidal-Martínez (2005) on the larval digenean *Oligogonotylus manteri*, there is a lack of information on parasite infrapopulations in aquatic hosts in tropical latitudes.

Therefore in the present investigation, the infrapopulations of the daniconematid (dracunculoid) nematode *Mexiconema cichlasomae* were analysed in both the definitive fish (*Cichlasoma urophthalmus*) and intermediate crustacean (*Argulus yucatanus*) hosts from a coastal lagoon in south-eastern Mexico. The effects of environmental factors on the temporal dynamics of *M. cichlasomae* in natural populations of its fish and crustacean host would clearly contribute to our understanding of how parasites might respond to extreme environmental changes in the light of GCC. Therefore, the aim of the present study was to determine the potential influence of rainfall or/and temperature from 2003 to 2010 on long-term fluctuations of the prevalence and mean abundance of *M. cichlasomae* in both its intermediate and definitive hosts in Celestun, a tropical coastal lagoon from Yucatan, south-eastern Mexico.

MATERIALS AND METHODS

Study site and sampling procedures

Celestun is a karstic tropical lagoon located at the northwest corner of the Yucatan Peninsula (20°52′47.50″N; 90°21′13.10″O) characterized by the input of freshwater from groundwater discharges that vary according to the rainfall regime (Herrera-Silveira *et al.* 1999). Celestun coastal lagoon has been described as a dynamic ecosystem (Herrera-Silveira *et al.* 1999), demonstrating natural significant intra-annual variability in its water column characteristics, which are due to seasonal rainfall, winds and temperature regimes prevailing in the zone (Pech *et al.* 2007). Although the regional climatic conditions are not always well defined in the study area, 3 seasons occur namely a dry season with low

precipitation levels (March to May, 0–50 mm and 14 °C–38 °C), a rainy season (June to October >500 mm and 21 °C–35 °C) and a winter frontal storm ‘Nortes’ season (November to February, 20–60 mm). The latter is characterized by relatively strong winds (>60 km/h), marked and rapid decreases in air temperature (31 °C–8 °C) and a small amount (10–60 mm), of cool (9 °C–18 °C) rainfall (Hernández-Guevara *et al.* 2008).

Biological aspects of the host-parasite system under study

Cichlasoma urophthalmus is an euryhaline species, abundant in freshwater canals and brackish waters of the Atlantic watersheds from the Rio Coatzacoalcos basin southward through Mexico, including the Yucatan Peninsula up to Nicaragua (Martínez-Palacios and Ross, 1992; Greenfield and Thomerson, 1997; Trexler *et al.* 2000). This fish species survives in a wider range of temperature (24 °C–38 °C) and salinities (4–40.3 ppt) (Martínez-Palacios, 1987). They are primarily carnivorous, feeding mainly on invertebrate (i.e. microcrustacea, mollusks, isopods and polychaetes) (Martínez-Palacios and Ross, 1988; Miller *et al.* 2005). Breeding occurs throughout the year, with a reproductive peak between May and September (rainy season). The maximum age reached by *C. urophthalmus* is 7 years old (Faunce *et al.* 2002). *Argulus yucatanus* is a crustacean ectoparasite infecting *C. urophthalmus* in coastal lagoons along the Peninsula of Yucatan. This ectoparasite has a proboscis to penetrate the host’s skin, feeding on blood (Avenant-Oldewage *et al.* 1994). *Argulus yucatanus* is known to be a vector of the nematode larvae of *Mexiconema cichlasomae* (Moravec *et al.* 1999).

This parasite is a dracunculoid (Family Daniconematidae). The nematodes are genetically related to Skrjabillanids (Mejía-Madrid and Aguirre-Macedo, 2011) and used as intermediate host to *A. yucatanus*. In the fish *M. cichlasomae* develop into mature male and female, the gravid females are approximately 2–3 times as long as male and produce thousands of larvae (Moravec *et al.* 1992). However, in spite of this information there are many aspects of their life cycle still unknown, such as recognition of their different stages of maturation in both hosts and the parasite’s larval morphogenesis.

Sampling procedure

Specimens of *C. urophthalmus* were collected by hook and line in the middle zone of Celestun lagoon (20°52′46.68″N; 90°21′15.4″O), on a monthly basis between March 2003 and December 2010 with a sample size of 15 fish per month. Three factors were considered when determining the sample size for detecting infections with *M. cichlasomae* and *Argulus*

yucatanus. First, the prevalence was based on that of 43% by of *M. cichlasomae* Moravec *et al.* (1992) and 63% by Salgado-Maldonado and Kennedy (1997). The other two factors included the accepted level of risk, $\alpha=0.05$ in this case, and the sensitivity of stereomicroscopy as a method for parasite identification. We assumed that such a diagnostic method has a sensitivity of 75% due to human error. Thus, assuming a Poisson distribution for the probability of identifying *M. cichlasomae*, the monthly sample size was obtained using the formula $n=4/\text{prev}$, where n is the fish sample size, the number 4 originated from $-\ln(\alpha=0.05 \times \text{sensitivity of the diagnostic method})$ and prev is the prevalence in the fish population (des Clers, 1994). In the case of larvae of *M. cichlasomae* in *A. yucatanus* due to low prevalence values (1.29% for $n=155$ *A. yucatanus*; Moravec *et al.* 1999), a statistically representative sample size with this method cannot be guaranteed. Nevertheless, we decided to present the data on these larvae to further our understanding of the biology of *M. cichlasomae*.

For the first 6 years of study of this host–parasite system, each month the fish were captured and taken together in a 200 L tank with lagoon water to the laboratory. Once there, the body surface of each fish was examined under a stereomicroscope especially for *A. yucatanus*. Certainly, this method can present some error to represent statistically the prevalence of this ectoparasite due to the detachment from the fish. Thus, in the last 2 years at the very moment of a capture, each fish is placed in an individual lagoon water-filled container and its external surface immediately examined. *Argulus yucatanus* were collected with the aid of forceps and allocated in the same container, numbered and transported to the laboratory with lagoon water. We did not find significant differences between the old and new techniques for prevalence (G -test; $G=2.74$ $P>0.05$) or mean abundance ($W=275.50$ $P>0.05$). Thus, we concluded that the data from both the ‘old’ and ‘new’ methods can be reliably compared.

In the laboratory each specimen (*A. yucatanus*) was transferred to a slide with a drop of lagoon water and a coverslip, for examination under a compound microscope (10X). Following a post-mortem examination of each fish the body cavity, mesenteries, swim bladder and kidney were examined thoroughly as these are the preferred microhabitats of *M. cichlasomae* (Vidal-Martínez *et al.* 2001). Each organ was compressed between two glass slides of 15×15 cm (0.5 cm thick) for observation under the stereomicroscope. Each nematode was placed in a Petri dish containing 0.7% saline solution and later fixed in 4% formalin at 80 °C (see Vidal-Martínez *et al.* 2001). The recognition of each stage of maturity of *M. cichlasomae* was based on previous work by Moravec *et al.* (1992), Moravec (1994), and Caspeta-Mandujano and Monjica (2004).

Additionally we obtained the water temperature (°C) monthly data from 2003 to 2010 ourselves, directly from site, with the aid of multiparameter Ysi model 85. The monthly rainfall data were obtained from the Climatologic Station (CELYC) of CNA (National Water Commission at Celestún, Yucatán, México), localized to 20°51'29"N; 90°22'59"O approximately to 2 km of the study site.

Data analysis

The prevalence and mean abundance, referred to as infection parameters, of *M. cichlasomae* in both the definitive and intermediate hosts were calculated according to the method of Bush *et al.* (1997). A single spectral analysis by Fourier series (Legendre and Legendre, 1998) was used to extract variability patterns and periodical cycles of the infection parameters of *M. cichlasomae* in both hosts, together with monthly cycles of rainfall and temperature, (Statistica v. 6 Statsoft©). This analysis requires data points equally spaced in time (Press *et al.* 1996), and our data sets fulfilled this requirement. Each temporal data set was transformed into sine curves of the same amplitude or harmonic frequencies of different amplitudes and phases that collectively smooth the original time series (Scharlemann *et al.* 2008) and were represented in a periodogram. Here harmonic frequencies, measured as spectral densities (strength of the frequency signal), represent a temporal scale of maximum variability in the temporal distribution (Platt and Denman, 1975). Any marked frequency peaks were interpreted as temporal scales of maximum variability to show trends of infection and environmental variables (temperature and rainfall).

Spectral density values of parasite infection parameters and environmental variables were compared using cross-correlation coefficients. Cross-correlation quantifies temporal associations between variables and provides a measure of the similarity between 2 different data sets at different time lags and determines the extent to which data sets exhibit correlated periodic variations. Time lags refer to delayed responses of dependent variables following fluctuations in independent variables (Olden and Neff, 2001). The time lag with the highest correlation coefficient is taken as the accurate time lag between the 2 time series (Wei, 1990), and the cross-correlation coefficients were calculated for a significance of $P<0.05$ (Thiel *et al.* 2004).

RESULTS

A total of 825 specimens of *C. urophthalmus*, based on monthly samples of 15 fish from the Celestun coastal lagoon, were collected between March 2003 and

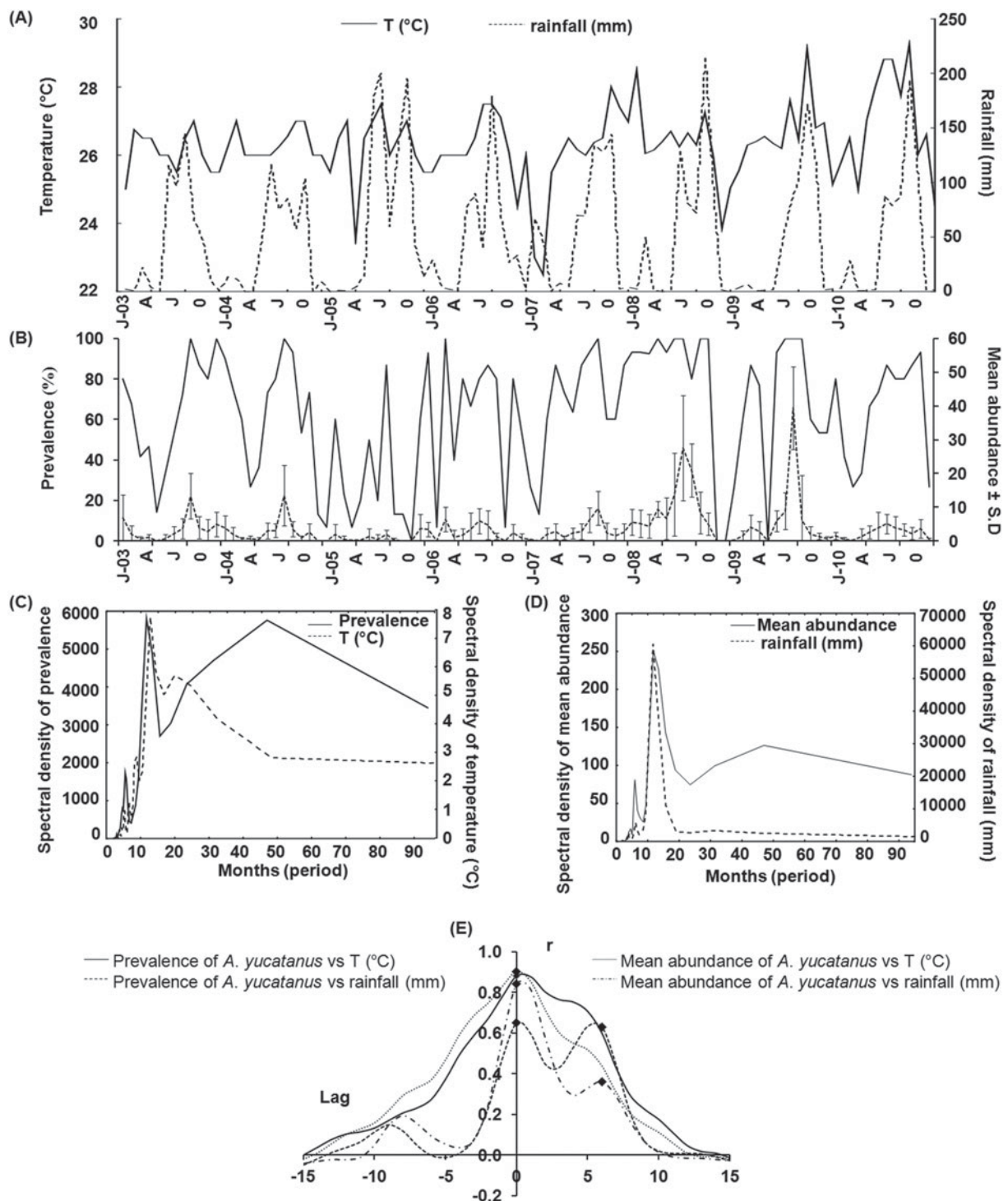


Fig. 1. *Argulus yucatanus* ectoparasite from the fish *Cichlasoma urophthalmus* in a Celestun (México) coastal lagoon from 2003 to 2010. (A) Shows temporal fluctuations in the infection parameters. Temperature (°C) and rainfall (mm) of Celestun Yucatan. (B) The prevalence (black line), mean abundance ± S.D. (dotted line) of *Argulus yucatanus* in *Cichlasoma urophthalmus*. (C) Spectral density of the prevalence of *A. yucatanus* (black line) and temperature (°C) (dotted line). (D) Spectral density of the mean abundance of *A. yucatanus* (black line) and rainfall (mm) (dotted line) by Fourier series. (E) Cross-correlations between the prevalence and mean abundance of *A. yucatanus* relative to temperature (°C), rainfall (mm).

December 2010, except in August 2007, when sampling was not possible due to the hurricane Dean.

Rainfall and temperature showed marked temporal fluctuations throughout the study period (Fig. 1A). The water temperature data showed

3 peaks every 12, 21 and 41 months (Fig. 1C) with the minimum at 25.2 °C and maximum at 29.2 °C and high frequency peaks of rainfall occurred every 12 months (Fig. 1D). Data on temperature and rainfall from Fig. 1A–D are also repeated in Figs 2A–D

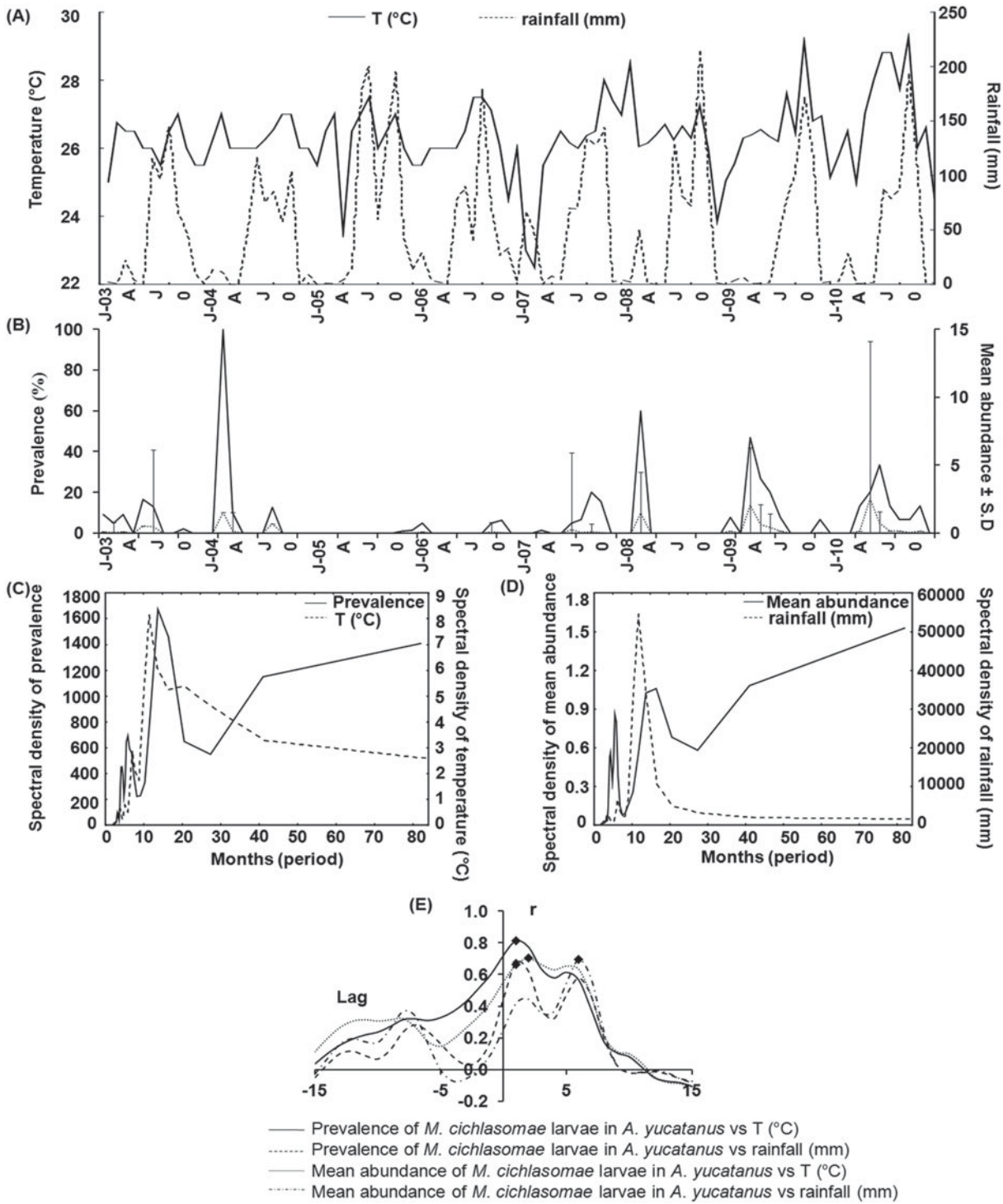


Fig. 2. *Mexiconema cichlasomae* larvae from ectoparasite *Argulus yucatanus* in a Celestun (México) coastal lagoon from 2003 to 2010 showing temporal fluctuations in the infection parameters. (A) Temperature (°C) and rainfall (mm) of Celestun Yucatan. (B) The prevalence (black line), mean abundance \pm S.D. (dotted line) of *Mexiconema cichlasomae* larvae in *Argulus yucatanus*. (C) Spectral density of prevalence *M. cichlasomae* larvae (black line) and temperature (°C) (dotted line). (D) Spectral density of mean abundance of *M. cichlasomae* larvae (black line) and rainfall (mm) (dotted line) by Fourier series. (E) Cross-correlations between the prevalence and mean abundance of *M. cichlasomae* larvae relative to temperature (°C), rainfall (mm).

and 3A–D to provide an overall effect of these two environmental factors on changes in the infection parameters of both *M. cichlasomae* and *A. yucatanus*.

Argulus yucatanus in *Cichlasoma urophthalmus*

Argulus yucatanus was found to infect *C. urophthalmus* between 2003 and 2010 (94 sampling temporal

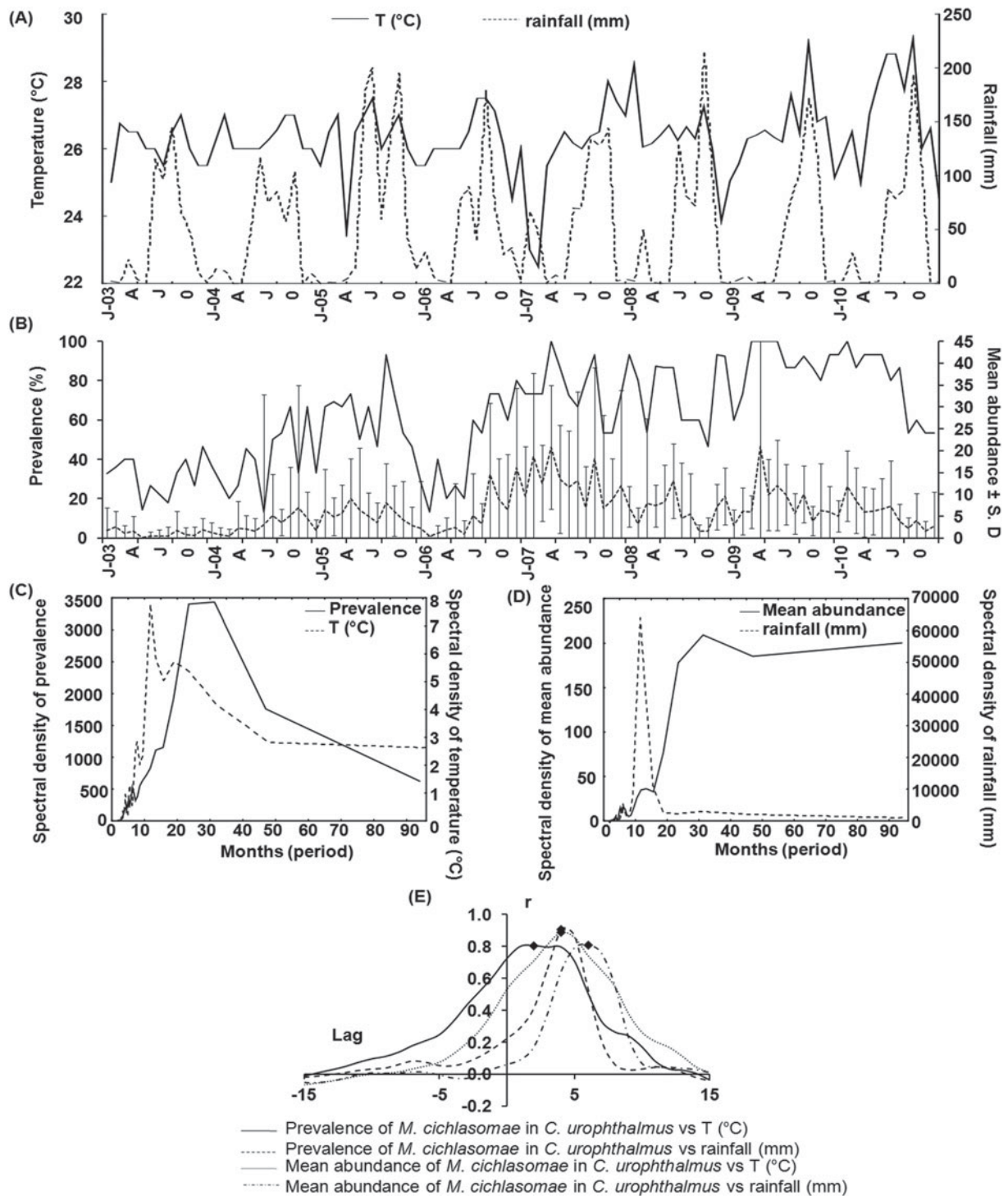


Fig. 3. Dracunculoid nematode *Mexiconema cichlasomae* from the fish *Cichlasoma urophthalmus* in a Celestun (México) coastal lagoon from 2003 to 2010 showing temporal fluctuations in the infection parameters. (A) Temperature (°C) and rainfall (mm) of Celestun Yucatan. (B) The prevalence (black line), mean abundance \pm S.D. (dotted line) of *Mexiconema cichlasomae* in *Cichlasoma urophthalmus*. (C) Spectral density of the prevalence of *M. cichlasomae* (black line) and temperature (°C) (dotted line) (D) spectral density of the mean abundance of *M. cichlasomae* (black line) and rainfall (mm) (dotted line) by Fourier series. (E) Cross-correlations between the prevalence and mean abundance of *M. cichlasomae* in *C. urophthalmus* relative to temperature (°C), rainfall (mm).

points) with prevalence and mean abundance values from 6 to 100%, and $4 \cdot 12 \pm 2 \cdot 84$ respectively (Fig. 1B).

The spectral analysis of prevalence and mean abundance showed 2 peaks of maximum variability

occurring every 12 and 45 months (Fig. 1C, D). Significant cross-correlation coefficients between prevalence or mean abundance of *A. yucatanus* and rainfall or temperature were observed at lag 0, suggesting an immediate response to infection to

Table 1. Cross-correlations between the prevalence and mean abundance of *Mexiconema cichlasomae* including L1 and L4 larvae, adult worms (male and female), gravid females and *Argulus yucatanus**(P* < 0.05, 1 lag = 1 month.)

	Prevalence		Mean abundance	
	r	Lag	r	Lag
<i>M. cichlasomae</i> (larvae) vs <i>A. yucatanus</i>	0.86	-1	0.7	-1
<i>M. cichlasomae</i> (larvae) vs <i>M. cichlasomae</i> (L4)	0.73	2	0.79	1
<i>M. cichlasomae</i> (adults) vs <i>M. cichlasomae</i> (L4)	0.82	0	0.86	0
<i>M. cichlasomae</i> (gravid female) vs <i>A. yucatanus</i> (L4)	0.9	0	0.89	0
<i>M. cichlasomae</i> (gravid female) vs <i>M. cichlasomae</i> (larvae)	0.74	2	0.83	2

changes in these environmental variables. Additionally, significant cross-correlation coefficients between prevalence, abundance and rainfall were observed at lag (6) (1 lag = 1 month), suggesting a delay in response to infection (Fig. 1E).

Mexiconema cichlasomae larvae in *Argulus yucatanus*

The prevalence of larval *M. cichlasomae* fluctuated between 0 to 100% and the average number of larvae was 0.13 ± 0.36 throughout the entire study (Fig. 2B). The periodograms of prevalence and mean abundance showed peaks of maximum variability every 12 and 40 months (Fig. 2C, D). From the cross-correlation analysis, the prevalence, mean abundance and rainfall correlated significantly at lag 1 and lag 6, whereas the prevalence and mean abundance correlated significantly with temperature at lag 1 and lag 2 (Fig. 2E).

In addition, cross-correlation analyses between the infection parameters of *M. cichlasomae* and those of *A. yucatanus* in *C. urophthalmus* showed significant negative correlations (Table 1). Positive cross-correlations were observed between the mean abundance of both larval and adult nematodes in *C. urophthalmus* (Table 1).

Mexiconema cichlasomae in *Cichlasoma urophthalmus*

Adult nematodes of *M. cichlasomae* (males, mature females, gravid females) and L4 larvae were present throughout the entire sampling period, with prevalences ranging from 20 to 100% and a mean abundance of 3.74 ± 4.40 (Fig. 3B). Spectral analysis of prevalences showed very similar patterns for all developmental stages, with peaks of maximum variability for prevalence and mean abundance occurring every 24–27 months (Fig. 3C), and 12 and 24 months respectively (Fig. 3D). Cross-correlation analyses between the prevalence and mean abundance of *M. cichlasomae* and rainfall showed significant associations at lags 4 and 6 (Fig. 3E). Similar significant results were found between the

prevalence, mean abundance of *M. cichlasomae* and the temperature at lags 2 and 4 (Fig. 3E). The spectral density analysis of prevalence and mean abundance of *M. cichlasomae* L4 showed similar peaks of maximum variability to those of adults every for 10 and 27 months (data not included). The prevalence and mean abundance of both adults and L4 showed significant cross-correlations at lag 0 (Table 1). Furthermore, significant associations were observed between the prevalence and mean abundance of gravid females and larvae of *M. cichlasomae* in *A. yucatanus* at lag 2 respectively (Table 1).

DISCUSSION

The present results showed significant annual peaks of both prevalence and mean abundance of *M. cichlasomae* in *A. yucatanus* and bi-annual peaks of maximum variability of *M. cichlasomae* in the definitive fish host associated with temporal patterns of rainfall and temperature, despite slight asynchronies in the transmission peaks of some stages in the life cycle of *M. cichlasomae*.

The maximum variability of both prevalence and abundance of *A. yucatanus* in *C. urophthalmus* were observed every 12 and 45 months. The first peak correlated with seasonal fluctuations in both rainfall and temperature at lag 0 suggesting that both environmental factors (rainfall and temperature) were acting simultaneously to trigger the infection levels of *A. yucatanus* in *C. urophthalmus*. This result is in contrast to that reported by Pech *et al.* (2010) who suggested that rainfall was the single key environmental factor affecting the percentage of infected hosts (snails and *C. urophthalmus*) at Celestun. It is clear that the effects of both environmental factors were evident either immediately (lag 0) or with delay (lag 6), reflecting periods of increases in both temperature and rainfall (the rainy season) or only in rainfall (the winter frontal storm).

A peak every 45 months or approximately 4 years appears to be a consequence of the processes acting at a larger temporal scale, suggesting the influence of natural disturbances such as El Niño Southern Oscillation (ENSO), which occurs every 3–7 years

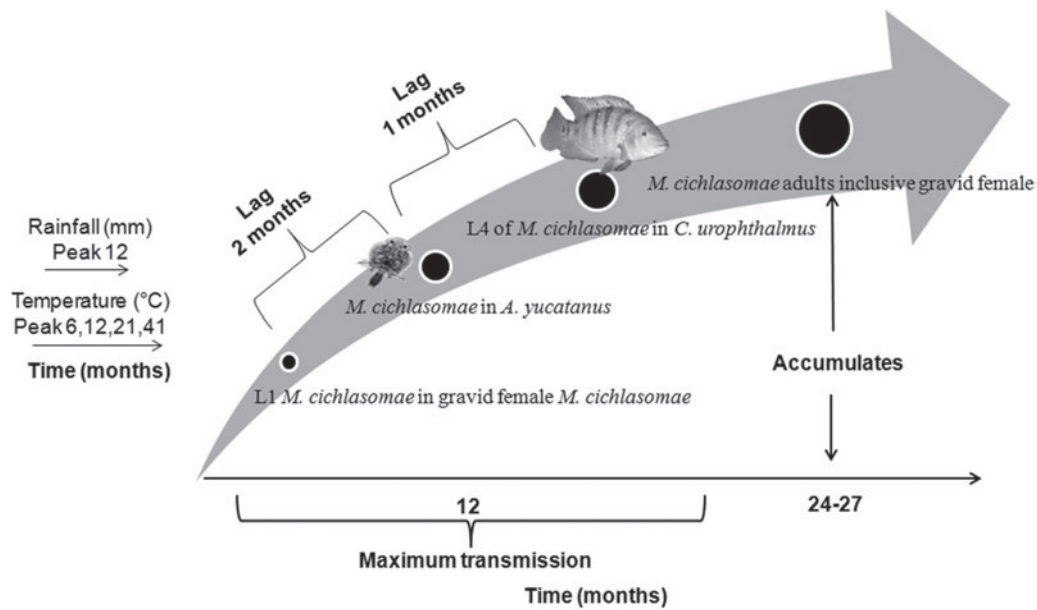


Fig. 4. Descriptive model of the temporal dynamics of *Mexiconema cichlasomae* in its intermediate host, the fish louse *Argulus yucatanus* and the Mayan cichlid *Cichlasoma urophthalmus*.

(Stenseth *et al.* 2003). This climatic phenomenon, which produces strong rainfall in both the Atlantic and Pacific coasts in the intertropical region (Stenseth *et al.* 2003), is likely to be a key environmental variable in this host-parasite system at relative intermediate temporal scales. Similar interpretations have been made on the occurrence of disease outbreaks in humans (e.g. dengue, malaria) and aquatic animals such as *Perkinsus marinus* in oysters to ENSO (Hay *et al.* 2000; Húbalek, 2005; Oliva *et al.* 2007; Soniat *et al.* 2009; Lafferty 2009, Colón-Gonzalez *et al.* 2011).

The infection parameters of *M. cichlasomae* larvae in *A. yucatanus* followed a similar pattern to those of *A. yucatanus* in *C. urophthalmus*, with peaks of maximum variability every 12 and 40 months. The peak at 12 months is not surprising since *A. yucatanus* is the intermediate host of *M. cichlasomae* (Moravec *et al.* 1999). The influence of rainfall and temperature on *A. yucatanus* also explains the significant cross-correlations found at lags 0, and 6, whereas the influence of ENSO explains the peak at 40 months.

The presence of larval *M. cichlasomae* in *A. yucatanus* is likely to be linked with the infection of *C. urophthalmus* with gravid females. In the present study we found a synchronic occurrence between the prevalence of gravid females of *M. cichlasomae* and both the prevalence and mean abundance of *A. yucatanus* in *C. urophthalmus*. This indicates that sufficient intermediate hosts had become infected with the larvae of *M. cichlasomae*, whereas the presence of gravid females throughout the year explains lags of up to 2 months in the occurrence of gravid females in the fish host and the maximum prevalence and mean abundance larval *M. cichlasomae* in *A. yucatanus*. This suggests a significant

association between maturation of gravid females and the number of *A. yucatanus*. Such synchronicity is similar to that in other species in the Daniconematidae family, where the presence of gravid female nematodes occurs at the same time as the number of free-living copepod intermediate hosts increases (Moravec *et al.* 1992).

A time lag of 2 months could be related to the time of transmission of larvae from the definitive cichlid fish host to *A. yucatanus* the intermediate host. Two possible methods of transmission could occur. First, May-Tec (2007), who found larvae of *M. cichlasomae* in the blood of *C. urophthalmus*, has suggested that species of *Argulus* become infected through ingestion of contaminated blood. Hence differences in the time lag between the presence of larvae in *A. yucatanus* and gravid females of *M. cichlasomae* may be attributed to the delay in the time taken for larvae of *M. cichlasomae* to migrate from the swim bladder to the peripheral blood of the cichlid fish host. *Argulus yucatanus* could therefore ingest the larvae during the course of a bloodmeal. This feeding behaviour is characteristic of life cycles in other nematode species of the family Skrjabillanidae, including *Molnaria intestinalis* and *Skrjabillanus scardinii* which use *Argulus* sp. as intermediate hosts (Tikhomirova, 1980; Molnar and Székely, 1998; Smith *et al.* 2007).

A second possible scenario is that *A. yucatanus* containing larvae of *M. cichlasomae* could be ingested by *C. urophthalmus* during a symbiotic process of removing or 'cleaning' *Argulus* from its skin surface. Such ingestion of infected *A. yucatanus* could be higher during the breeding season of *C. urophthalmus* due to aggregation. This behaviour may also explain the low prevalence of infection of *M. cichlasomae* in *A. yucatanus* on the surface of *C. urophthalmus*, but

further experimental approaches are needed to support such a transmission process.

Peaks of maximum variability every 12 and 24–27 months are more likely to be due to the accumulation of nematodes throughout time, as transmission occurs throughout the year. This accumulation can be related with the age of *C. urophthalmus*, which has a life span up to 7 years (Faunce *et al.* 2002), i.e. enough time to accumulate nematodes as each individual fish grows. Support for this interpretation comes from the fact that in fish populations, intensity of infection by parasite increases with age or size of fish host (Poulin, 2000). Furthermore, a number of authors have reported that *M. cichlasomae* and other helminth parasites in tropical areas respond to seasonal changes on a yearly basis (Salgado-Maldonado, 1993; Jiménez-García and Vidal-Martínez, 2005; Violante-González *et al.* 2008) but most of these studies have been undertaken over a short time scale of 1 year or less. However, the present results suggest that the occurrence of bi-annual peaks in the infection dynamics of *M. cichlasomae* is not only due to the accumulation of infective stages through time, but also to changes in both rainfall and temperature. This is in contrast to the work of Pech *et al.* (2010) where rainfall was found to be the key factor in triggering host infection parameters in parasite infracommunities in tropical aquatic hosts.

The present investigation has shown that rainfall and temperature influence the infection dynamics of *M. cichlasomae* in its definitive and intermediate hosts at different time scales. Within 12 months, there is a peak in the mean abundance of gravid females of *M. cichlasomae* in the definitive fish host, presumably due to first-stage larvae being released into the bloodstream and then appearing in *A. yucatanus* 2 months later. Ultimately, adult worms of *M. cichlasomae*, including gravid females, accumulate through time, reaching peaks of abundance every 24–27 months (Fig. 4). What happens with fish carrying a large number of nematodes every 2 years? There are 2 possibilities: the first being senescence of old nematodes, and the second being parasite-induced host mortality. Both options are being analysed elsewhere (Vidal-Martínez *et al. manuscript in preparation*). Meanwhile, we conclude that the temporal dynamics of *M. cichlasomae* showed yearly fluctuations in infection levels associated with annual seasonal increases in rainfall and temperature, and bi-annual peaks due to the accumulation of infective stages.

ACKNOWLEDGEMENTS

This study was part of the Ph. D. thesis of A.L.M.T., who is grateful to CONACYT-México (216405) for providing 4 years scholarship. Sincere and grateful thanks are extended to all at Laboratorio de Patología Acuática

CINVESTAV-IPN Unidad Mérida including Clara Vivas-Rodríguez, Gregory Arjona-Torres, Nadia Herrera, Francisco Puc, Geny Ail and Trinidad Sosa who helped with field and laboratory work at different times over the past 8 years.

FINANCIAL SUPPORT

This study was partly supported by grant No. 44590 'Invertebrados como hospederos intermediarios de helmintos de *Lutjanus griseus* y otros peces de importancia comercial en dos lagunas costeras de Yucatán' given to M.L.A.-M. by CONACyT-Mexico D 44590-Q. We are indebted to SEP-PROMEP for an award to support our project 'Propuesta sobre Calentamiento Global y Cambio Climático de la Red Académica de Instituciones SEP-PROMEP del Sureste: área Sensibilidad Marina' and to a FOMIX Yucatán award in support of the project 'Sensibilidad y vulnerabilidad de los ecosistemas costeros del sureste de México ante el Cambio Climático Global' YUC-2008-C06-108929.

REFERENCES

- Abell, S., Gadeka, P., Pearce, C. and Congdon, B. (2006). Seasonal resource availability and use by an endangered tropical mycophagous marsupial. *Biological Conservation* **132**, 533–540.
- Aguirre-Macedo, M. L., Vidal-Martínez, V. M. and Lafferty, K. D. (2011). Trematode communities in snails can indicate impact and recovery from hurricanes in a tropical coastal lagoon. *International Journal for Parasitology* **41**, 1403–1408.
- Avenant-Oldewage, A., Swanepoel, J. H. and Knight, E. (1994). Histomorphology of the digestive tract of *Chonopeltis australis* (Crustacea: Branchiura). *The South African Journal of Zoology* **29**, 74–81.
- Benedetti-Cecchi, L., Acunto, S., Bulleri, F. and Cinelli, F. (2000). Population ecology of the barnacle *Chthamalus stellatus* in the northwest Mediterranean. *Marine Ecological Progress Series* **198**, 157–170.
- Bush, A. O., Lafferty, K. D., Lotz, J. M. and Shostak, A. W. (1997). Parasitology meets ecology on this own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.
- Caspeta-Mandujano, J. M. and Mejía-Mojica, H. (2004). Seasonal dynamics of the occurrence and maturation of *Rhabdochona Canadensis* in its definitive host, *Notropis boucardi* of the Chalma River, State of Morelos, México. *Helminthologia* **41**, 121–123.
- Coley, P. D. and Aide, T. M. (1991). Comparisons of herbivory and plant defenses in temperate and tropical broad-leaved forest. In *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (ed. Price, P. W., Lewinshom, T. M., Fernandes, G. W. and Benson, W. W.), pp. 25–49. Wiley and Sons, New York, USA.
- Colón-González, F., Lake, I. and Bentham, G. (2011). Climate variability and dengue fever in warm and humid Mexico. *The American Journal of Tropical Medicine and Hygiene* **84**, 757–763.
- Des Clers, S. (1994). *Sampling to Detect Infections and Estimate Prevalence in Aquaculture*. Pisces Press, Stirling, Scotland.
- Easterling, D. R., Evans, P., Groisman, T. R., Kunkel, K. E. and Ambenje, P. (2000). Observed variability and trends in extreme climate events: A brief review. *American Meteorological Society* **81**, 417–425.
- Faunce, C. H., Patterson, H. M. and Lorenz, J. J. (2002). Age, growth, and mortality of the Mayan cichlid (*Cichlasoma urophthalmus*) from the southeastern Everglades. *Fishery Bulletin* **100**, 42–50.
- Fiorillo, R. A. and Font, W. F. (1999). Seasonal dynamics and community structure of helminths of spotted sunfish, *Lepomis miniatus* (Osteichthyes: Centrarchidae) from an oligohaline estuary in southeastern Louisiana, U.S.A. *Journal of the Helminthological Society of Washington* **66**, 101–110.
- Ghil, M. (2002). Natural climate variability. In *Encyclopedia of Global Environmental Change* (ed. MacCracken, M. C. and Perry, J. S.), pp. 544–549. John Wiley & Sons, Ltd, Chichester, UK.
- Githeko, A. K., Lindsay, S. W., Confalonieri, U. E. and Patz, J. A. (2000). *Climate change and vector-borne diseases: a regional analysis*. Bulletin of the World Health Organization, N. 78 (9).
- Greenfield, D. W. and Thomerson, J. E. (1997). *Fishes of the Continental Waters of Belize*. University of Florida Press, Gainesville, FL, USA.
- Hay, S. I., Myers, M. F., Burke, D. S., Vaughn, D. W., Endy, T., Ananda, N., Shanks, G. D., Snow, R. W. and Rogers, D. J. (2000).

- Etiology of interepidemic periods of mosquito-borne disease. *Proceedings of the National Academy of Sciences, USA* **97**, 9335–9339.
- Herrera-Silveira, J. A., Martín, M. B. and Díaz-Arce, V.** (1999). Variaciones del fitoplancton en cuatro lagunas costeras del estado de Yucatán, México. *Revista de Biología Tropical* **47**, 47–56.
- Hernández-Guevara, N. A., Pech, D. and Ardisson, P.-L.** (2008). Temporal trends in benthic macrofauna composition in response to seasonal variation in a tropical coastal lagoon, Celestun, Gulf of Mexico. *Marine and Freshwater Research* **59**, 772–779.
- Hubálek, Z.** (2005). North Atlantic weather oscillation and human infectious diseases in the Czech Republic, 1951–2003. *European Journal of Epidemiology* **20**, 263–270. doi:10.1007/s10654-004-6518-3.
- Hubálek, Z., Halouzka, J. and Juricová, Z.** (2003). Longitudinal surveillance of the tick *Ixodes ricinus* for borreliae. *Medical and Veterinary Entomology* **17**, 46–51.
- Jiménez-García, M. I. and Vidal-Martínez, V. M.** (2005). Temporal variation in the infection dynamics and maturation cycle of *Oligogonotylus manteri* (Digenea) in the cichlid fish, *Cichlasoma urophthalmus*, from Yucatán, México. *Journal of Parasitology* **91**, 1008–1014.
- Kennedy, C. R.** (1993). The dynamics of helminth communities in eels *Anguilla anguilla* in a small stream: long term changes in richness and structure. *Parasitology* **107**, 71–78.
- Kerans, B. L., Stevens, R. I. and Lemmon, J. C.** (2005). Water temperature affects a host–parasite interaction: *Tubifex tubifex* and *Myxobolus cerebralis*. *Journal of Aquatic Animal Health* **17**, 216–221.
- Knipes, A. K. and Janovy, J. Jr.** (2009). Community structure and seasonal dynamics of Dactylogyrus spp. (Monogenea) on the fathead minnow (*Pimephales promelas*) from the Salt Valley Watershed, Lancaster County, Nebraska. *Journal of Parasitology* **95**, 1295–1305.
- Krasnov, B. R., Korralo-Vinarskaya, N. P., Vinarski, M. V., Shenbrot, G. I., Moullot, D. and Poulin, R.** (2008). Searching for general patterns in parasite ecology: host identity versus environmental influence on gamasid mite assemblages in small mammals. *Parasitology* **135**, 229–242. doi:10.1017/S003118200700368X.
- Lafferty, K.** (2009). The ecology of climate change and infectious diseases. *Ecology* **90**, 888–900.
- Leong, T. S.** (1986). Seasonal occurrence of metazoan parasites of *Puntius binotus* in an irrigation canal, Pulau Pinang, Malaysia. *Journal of Fish Biology* **28**, 9–16.
- Legendre, P. and Legendre, L.** (1998). *Numerical Ecology*. 2nd English Edn. Elsevier Science BV, Amsterdam, The Netherlands.
- Luque, J. L. and Poulin, R.** (2008). Linking ecology with parasite diversity in Neotropical fishes. *Journal of Fish Biology* **72**, 189–204. doi:10.1111/j.1095-8649.2007.01695.x.
- Mas-Coma, S., Valero, M. A. and Bargues, M. D.** (2009). Climate change effects on trematodiasis, with emphasis on zoonotic fascioliasis and schistosomiasis. *Veterinary Parasitology* **163**, 264–280. doi:10.1016/j.vetpar.2009.03.024.
- Marcogliese, D. J.** (2008). The impact of climate change on the parasites and infectious diseases of aquatic animals. *Scientific and Technical Review of the Office International des Epizooties* **27**, 467–484.
- Martin, L. B., Pless, M., Svoboda, J. and Wikelski, M.** (2004). Immune activity in temperate and tropical house sparrows: A common-garden experiment. *Ecology* **85**, 2323–2331.
- Martínez, J. and Merino, S.** (2011). Host-parasite interactions under extreme climatic conditions. *Current Zoology* **57**, 390–405.
- Martínez-Palacios, C. A.** (1987). Aspects of the biology of *Cichlasoma urophthalmus* (Günther) with particular reference to its culture in Celestun Lagoon, Yucatan, Mexico. Ph.D. Thesis, University of Stirling, Stirling, UK.
- Martínez-Palacios, C. A. and Ross, L. G.** (1988). The feeding ecology of the Central American cichlid *Cichlasoma urophthalmus* (Günther). *Journal of Fish Biology* **33**, 665–670.
- Martínez-Palacios, C. A. and Ross, L. G.** (1992). The reproductive biology and growth of the Central American cichlid *Cichlasoma urophthalmus* Günther. *Journal Applied Ichthyology* **8**, 99–109.
- May-Tec, A. L.** (2007). Aspectos biológicos del ciclo de vida de *Mexiconema cichlasomae* (Nematoda: Daniconematidae) en *Cichlasoma urophthalmus* y en su hospedero intermediario *Argulus* sp. en Celestun, Yucatan. Tesis Licenciatura en Biología. Instituto Tecnológico Agropecuario N° 2.
- Mejia-Madrid, H. H. and Aguirre-Macedo, M. L.** (2011). Systematics of *Mexiconema cichlasomae* (Nematoda: Daniconematidae) Based on Sequences of SSU rDNA. *Journal of Parasitology* **97**, 160–162. doi:10.1645/GE-2569.1.
- Miller, R. R., Winckley, W. L. and Norris, M. S.** (2005). *Freshwater Fishes of Mexico*. The University of Chicago Press, Chicago, ILL, USA.
- Molnár, K. and Székely, C.** (1998). Occurrence of Skrajabillanid nematodes in fishes of Hungary and in the intermediate host. *Argulus foliaceus* L. *Acta Veterinaria Hungarica* **46**, 451–463.
- Moravec, F.** (1994). *Parasitic nematodes of freshwater fishes of Europe*. Academia and Kluwer Academy Publishers, Praha, Czech Republic.
- Moravec, F.** (2004). Some aspects of the taxonomy and biology of dracunculoid nematodes parasitic in fishes: A review. *Folia Parasitologica* **51**, 1–13.
- Moravec, F.** (2006). *Dracunculoid and anguillicoloid nematodes parasitic in vertebrates*. Academia, Praha, Czech Republic.
- Moravec, F.** (2007). Some aspects of the taxonomy and biology of adult spirurine nematodes parasitic in fishes: A review. *Folia Parasitologica* **54**, 239–257.
- Moravec, F., Magi, M. and Macchioni, F.** (2008). Redescription of the gonad-infecting nematode *Philometra saltatrix* Ramachandran, 1973 (Philometridae) based on specimens from the type host *Pomatomus saltatrix* (L.) (Osteichthyes) from the Tuscan Sea, Italy. *Folia Parasitologica* **55**, 219–223.
- Moravec, F. and Salgado-Maldonado, G.** (2007). A new species of *Philometra* (Nematoda, Philometridae) from the gonads of the rock hind *Epinephelus adscensionis* (Osteichthyes) from the southern Gulf of Mexico. *Acta Parasitologica* **52**, 376–381. doi:10.2478/s11686-007-0044-x.
- Moravec, F., Vidal-Martínez, V. M. and Aguirre-Macedo, M. L.** (1999). Branchiurids (*Argulus*) as intermediate host of the Daniconematid nematode *Mexiconema cichlasomae*. *Folia Parasitologica* **46**, 79.
- Moravec, F., Vidal-Martínez, V. M. and Salgado-Maldonado, G.** (1992). *Mexiconema cichlasomae* gen. et sp. (Nematoda: Daniconematidae) from *Cichlasoma* spp. (Pices) from México. *Folia Parasitologica* **39**, 33–40.
- Olden, J. D. and Neff, B. D.** (2001). Cross-correlation bias in lag analysis of aquatic time series. *Marine Biology* **138**, 1063–1070.
- Oliva, M. E., Barrios, I., Thatje, S. and Laudien, J.** (2007). Changes in prevalence and intensity of infection of *Proflicollis altmani* (Perry, 1942) cystacanth (Acanthocephala) parasitizing the mole crab *Emerita analoga* (Stimpson, 1857): an El Niño cascade effect?. *Helgolander Marine Research*. doi:10.1007/s10152-007-0082-7.
- Parmesan, C. and Galbraith, H.** (2004). *Observed Ecological Impacts of Climate Change in North America*. Pew Center on Global Climate Change, Arlington, VA, USA.
- Patz, J. A., Campbell-Lendrum, D., Holloway, T. and Foley, J. A.** (2005). Impact of regional climate change on human health. *Nature, London* **438**, 310–317. doi:10.1038/nature04188.
- Platt, D. and Denman, K. L.** (1975). Spectral analysis in ecology. *Annual Review of Ecology and Systematics* **6**, 189–210.
- Pech, D., Ardisson, P. L. and Hernández-Guevara, N. A.** (2007). Benthic community response to habitat variation: A case of study from a natural protected area, the Celestun coastal. *Continental Shelf Research* **27**, 2523–2533. doi:10.1016/j.csr.2007.06.017.
- Pech, D., Aguirre-Macedo, M. L., Lewis, J. W. and Vidal-Martínez, V. M.** (2010). Rainfall induces time-lagged changes in the proportion of tropical aquatic hosts infected with metazoan parasites. *International Journal for Parasitology* **40**, 937–944. doi:10.1016/j.ijpara.2010.01.009.
- Poulin, R.** (2000). Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. *Journal of Fish Biology* **56**, 123–137.
- Poulin, R. and Mouritsen, K. N.** (2006). Climate change, parasitism and the structure of intertidal ecosystems. *Journal of Helminthology* **80**, 183–191. doi:10.1079/JOH2006341.
- Press, W. H., Teukolsky, S. A., Vetterling, W. T. and Flannery, B. P.** (1996). *Numerical Recipes in Fortran 77: The Art of Scientific Computing*. Cambridge University Press, Cambridge, UK.
- Salgado-Maldonado, G.** (1993). Ecología de Helminthos parásitos de *Cichlasoma urophthalmus* (Günther) (Pises: Cichlidae) en la península de Yucatán, México. Tesis de doctorado. Centro de investigación y de Estudios avanzados del Instituto Politécnico Nacional, México.
- Salgado-Maldonado, G. and Kennedy, C. R.** (1997). Richness and similarity of helminth communities in the tropical cichlid fish *Cichlasoma urophthalmus* from the Yucatan Peninsula, Mexico. *Parasitology* **107**, 71–78.
- Scharlemann, J. P. W., Benz, D., Hay, S. I., Purse, B. V., Tatem, A. J., Wint, G. R. W., and Rogers, D. J.** (2008). Global data for ecology and epidemiology: a novel algorithm for temporal Fourier processing MODIS data. *PLoS One* **3**, e1408. 1, 1371–1408. doi:10.1371/journal.pone.0001408.
- Simková, A.** (2005). Associations between fish reproductive cycle and the dynamics of metazoan parasite infection. *Journal of Parasitology Research* **95**, 65–72. doi:10.1007/s00436-004-1261-y.
- Smith, J. L., Wootten, R. and Sommerville, C.** (2007). The pathology of the early stages of the crustacean parasite, *Lernaeocera branchialis* (L.), on Atlantic cod, *Gadus morhua* L. *Journal of Fish Diseases* **30**, 1–11.

- Soniat, M. T., Hofmann, E. E., Klinck, M. J. and Powell, N. E.** (2009). Differential modulation of eastern oyster (*Crassostrea virginica*) disease parasites by the El-Niño-Southern Oscillation and the North Atlantic Oscillation. *International Journal of Earth Sciences* **98**, 99–114. doi: 10.1007/s00531-008-0364-6.
- Steinauer, M. and Font, W.** (2003). Seasonal dynamics of the helminthes of bluegill (*Lepomis macrochirus*) in a subtropical region. *Journal of Parasitology* **89**, 324–328.
- Stenseth, N., Ottersen, G., Hurrell, J., Mysterud, A., Lima, M., Chan, K., Yoccoz, N. and Ådlandsvik, B.** (2003). Review article. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings The Royal Society of London, B* **270**, 2087–2096. doi: 10.1098/rspb.2003.2415.
- Trexler, J. C., Loftus, W. F., Jordan, F., Lorenz, J. J., Chick, J. H. and Kobza, R. M.** (2000). Empirical assessment of fish introductions in a subtropical wetland: an evaluation of contrasting views. *Biological Invasions* **2**, 265–277.
- Thiel, M., Romano, M. C., Schwarz, U., Kurths, J. and Timmer, J.** (2004). Surrogate- based hypothesis test without surrogates. *International Journal of Bifurcation and Chaos* **14**, 2107.
- Tikhomirova, V. A.** (1980). On nematodes of the family Skrjabillanidae (Nematoda: Camallanata). *Parazitologiya* **14**, 258–262.
- Ujvari, B., Andersson, S., Brown, G., Shine, R. and Madsen, T.** (2010). Climate-driven impacts of prey abundance on the population structure of a tropical aquatic predator. *Oikos* **119**, 188–196. doi: 10.1111/j.1600-0706.2009.17795.x.
- Vidal-Martínez, V. M., Scholz, T., Aguirre-Macedo, M. L., Gonzalez-Solis, D. and Mendoza-Franco, E. F.** (2001). *Atlas of the Helminth Parasites of Cichlid Fishes of México*. Academia, Prague, Czech Republic.
- Vincent, A. and Font, W.** (2003). Host specificity and population structure of two exotic helminths, *Camallanus cotti* (nematoda) and *Bothriocephalus acheilognathi* (cestoda), parasitizing exotic fishes in Waianu Stream, O’Ahu, Hawaii. *Journal of Parasitology* **89**, 540–544.
- Violante-González, J., Aguirre-Macedo, M. L. and Vidal-Martínez, V. M.** (2008). Temporal variation in the helminth parasite communities of the pacific fat sleeper, *Dormitor latifrons*, from Tres Palos Lagoon, Guerrero, Mexico. *Journal of Parasitology* **94**, 326–334.
- Walker, P. D., Flik, G. and Wendelaar Bonga, S. J.** (2004). The biology of parasites from the genus *Argulus* and a review of the interactions with its host. In *Host-Parasite Interactions*. (ed. Wiegertjes, G. F. and Flik, G.), pp 107–129. Garland Science/BOIS Scientific Publishers. Hampshire, UK.
- Wei, W. W. S.** (1990). *Time Series Analysis: Univariate and Multivariate Methods*. Addison-Wesley, New York, USA.
- Yildiz, K. and Kumantas, A.** (2002). *Argulus foliaceus* infection in a goldfish (*Carassius auratus*). *Israel Journal of Veterinary Medicine* **57**, 118–120.
- Zander, C. D.** (2003). Four-year monitoring of parasite communities in gobiid fishes of the southwestern Baltic. I. Guild and component community. *Journal of Parasitology Research* **90**, 502–511.
- Zander, C. D.** (2004). Four-year monitoring of parasite communities in gobiid fishes of the southwestern Baltic. II. Infracommunity. *Journal of Parasitology Research* **93**, 17–29.
- Zander, C. D.** (2005). Four-year monitoring of parasite communities in gobiid fishes of the southwest Baltic. III. Parasite species diversity and applicability of monitoring. *Journal of Parasitology Research* **95**, 136–144.