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Trematode communities in snails can indicate impact and recovery from hurricanes in a tropical coastal lagoon

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ABSTRACT

In September 2002, Hurricane Isidore devastated the Yucatán Peninsula, Mexico. To understand its effects on the parasites of aquatic organisms, we analyzed long-term monthly population data of the horn snail *Cerithidea pliculosa* and its trematode communities in Celestún, Yucatán, Mexico before and after the hurricane (February 2001 to December 2009). Five trematode species occurred in the snail population: *Mesostephanus appendiculatoides*, *Euhaplorchis californiensis*, two species of the genus *Renicola* and one Heterophyidae gen. sp. Because these parasites use snails as first intermediate hosts, fishes as second intermediate hosts and birds as final hosts, their presence in snails depends on food webs. No snails were present at the sampled sites for 6 months after the hurricane. After snails recolonised the site, no trematodes were found in snails until 14 months after the hurricane. It took several years for snail and trematode populations to recover. Our results suggest that the increase in the occurrence of hurricanes predicted due to climate change can impact upon parasites with complex life cycles. However, both the snail populations and their parasite communities eventually reached numbers of individuals and species similar to those before the hurricane. Thus, the trematode parasites of snails can be useful indicators of coastal lagoon ecosystem degradation and recovery.
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1. Introduction

The increased intensity and frequency of hurricanes is a matter of concern for several reasons, including the observation that biological diversity and abundance can remain low for several years after a hurricane (Crabbe et al., 2008; Smith et al., 2009). For instance, damage caused by two consecutive hurricanes had effects that cascaded through a forest food web for over 2 years (Spiller and Shoeder, 2007). Recovery time from a hurricane can depend on the severity of the event, the frequency of hurricanes, and the effects of other stressors (Savage, 1993; Michener et al., 1997; Ward et al., 2006; Willig et al., 2007). Because parasites depend on free-living biodiversity (e.g. intermediate hosts) (Hechinger and Lafferty, 2005; Hudson et al., 2006), parasitism (e.g. species composition, species richness, community structure) might change following extreme weather events such as hurricanes (Marcogliese, 2001). For instance, trematodes parasitising fishes disappeared after Hurricane Katrina; although some trematodes started to reappear within 6 months, prevalences were still low 2 years later (Overstreet, 2007).

Since 2001, one of the current authors (M.L. Aguirre-Macedo CINVESTAV-IPN Unidad Mérida, Mexico) has been collecting data on the helminth parasites of snails and fishes as part of a long-term ecological monitoring program at a Celestún coastal lagoon in Yucatan, Mexico for the Mexican organization for Long-Term Ecological Research (MEX-LTER, Mexico). Unexpectedly, these data turned out to be useful for studying the effect of hurricanes.

In September 2002, the category-three Hurricane Isidore passed slowly through the Yucatán Peninsula, until degrading into a tropical storm 31 h later (Fig. 1A). The hurricane devastated the area, causing extensive damage to the vegetation, agriculture and domestic and industrial facilities (Pasch et al., 2004). It also impacted upon many animal populations living in the area (Palacios-Sánchez and Vega-Cendejas, 2010), including gastropod snails and other invertebrates at Celestún. To ascertain how host and parasite communities respond to hurricanes, we examined data on the trematodes of the horn snail *Cerithidea pliculosa* from Celestún, Yucatán, Mexico collected monthly over 20 months before the hurricane (BH) and 87 months after the hurricane (AH). The continued sampling from February 2001 through December 2009 allowed us to describe snail abundance and trematode community structure before and after the hurricane.

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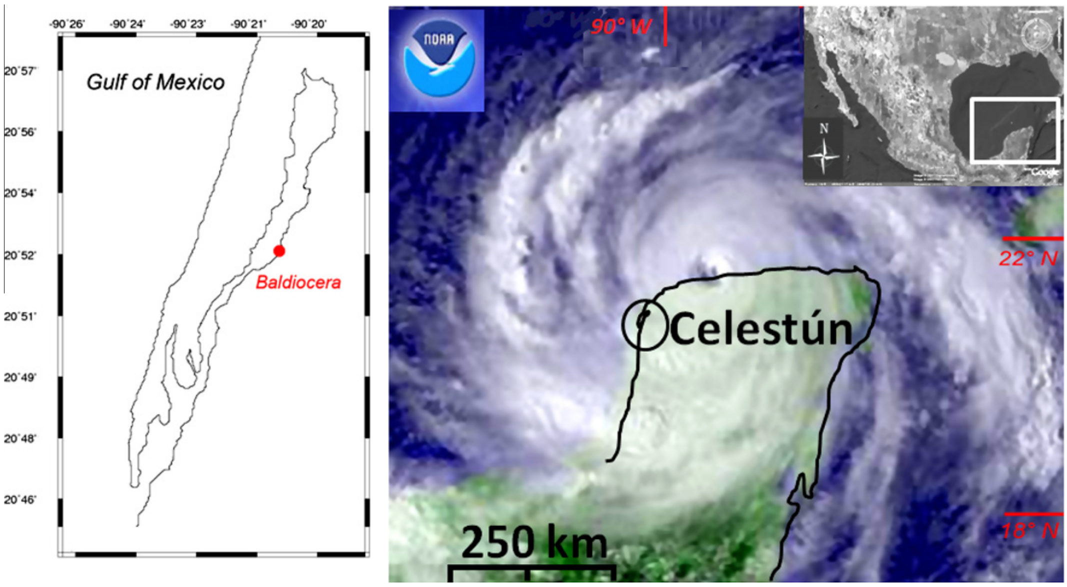

Fig. 1. Study area and Hurricane Isidore on the Yucatán Peninsula, Mexico.

2. Materials and methods

2.1. Study area

Celestún is a shallow (1 m depth average) coastal lagoon in the northwest of the Yucatán Peninsula (20°45′ and 20°58′N; 90°15′and 90°25′W) (Fig. 1). The water body has an area of 28.1 km^2 and is 22.5 km in length with a 410 m wide inlet at the southern end connecting to the sea. The site is a National Protected Area renowned for its diversity and abundance of aquatic birds. Due to its karstic origin, the Yucatan Peninsula has no rivers. Underground currents flow from the centre of the Peninsula to the coastal zone, discharging freshwater at the margins of coastal lagoons as freshwater springs. Springs, combined with tidal flushing at the mouth of the lagoon, create an estuarine salinity gradient (Herrera-Silveira, 1994). Our study site, Baldiocera (Fig. 1), is a spring on the west margin of Celestún, approximately 12.84 km from the mouth at 20°52′N and 90°21′W. Mangroves border the coastal lagoon and spring margins. Several studies describe the fishes (Vega-Cendejas, 2004; García-Hernández et al., 2009), benthic community (Pech et al., 2007), submerged vegetation and phytoplankton (Herrera-Silveira and Morales-Ojeda, 2009), and some parasites of fishes and birds (Salgado-Maldonado and Kennedy, 1997; Scholz et al., 1997; Vidal-Martínez and Poulin, 2003; Pech et al., 2010).

2.2. Data collection

From February 2001 to December 2009, we collected data on snail count and biomass density from 10 random quadrats (0.5 m^2) at the intertidal edges of the Baldiocera spring during low tide. At each sampling, salinity (PPT) was measured with an ATAGO refractometer, and water temperature (°C) with a YSI 50 multiparametric probe, while data on rainfall were obtained from the National Meteorological Service of Mexico (SMN). The physical data were highly correlated with rainfall (temperature, $r = 0.23$, $P = 0.01$; salinity, $r = 0.46$ $P = 0.0001$), so we used this measure in subsequent analyses. Total shell lengths of snails (in mm) were measured with a caliper. Snails were then dissected at the laboratory and the trematode species identified in situ. Using length-weight regressions, we estimated snail biomass density per square metre and used this as a measure of the snail population.

The scale of the hurricane was such that no unimpacted reference site existed (a limitation common to most hurricane impact studies). Data collected 20 months before and 87 months after Hurricane Isidore led to a before–after comparison. To estimate trematode species richness and the percentage of infected hosts (PIH) before the hurricane, we dissected a subsample of 70 snails per month, however for a year after the hurricane, sample sizes were limited by low snail density. Voucher specimens of trematode species collected were deposited at the Colección del Laboratorio de Parasitología (CHCM) CINVESTAV del IPN, Unidad Mérida (Yucatán, Mexico).

2.3. Data analysis

PIH combined across trematode species (see Pech et al., 2010) was calculated for each monthly sample. We determined Jackknife estimators of parasite species richness for each sample (Zelmer and Esch, 1999). We also used bootstrapping (resampling with replacement) to estimate the total number of parasite species expected in a sample of 500 snails (the results were qualitatively identical, so we present the jackknifed estimate).

Although the effects of the hurricane were visually striking, changes in parasites over time could have also been affected by temporal trends, snail demography or environmental forcing. To investigate the possible influence of variables not directly related to the hurricane, we ran general linear models for snail density, PIH and trematode richness using rainfall and snail size as potential covariates but excluded data from 40 months immediately after the hurricane (i.e., to understand the relationship between variables independent of the hurricane). To statistically assess impact and recovery, we used intervention analysis (Box and Tiao, 1975) which determines whether known events have changed the course of a time series. A separate intervention analysis was run for snail density, PIH and trematode species richness. The intervention model hypothesised a temporary "pulse" impact, $y = n - h\ d^t$ where h is the initial impact of the hurricane and d (0–1) is measure of the duration of the impact over time, t. For background noise, n, we assumed the signal followed a moving average and we investigated a potential role for seasonality

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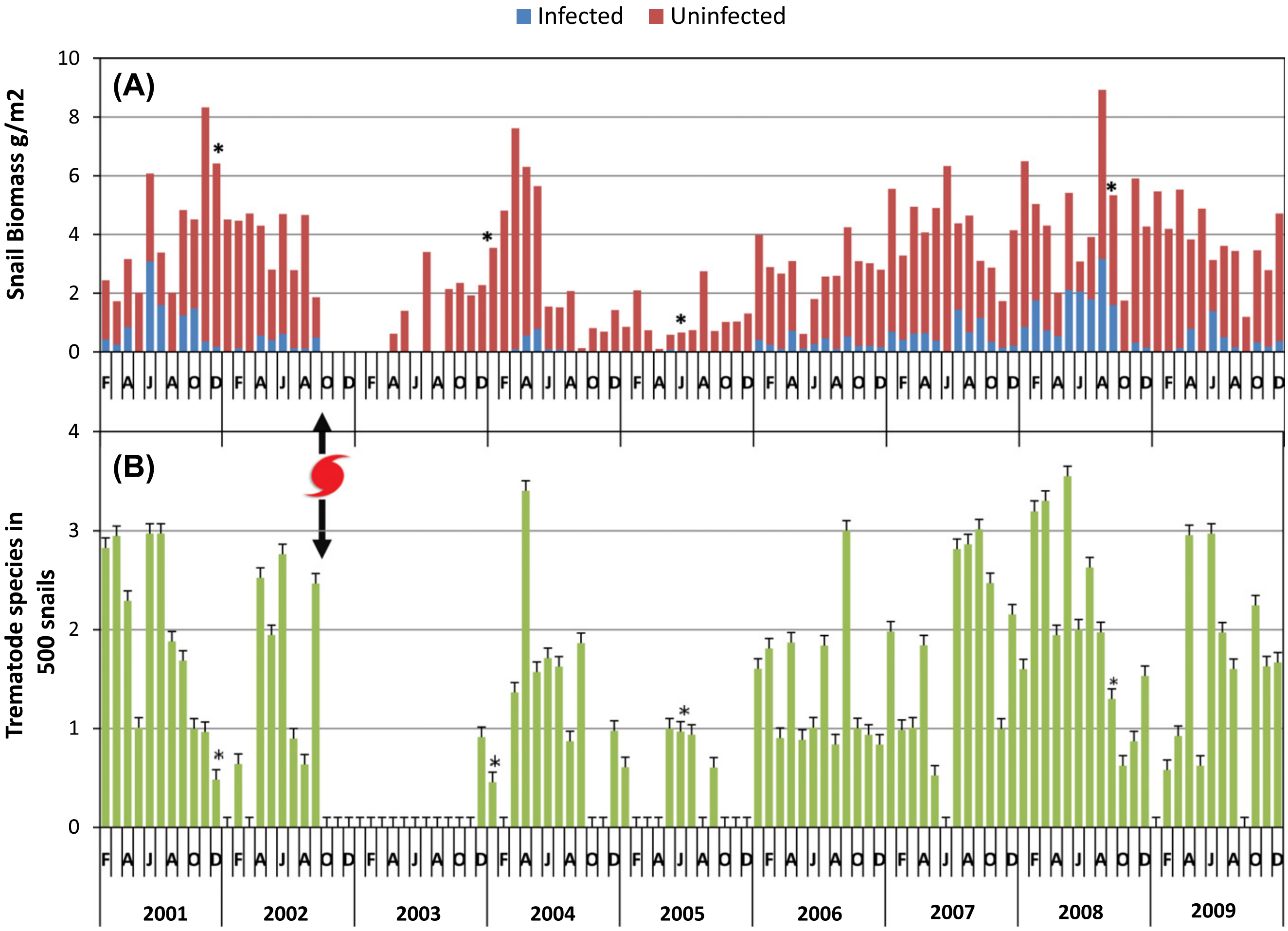

Fig. 2. Biomass of *Cerithidea pliculosa* (uninfected and infected) per month (A) and Jackknife estimate of the trematode species per host per month (B) in Celestún, Yucatán, Mexico over 9 years of monitoring. (∗) Months with no sampling but estimated values are included for illustrative purposes. The arrow indicates the time of Hurricane Isidore.

(salinity and rainfall were highly seasonal). Analyses were conducted with the transfer function analysis for time series in the statistical software JMP 8.0®, SAS Institute Inc. We estimated time to recovery as the number of months before the time series returned to 90% of the initial value (or months to recovery = $-2.3/\ln(d)$).

Finally, we tracked the trajectory of the trematode community over time with non-metric multi-dimensional scaling (NMDS). Specifically, a similarity matrix was built using Bray–Curtis distances of the trematode species prevalence per sample. We then took the mean of the monthly samples from each October to September (± S.E.) for the two main NMDS axes. We connected the means with time vectors to illustrate how variation in the trematode community was associated with the hurricane. The year for the month of October is listed next to each mean in Fig. 3. Not all years had 12 monthly samples (see Fig. 2). In particular, note that the sample year labelled "2000" in the NMDS was sampled from February 2001 to September 2001 and the sample year labelled "2009" was sample from October to December 2009.

3. Results

Before the hurricane, five trematode species infected the snail population (Table 1): *Mesostephanus appendiculatoides* (prevalence range 1–26%), *Euhaplorchis californiensis* (3%), two species of the genus *Renicola* (1–35%, 3–32%) and one Heterophyidae gen. sp. (1–26%), all of them having birds as definitive hosts. Snail biomass, PIH and trematode richness varied considerably over the 9 years of the study (Fig. 2), but did not appear to be significantly correlated with seasonality, rainfall or snail size (this is contrary to past studies showing a weak positive association (with a 6 month lag) between PIH and rainfall before the hurricane (Pech et al., 2010)).

The hurricane impacted upon snails. In the period before the hurricane, host density ranged between 1.70 and 8.30 g of snail (g)/m^2. The intervention analysis for snail density ($R^2 = 0.37$) indicated that, before the hurricane, expected snail density was 4.30 (0.39 S.E.) g/m^2. The statistical model suggested that the hurricane resulted in an immediate decrease of 3.90 g (0.72 S.E.) snails/m^2 (t-Ratio = −5.30, $P < 0.001$). Snails were not seen at the site for 6 months after the hurricane, indicating a dramatic and persistent effect on the snail population. Average snail biomass remained low (0.60–3.40 g/m^2) for 12 months AH. Snail biomass recovered slowly ($d = 0.971$ (.009 S.E.)), (t-Ratio = 101.30, $P < 0.0001$), reaching 90% of the previous values after approximately 59–114 months (Fig. 2A).

The hurricane also impacted trematodes. Before the hurricane, PIH was between 2.5% and 50% (Fig. 2A). The intervention analysis for PIH ($R^2 = 0.33$), suggested that PIH was 17.5% (2.90 S.E.) before the hurricane. The hurricane resulted in an estimated decrease in the PIH of 22.6% (5.20 S.E.) (t-Ratio = −4.35, $P < 0.001$; note that while this implies that that PIH could have been negative after the hurricane, this is an artifact resulting from the errors around the two estimates). Despite the reappearance of snails at the sixth month AH (Fig. 2A), no trematodes were recovered from the snails until the 14th month AH (Table 1). PIH recovered slowly ($d = 0.972$

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Table 1
Frequency and prevalence of the trematode species in *Cerithidea pliculosa* in Celestún, Yucatán, Mexico before the Hurricane Isidore (BH) and time of first record after the hurricane (AH).

Trematode species	CHCM[a] Accession No.	Months present BH (prevalence range)	Months to first record AH (prevalence)	Second intermediate host
Heterophyidae gen. sp.	522	13/20 (1–26)	14 (1)	Fishes
Renicola sp. 1	523	14/20 (1–35)	17 (0.6)	Fishes or molluscs
Renicola sp. 2	524	2/20 (3–32)	18(0.8)	Fishes or molluscs
Mesostephanus apendiculatoides	525	3/20 (1–6)	18 (1)	Fishes
Euhaplorchis californiensis	526	1/20 (3)	54 (3)	Fishes

[a] Colección Helmintologica del CINVESTAV Unidad Mérida, Mexico.

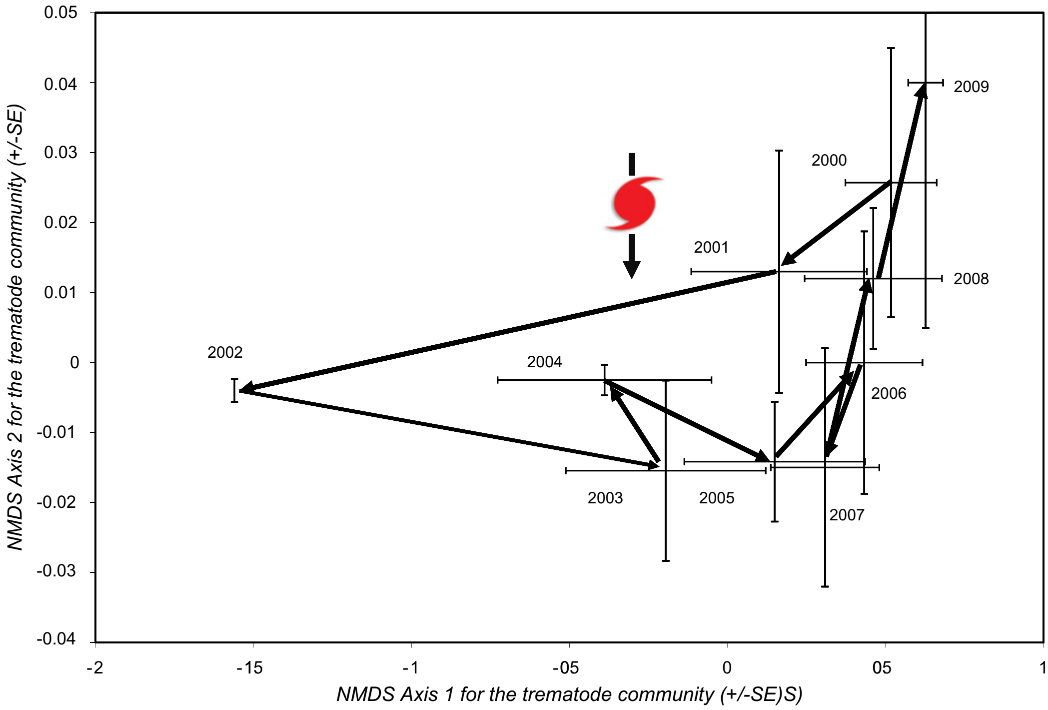

Fig. 3. Non-metric multidimensional scaling (NMDS) plot of the trematode community of *Cerithidea pliculosa* over time in Celestún, Yucatán, Mexico. Hurricane Isidore is indicated in the timeline.

(0.011 S.E.)), (t-Ratio = 88.71, $P < 0.0001$), reaching 90% of October 2002 levels after approximately 58–134 months. As indicated by the intervention analysis for species richness ($R^2 = 0.30$), before the hurricane, jacknifed species richness was 1.72 (0.20 S.E.) (Fig. 2B). The hurricane resulted in an estimated decrease of 1.99 (0.42 S.E.) species (t-Ratio = −4.74, $P < 0.001$). Species richness also recovered slowly ($d = 0.963$ (0.014 S.E.)), (t-Ratio = 68.52, $P < 0.0001$), reaching 90% of October 2002 levels after approximately 44–99 months. The first species to appear was Heterophyid gen. sp. and the last one, 56 months AH, was *E. californiensis* (Table 1). The NMDS analysis illustrates how trematode community structure in the snail host changed dramatically AH and returned back to the BH condition by the end of the study (Fig. 3). BH Heterophyid gen. sp., *Renicola* sp. 1 and *M. apendiculatoides*, were the most frequently found species (Fig. 4). For the 5 years AH, all species were reduced, particularly *M. apendiculatoides* (Fig. 4).

4. Discussion

The hurricane led to dramatic declines in snails and trematodes, followed by a slow recovery. Although not detected by our monthly sampling, during and for several days AH, heavy rain reduced salinity (Jiang and Halverson, 2008), and water quality (turbidity, dissolved oxygen, pH and nutrient concentrations) (Herrera-Silveira, J.A., 1993. Ecología de los productores primarios en la laguna de Celestún, México: Patrones de variación espacial y temporal. Doctoral Thesis, Universidad de Bacelona, España; Morales-Ojeda, S.M., 2004. Efecto del Huracán Isidoro en las características hidrobiológicas de cuatro localidades en la costa norte de Yucatán. BSc Thesis, Universidad Autónoma de Yucatán, Mexico). These factors probably killed snails. The food for snails was also likely impacted (Herrera-Silveira, 1993, Doctoral Thesis; Morales-Ojeda, 2004, BSc Thesis, see above). Snails recruited back to the system from unknown sources (most probably from neighbouring localities) 6 months after the hurricane, but time needed for individual growth and local reproduction kept snails from reaching their pre-hurricane biomass for several years. Furthermore, in 2005 high storm activity, including the presence of Hurricane Emily in July and Tropical Storm Stan in September (Franklin and Brown, 2006), corresponded with a sharp drop in the snail biomass/m^2. Had these storms not occurred, the expected time to recovery would probably have been shorter.

It is not surprising that the initial snails that recovered were uninfected. Other hosts in the life cycle, particularly birds, might have taken longer to recover and bring parasites back into the system. Although there are no data available on the effect of Hurricane

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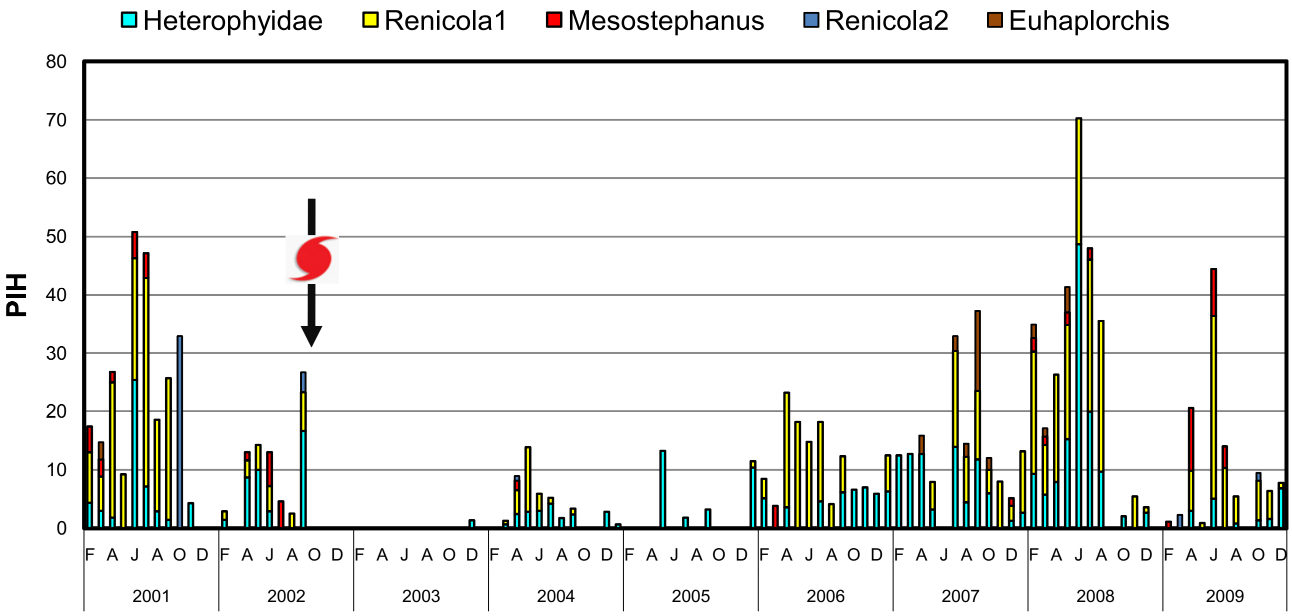

Fig. 4. Percentage of infected hosts (PIH) for trematode species infecting *Cerithidea pliculosa* in Celestún, Yucatán, Mexico over 9 years of monitoring. The arrow indicates the time of hurricane Isidore.

Isidore on the bird community, other studies have reported changes in bird feeding behaviour and nesting after hurricanes (Linch, 1991; Schmitz and Baldassarre, 1992). Bird abundance and diversity drive the abundance and diversity of trematode communities in snails in estuaries (Hechinger and Lafferty, 2005). Hurricanes can defoliate mangrove forests (Smith et al., 2009), preventing nesting and roosting by birds (Rittenhouse et al., 2010). Trematode communities are richer near mangroves (Lafferty et al., 2005) and experimental removal of perch sites in mangroves leads to reductions in the incidence of infection of snails (Smith, 2001). Unfortunately, we do not know the length of the time delay between the recovery of the bird community and the recovery of the trematode community. Impacts of the hurricane on second intermediate hosts in the life cycle could also have led to the changes we saw (Hechinger et al., 2007). Despite the dramatic impacts of hurricanes, natural communities tend to recover with time (Savage, 1993; Michener et al., 1997; Ward et al., 2006; Willig et al., 2007). Huspeni and Lafferty (2004) tracked trematode communities in snail hosts after a wetland restoration project, finding that recovery of a similar trematode community took 6 years, a period consistent with our observations. Interestingly, the trematode species that were initially most common at Celestún were the first to recover and the relative abundance of trematode species was relatively consistent throughout the study.

Increases in extreme weather events may have the unexpected consequence of decreasing the diversity of parasites, an argument that goes counter to the general expectation that climate change will increase infectious disease (Marcogliese, 2001; Lafferty, 2009). Because disturbances to food webs interfere with trematode life cycles, changes in trematode prevalence or richness are a proxy for links in the food web and one that can be relatively easy to assess over time (Hechinger and Lafferty, 2005). Changes in parasite communities can indicate other types of ecological impacts such as acidification (Cone et al., 1993; Marcogliese and Cone, 1997) and pulp mill effluent (Valtonen et al., 2003). This supports the idea that some parasites can be useful indicators of species-rich ecosystems with complex food webs (Huspeni et al., 2005).

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