

Seasonal dynamics of the cestode fauna in spiny dogfish, *Squalus acanthias* (Squaliformes: Squalidae)

MARIA PICKERING* and JANINE N. CAIRA

Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Rd. Unit 3043, Storrs, Connecticut 06269-3043, USA

(Received 30 October 2013; revised 2 December 2013; accepted 3 December 2013; first published online 25 February 2014)

SUMMARY

This study furthers understanding of cestode infections in a marine environment through time and space by following seasonal fluctuations in infection parameters of three cestode species (*Gilquinia squali*, *Trilocularia gracilis* and *Phyllobothrium squali*) parasitizing spiny dogfish (*Squalus acanthias*) in the northwest Atlantic and comparing them to work previously published from the northeast Atlantic on *T. gracilis*. For each cestode species, host size, season and presence of the other cestode species were analysed using generalized linear models to determine if they were good predictors of prevalence and intensity. Infection parameters differed across season for the three cestode species. However, within *T. gracilis* seasonal trends were found to be remarkably similar on both sides of the Atlantic, differing only in a somewhat delayed decline in prevalence in the northwest Atlantic. The differences seen in infection measures across cestode species likely reflect the unique life history strategies of different parasite species. While general trends appear to be maintained across disparate localities, variation seen is likely due to differences in accessibility to intermediate hosts and host diet across sites. The knowledge gained from understanding cestode infections in the vast ocean environment allows us to speculate about the factors driving fluctuations in parasite infections in elasmobranchs.

Key words: seasonality, tapeworms, sharks, *Squalus*, *Trilocularia*, *Gilquinia*, *Phyllobothrium*, Irish Sea, Rhode Island.

INTRODUCTION

Studies examining changes in assemblages of parasites across space and time have sparked considerable interest in the field of parasite community ecology. However, few studies have included replication over multiple years and those that have, yielded contradictory results; studies involving comparisons across disparate localities are even less common (González and Poulin, 2005). This study focuses on trends in prevalence and intensity in the three cestode species parasitizing the spiral intestine of the spiny dogfish, *Squalus acanthias* L., across seasons over a 3-year period in the northwestern Atlantic Ocean. This work was designed to allow comparison with a previous study of one of the species, in the northeastern Atlantic, which suggested that the prevalence of *Trilocularia gracilis* in *S. acanthias* varies among seasons (McCullough *et al.* 1986). In combination, these studies provide an opportunity for comparison of infection parameters across disparate parts of the geographical distribution of this host species, as well as across cestode species within one locality.

Squalus acanthias is considered to be the most abundant shark species in the world, and is important to many commercial fisheries (Compagno *et al.* 2005;

Gallucci *et al.* 2009). Despite such fishing pressure, this relatively small shark species remains widely distributed in temperate to subarctic and subantarctic waters globally, inhabiting the Atlantic and South Pacific Oceans (Compagno *et al.* 2005; Ebert *et al.* 2010). While the ecology of *S. acanthias* has been studied extensively (e.g. Gallucci *et al.* 2009), much less is known about the ecology of its cestodes. Basic parasite survey data for this shark indicate that its tapeworm fauna consists of three species: *Gilquinia squali* (Fabricius, 1794) Dollfus, 1930, *Phyllobothrium squali* Yamaguti, 1952, and *T. gracilis* (Olsson, 1867) Olsson, 1869 (see McCullough and Fairweather, 1983). The infection parameters of the latter species (as *Trilocularia acanthiaevulgaris*) in *S. acanthias* were monitored through time in a study conducted in the northeastern Atlantic Ocean in the Irish Sea (McCullough *et al.* 1986).

McCullough *et al.* (1986) observed seasonal fluctuations in the prevalence and abundance (= mean worm burden) of *T. gracilis*. In male sharks they found peak infections occurring in June and July for each of the 2 years sampled. They also noted increased development of proglottids on the strobila, as well as a greater number of free proglottids produced during these peak months, indicating substantial reproductive effort. Free proglottids were no longer found by August and September and the overall prevalence of worms also declined sharply at that time. The mean number of worms

* Corresponding author. Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Road, Unit 3043, Storrs, CT 06269, USA. E-mail: maria.pickering@uconn.edu

in female sharks showed no seasonal pattern or peak, although far fewer female sharks were examined than males (43 females; 181 males). McCullough *et al.* (1986) hypothesized that the seasonal trends seen in male sharks may be due to one of several factors which included water temperature, cyclical changes in levels of reproductive hormones and thyroid activity associated with migration and mating of hosts, or, alternatively, diet and the availability of infected intermediate hosts.

In order to place these previous findings in a more global context and to better characterize the widely distributed cestode species with complex life cycles parasitizing *S. acanthias*, this study explored seasonal fluctuations in all three cestode species in a geographic region removed from that of the McCullough *et al.* (1986) Irish Sea study – the northwestern Atlantic Ocean off Rhode Island, USA. If cestode species exhibit similar patterns globally, we would expect to find the highest prevalence, intensity and egg production occurring in the summer months for *T. gracilis* in the northwestern Atlantic. Furthermore, given the different evolutionary histories of the three cestode species, we might expect to see different trends among the species comprising this community. If, however, cestode patterns are more dependent on shared ecological conditions (e.g. proximal environmental conditions) rather than evolutionary history, we expect to see similarities among the cestode species. Discovering the drivers of fluctuations of elasmobranch cestode infections will further our understanding of the transmission dynamics of organisms with complex life cycles in the vast ocean environment.

MATERIALS AND METHODS

Sampling and cestode identification

Between February 2007 and October 2009, 217 spiny dogfish, *S. acanthias*, were obtained from a commercial trawler working off the coast of Rhode Island, USA from the region circumscribed by 41°18'53.99" N, 71°42'29.99"W; 41°10'30.00"N, 71°16'18.00"W; 40°53'30.06"N, 71°40'23.97"W. Sharks were examined seasonally (i.e. winter [Dec–Feb], spring [Mar–May], summer [June–Aug], autumn [Sept–Nov]) during the 3-year period. For each shark, total length and sex were recorded, and the spiral intestine was removed, opened with a longitudinal mid-ventral incision and immediately examined under a stereomicroscope for cestodes. Cestodes recovered were either fixed in 95% ethanol or 4% seawater-buffered formalin. The spiral intestine of each shark was then fixed in 4% seawater-buffered formalin and later transferred to 70% ethanol for storage and subsequent more careful examination for additional cestodes using a stereomicroscope. Cestodes were prepared as whole mounts on glass slides using standard

protocols (e.g. Pickering and Cairns, 2008), identified, sorted by species and counted.

Water temperature data

Average surface water temperature for the 30 days prior to each collection date was estimated from data obtained from NOAA's National Oceanographic Data Center (NODC) website (http://www.nodc.noaa.gov/dsdt/cwtg/natl_tmap.html). Stations used were those closest to the collection sites, either Newport, RI (Station ID: 8452660; 41°30.3'N, 71°19.6'W) or Montauk, NY (Station ID: 8510560; 41°2.9'N, 71°57.6'W). For comparative purposes, average monthly water temperatures for the coastal water of Ireland from 1961–1990 were obtained from The Irish Meteorological Service Online (http://www.met.ie/marine/marine_climatology.asp), as they included the dates of the McCullough *et al.* (1986) study (i.e. 1981–1983).

Statistical analyses

All statistical analyses were performed using R software (R Development Core Team, 2011). Measures of infection explored were prevalence and mean intensity for each cestode species, all calculated following Bush *et al.* (1997). These infection parameters were analysed separately for each cestode species using generalized linear models (GLMs). For prevalence data, a logistic regression specifying a binomial distribution with a logit-link was used. For intensity data, because of the heavily aggregated nature of worm count data, a negative binomial regression model was used. Season, shark total length (binned by size class), year and presence of other cestode species were included as categorical variables in the model. Only main effects are reported here. Post-hoc tests (Wald's test and ANOVA [Type III]) were used to help interpret the overall significance of the variables.

Comparing northwestern Atlantic data to Irish Sea data

For comparative purposes, the McCullough *et al.* (1986) data for prevalence and abundance were averaged by season, in order to allow direct comparison with our data for the northwestern Atlantic. However, given that their sample sizes for each collection event were not reported, it was not possible to generate s.e. bars for each seasonal mean.

RESULTS

Sample sizes per seasonal collection event ranged from 10 to 30 sharks with a mean of 18 ± 6 . In total, the 217 shark specimens examined, which consisted

Table 1. Seasonal data from collections of three cestode species found parasitizing shark, *Squalus acanthias* over 3 years from off the coast of Rhode Island, northwestern Atlantic. Prevalence, mean intensity \pm s.d. (MI \pm s.d.), mean abundance \pm s.d. (MA \pm s.d.) of cestode species, and total worm counts reported by season

		Winter	Spring	Summer	Autumn
<i>Gilquinia squali</i>	shark <i>n</i> =	44	60	55	58
	Infected sharks (Prevalence %)	31 (71)	37 (62)	29 (53)	27 (47)
	MI \pm s.d. (Range)	3.97 \pm 3.98 (1–15)	2.8 \pm 1.8 (1–8)	2.3 \pm 1.5 (1–6)	1.8 \pm 1.2 (1–6)
	MA \pm s.d.	2.8 \pm 3.8	1.7 \pm 1.97	1.2 \pm 1.6	0.8 \pm 1.2
	Total worm <i>n</i> =	123	103	68	49
<i>Trilocularia gracilis</i>	Infected sharks (Prevalence %)	19 (43)	21 (35)	34 (62)	41 (71)
	MI \pm s.d. (Range)	5.2 \pm 7.4 (1–34)	4.1 \pm 7.4 (1–32)	21.4 \pm 50.3 (1–252)	13.6 \pm 26.5 (1–154)
	MA \pm s.d.	2.2 \pm 5.5	1.4 \pm 4.7	13.3 \pm 40.7	9.6 \pm 23.1
	Total worm <i>n</i> =	98	86	729	559
	<i>Phyllobothrium squali</i>	Infected sharks (Prevalence %)	2 (5)	3 (5)	4 (7)
MI \pm s.d. (Range)		1 \pm 0 (1–1)	1 \pm 0 (1–1)	1.3 \pm 0.5 (1–2)	2.3 \pm 3.4 (1–12)
MA \pm s.d.		0.05 \pm 0.2	0.05 \pm 0.2	0.1 \pm 0.3	0.4 \pm 1.6
Total worm <i>n</i> =		2	3	5	25

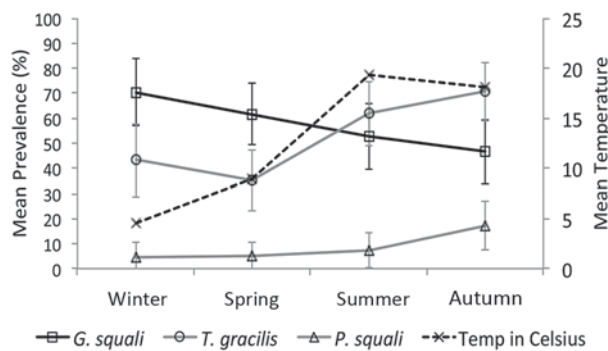


Fig. 1. Seasonal mean prevalence of three cestode species infecting *Squalus acanthias* off Rhode Island from 2007–2009; average temperature (°C) is also reported. Bars represent 95% confidence intervals.

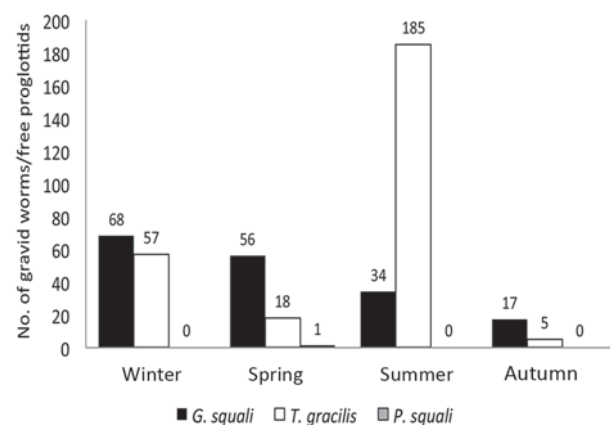


Fig. 2. Total number of gravid worms or free proglottids recovered by season over 3 years from Rhode Island, USA.

of 189 females and 28 males, yielded 1850 individual cestodes, specifically 1472 specimens of *T. gracilis*, 343 specimens of *G. squali*, and 35 specimens of *P. squali*. Mean prevalence and intensity data for the three cestode species are given in Table 1. Mean prevalence across seasons over the 3 years of the study for each of the three cestode species is shown in Fig. 1, as is average water temperature by season. Number of gravid worms or, in the case of the hyperapolytic *T. gracilis*, free proglottids by season and species is shown in Fig. 2. Unfortunately, the skewed nature of the sex ratio of sharks examined (i.e. 87% female) prevented statistical analysis of the effect of sex on measures of infection across season.

Gilquinia squali: Both season and shark total length were found to be significant predictors ($\chi^2 = 8$, D.F. = 3, $P = 0.046$; $\chi^2 = 5.9$, D.F. = 1, $P = 0.015$, respectively) of prevalence of *G. squali* with larger

sharks being infected more often. Prevalences seen in winter and spring were not significantly different from one another ($\chi^2 = 2.8$, D.F. = 1, $P = 0.096$), but prevalence in winter and spring was significantly higher than in autumn ($\chi^2 = 8.5$, D.F. = 2, $P = 0.004$; $\chi^2 = 4$, D.F. = 1, $P = 0.044$, respectively); summer prevalence did not significantly differ from winter, spring, or autumn ($\chi^2 = 1.9$, D.F. = 1, $P = 0.16$; $\chi^2 = 3.2$, D.F. = 1, $P = 0.07$; $\chi^2 = 0.004$, D.F. = 1, $P = 0.95$, respectively) (see Fig. 1). Of the parameters examined, only season was found to have had a significant effect on intensity ($\chi^2 = 16.5$, D.F. = 3, $P < 0.001$). Seventy-one per cent of gravid worms were found in the winter and spring.

Trilocularia gracilis: The overall effect of season was significant with respect to the prevalence ($\chi^2 = 17.8$, D.F. = 3, $P < 0.001$) and intensity

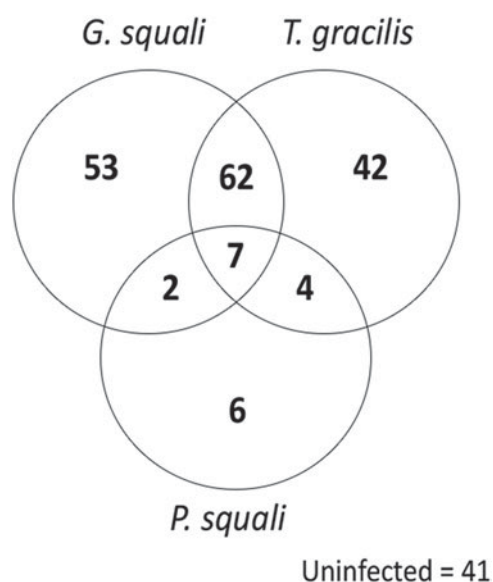


Fig. 3. Venn diagram showing total number of sharks (of $n = 217$) from Rhode Island, USA infected by all combinations of the three cestode species.

($\chi^2 = 24.3$, D.F. = 3, $P < 0.001$) of *T. gracilis*. In fact, the combined season model (winter + spring and summer + autumn) was found to be the best model, and was significant for both prevalence ($\chi^2 = 16.8$, D.F. = 1, $P < 0.001$) and intensity ($\chi^2 = 21.4$, D.F. = 1, $P < 0.001$). The higher water temperatures found in the summer and autumn were associated with higher prevalence and infection intensities (see Fig. 1). Seventy per cent of gravid-free proglottids were found in the summer.

Phyllobothrium squali: The rarity of *P. squali* in sharks collected in all seasons prevented meaningful statistical analysis. As a consequence only descriptive statistics (Table 1) are reported for this species. This species exhibited relatively low infections overall; both prevalence and intensity were higher in the autumn than at other times of the year. Only a single gravid worm was found; it was found in the spring.

Multiple infections

Out of the 176 sharks (158 female and 18 male) parasitized by cestodes, the majority (57% or 101 sharks) were parasitized by only a single cestode species. Approximately 39% (68 sharks) of infected sharks hosted two species, and only 4% of infected sharks (seven sharks) were parasitized by all three species of cestode. These data are summarized by cestode species in Fig. 3.

Comparison to the Irish Sea data for T. gracilis

For comparative purposes, the mean prevalences of *T. gracilis* across seasons recorded in our study and also in McCullough *et al.*'s (1986) study are shown

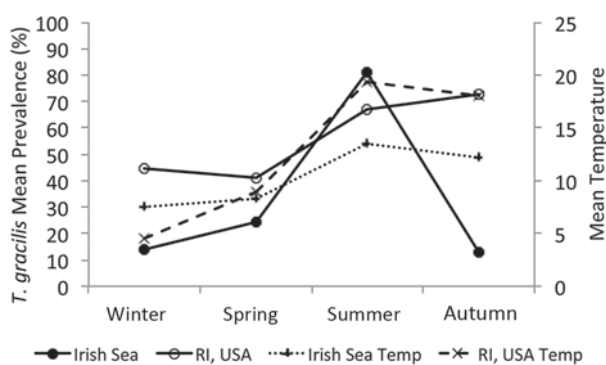


Fig. 4. Seasonal mean prevalence of *Trilocularia gracilis* from Irish Sea (2 years) and Rhode Island coast (3 years). (Modified Irish Sea data from McCullough *et al.* 1986). Average temperature by season for Irish Sea and Rhode Island coast.

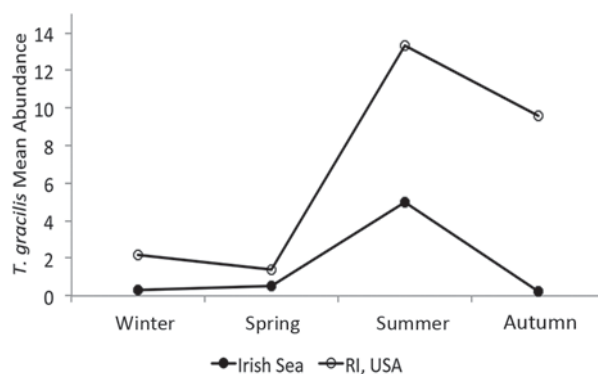


Fig. 5. Seasonal mean abundance of *Trilocularia gracilis* from Irish Sea (2 years) and Rhode Island coast (3 years). (Modified from McCullough *et al.* 1986).

in Fig. 4. The trend in prevalence across seasons was similar between the two localities, most strikingly, both localities see a dramatic increase occur between spring and summer seasons. However, the overall prevalence of *T. gracilis* in sharks in Rhode Island in autumn, winter, and spring was higher than in the Irish Sea. While the Irish Sea data showed a sharp decline in prevalence in the autumn, this was not the case in Rhode Island, the peak in prevalence seen in the summer continued through the autumn. Trends in abundance of *T. gracilis* were also similar between localities. However, the overall mean abundance in all four seasons was higher in sharks in Rhode Island than in the Irish Sea (Fig. 5).

DISCUSSION

The impetus of this study was, in part, to place the results of McCullough *et al.* (1986) into a global perspective – to determine whether the seasonal trends they observed in *T. gracilis* in the Irish Sea would be detected in a locality relatively far removed from that of their study (i.e. the northwestern Atlantic Ocean). In addition, we were interested

in determining whether the two other species that comprise the cestode fauna of *S. acanthias*, specifically, *G. squali* and *P. squali*, would show the same seasonal pattern as *T. gracilis* and whether it was like that seen in the northeastern Atlantic. In regards to the hypotheses put forth by McCullough *et al.* (1986) to explain their results, similarities between localities would provide support for both their water temperature and host hormones hypotheses, while differences between localities might indicate seasonal trends are more likely attributable to host diet and access to intermediate hosts, which, given that cestodes are trophically transmitted, are intimately tied.

When comparing our results to those of McCullough *et al.* (1986), at the outset it is important to recognize the difference in host sex ratio between the two studies. Whereas McCullough *et al.*'s (1986) sample consisted predominantly of male sharks, ours was much more heavily skewed towards females (specifically, 1:4 *vs* 6.75:1 females to males, respectively). Given that *S. acanthias* travels in schools segregated by sex and size (Compagno *et al.* 2005) and there is evidence that different sexes have a preference for different water depths and salinities (Shepherd *et al.* 2002), perhaps balanced sex ratios were unlikely, for in the cases of both studies samples were largely dependent upon commercial fishers who have fishing preferences for specific fishing grounds. Nonetheless, this difference is important to recognize.

Despite difference in sex ratios, the overall trend in infection parameters of *T. gracilis* was remarkably similar between the two localities. Both studies found similarly low prevalences and intensities of infection in the spring and high prevalence and intensity of infection during the summer months. Both studies also saw peak reproduction, as indicated by the number of free gravid proglottids produced, occurring in the summer months. However, some differences were seen. While Irish Sea sharks showed declining prevalence and intensity of *T. gracilis* in autumn, this substantial decline was not seen in Rhode Island sharks until winter. Average annual prevalence was higher in Rhode Island than in the Irish Sea (53% *vs* 32%, respectively), and at no time did seasonal prevalence in Rhode Island drop below 35%. In contrast, the Irish Sea prevalence rates remained below 35% except during the summer.

One of the hypotheses proposed by McCullough *et al.* (1986) for the seasonal trends they observed in prevalence, abundance and reproductive output of *T. gracilis* in the Irish Sea was that these parameters may be tied to water temperature. Indeed, surface water temperature data over a 30-year period (1961–1990) obtained from the Irish Meteorological Service indicate that average water temperatures in the months with the highest prevalence of *T. gracilis* (i.e. June and July) were relatively high, but the

highest temperatures were in August and September, months in which McCullough *et al.* (1986) saw a sharp decline in *T. gracilis* prevalence. Water temperatures in the northwestern Atlantic when infections of *T. gracilis* were at their highest prevalence in summer and autumn were at average temperatures much higher than those seen in Ireland (see Fig. 4). Our study suggests that water temperature is a good predictor of the intensity of *T. gracilis* infections (higher temperatures, higher infections). However, the difference in the Irish Sea data (i.e. sharp decline of *T. gracilis* in the autumn while temperatures are still relatively high), as well as different patterns in the other cestode species, suggest that the relationship between temperature and infection is more complex than a direct one. Perhaps these patterns reflect how temperature affects other aspects of the life cycle (e.g. encounters with intermediate hosts, etc.). Surface water temperature can be used as a proxy for the more complex seasonal interactions that appear to be occurring and driving these patterns.

It should be noted that Henderson *et al.* (2002), who also surveyed the metazoan parasites of the *S. acanthias* from off the coast of Ireland for one year, not only found the prevalence of *T. gracilis* to be highest in the spring rather than the summer, but also found prevalence to be substantially lower (~24%), than seen in either McCullough *et al.*'s (1986) or our study. However, given the limited time frame of their study, and perhaps more importantly, that their sharks were frozen prior to examination, a suboptimal method for the preservation of cestodes which can lead to their destruction and likely resulted in an underestimate of infection rates, we have refrained from any further comparisons. It is also possible that the dramatic decline of *S. acanthias* in the northeastern Atlantic (Pawson *et al.* 2009) from the time of McCullough *et al.*'s (1986) to Henderson *et al.*'s (2002) study influenced the transmission success of the cestode fauna, leading to the low numbers seen in the latter study. This idea is further supported by the conspicuous absence of *G. squali* larvae seen in North Sea whiting in the 1990s (K. MacKenzie, personal communication, 18 November 2013) despite its presence in the 1960s and 1970s (MacKenzie, 1965, 1975).

General trends across cestode species

Seasonal infection parameters differed across the three cestode species comprising the fauna of *S. acanthias* (see Figs 1 and 2). Given that the two most common cestode species parasitizing *S. acanthias* were found to show different seasonal trends, while there may be a relationship between infection parameters and water temperature, it is clearly not a consistent one. In addition, given the differences seen between species, it seems unlikely that seasonal

variation in infection parameters is due to changes in host hormones associated with migration or reproduction as was suggested by McCullough *et al.* (1986), for both species occupy the same habitat (i.e. the spiral intestine) and thus, are likely exposed to the same hormone levels. It is of course possible that the two species respond differently to changes in temperature and/or hormones.

However, given that the three species of cestodes examined here collectively represent two distinct orders of cestodes (*G. squali* is a trypanorhynch, and *T. gracilis* and *P. squali* are tetraphyllideans), an explanation involving differences in life history strategies is plausible. Marine cestodes are trophically transmitted, and exhibit complex life cycles that typically involve a diversity of larval forms passing through at least three hosts over the course of their development (e.g. Sakanari and Moser, 1989; Palm, 2004). Thus the seasonal differences seen between *G. squali* and *T. gracilis* may reflect their different life histories. While the complete life cycle of both species is unknown, by examining the little that is known about their intermediate hosts, we can hypothesize about some of the trends seen here. In the case of *G. squali*, data exist only for the last larval stage and suggest that certain bony fish serve as appropriate penultimate hosts. Plerocercoid larvae have been reported from the eyes of fish, specifically the salmonid *Oncorhynchus tshawytscha* in British Columbia (Kent, 2000) and the gadiform *Merlangius merlangus* in the North Sea (MacKenzie, 1965, 1975). The flatfish *Citharichthys stigmaeus* in the northeast Pacific was also reported as a potential intermediate host (Kuitunen-Ekbaum, 1933). The limited distributions of these fish species, in comparison to the widespread distribution of *S. acanthias*, lead us to believe that other fish species may serve as appropriate hosts for plerocercoids, particularly since neither of the aforementioned fish species is found off Rhode Island. Indeed, the larval stages of marine cestodes generally exhibit relaxed specificity for their intermediate hosts (Palm and Caira, 2008; Jensen and Bullard, 2010). Furthermore, spiny dogfish are opportunistic feeders – ingesting a wide variety of prey that includes a diversity of both pelagic and benthic fish (Stehlik, 2007). Stomach content data for spiny dogfish in the northwest Atlantic (Stehlik, 2007) include additional gadiform fishes, such as *Melanogrammus aeglefinus* (haddock), *Merluccius bilinearis* (silver hake), *Urophycis chesteri* (long-finned hake) and *Urophycis chuss* (red hake). Determination of additional hosts of plerocercoids of *G. squali* and the time of year they are most commonly present and consumed by spiny dogfish will greatly help to understand the transmission dynamics of this cestode. It is interesting to note that in the case of plerocercoid infections of *G. squali* in *M. merlangus* in the North Sea, MacKenzie (1975) found no regular seasonal pattern, and the prevalence

of infections with plerocercoids was highest (9.8%) in larger fish with a total length of about 30 cm. Although one of these fish was found to host 18 plerocercoids, 75.5% of infected fish hosted only a single plerocercoid. If this low intensity and prevalence is typical of plerocercoid infections in other fish species, it has interesting implications for our Rhode Island adult worm data. The highest intensity of *G. squali* in Rhode Island was in two female sharks, each of which hosted 15 adult worms. Either these sharks acquired their infections by consuming multiple fish each infected with a small number of plerocercoids, or they consumed a single heavily infected intermediate/paratenic host. It has been shown that other species of parasite that infect fish eyes can inhibit vision (Owen *et al.* 1993). If infections of plerocercoids in the eye of the intermediate host affect the host's vision and thus predator avoidance behaviour, they are more likely to be eaten, which may account for a relatively high prevalence of *G. squali* in definitive hosts (58%) compared to the relatively low (<10%) infection rates in intermediate hosts.

Our data contribute to understanding duration of infection. If these cestodes are long lived in their definitive host, we would expect to see an accumulation of worms over time (assuming no acquired immunity), in which case infection intensity would be positively correlated with host size. But, host size was not found to have a significant effect on intensity; larger sharks did not harbour significantly higher intensities of infection with *G. squali* than smaller sharks. This leads us to believe that *G. squali* is relatively short lived within its shark definitive host. However, prevalence of *G. squali* was significantly affected by shark size – larger sharks were more likely to be infected. This may account for the fact that the highest percentage of intermediate hosts infected are of the 30 cm size class (MacKenzie, 1975), and only sharks of a certain size or above are able to capture and consume them. Alternatively, it is possible that larger, older sharks have been around longer, which increases their chances of encountering an infected intermediate host.

With respect to its life cycle, *T. gracilis* is very unusual among cestodes in that its definitive host also appears to serve as its final intermediate host (McCullough and Fairweather, 1983, 1984; Pickering and Caira, 2013). Juveniles of this species initially occupy the stomach of *S. acanthias* and subsequently migrate posteriorly to the spiral intestine where they develop into the hyperapolytic adult form. While the complete life cycle is unknown, these observations led McCullough *et al.* (1986) to suggest that the life cycle of *T. gracilis* is unusual in including only two (rather than three) host species and perhaps *S. acanthias* consumes the first intermediate host of *T. gracilis* directly. The first intermediate host in the life cycle of most cestodes is considered to be

a small invertebrate (see Jensen and Bullard, 2010) able to consume eggs containing oncospheres. This would require that *S. acanthias* consume such small prey items. Indeed stomach content analyses show that both euphausiids and shrimps are included among the prey items consumed by *S. acanthias*, and, in fact, there is evidence that dogfish may be a major predator of euphausiids during the summer in some areas (Hanchet, 1991; Sameoto *et al.* 1994). Infection with *T. gracilis* was also found to have no relationship to host size, indicating that dogfish, small or large, are equally susceptible to infection; stomach content data support this, as sharks of all sizes are known to consume small crustaceans (Stehlik, 2007).

The low prevalence and intensity of *P. squali* throughout the 3 years of this study is puzzling in the context of the maintenance of a viable population of this cestode species. The vast majority of sharks infected with *P. squali* hosted only a single worm, although a few hosted two worms and a single shark collected in the autumn was infected with 12 worms – all juveniles. However, *P. squali* appears to be more prevalent in other localities. Of note, Vasileva *et al.* (2002) reported *P. squali* infecting 43% of sharks in spring months and 60% of sharks in summer months in the Black Sea. It is possible these areas of high prevalence allow the life cycle to continue successfully, providing enough progeny to account for areas with a dearth of infection. The large size discrepancy in size between the single gravid worm found in the spring in Rhode Island and the immature worms seen throughout the remainder of the year, suggests that maturation is a relatively long process, and that the lifespan of this cestode may be substantially longer than that of the two other species.

In conclusion, this study has demonstrated that seasonal trends are exhibited by elasmobranch cestodes, but these trends differ across cestode species and likely reflect their different life history strategies and evolutionary histories. While some general trends observed may be maintained across disparate localities, one is likely to see spatial variation due to differences in accessibility to intermediate hosts and host diet across sites. We predict that the more similar intermediate hosts and definitive host diets are across localities, the more similar the seasonal trends observed in their parasite species will be. Given the intimate interaction between hosts and their parasites, much can be inferred about the former species from the latter. Investigations to further determine intermediate hosts and diet in different localities, not only will inform us about the maintenance of cestodes in the vast ocean environment, but will also provide knowledge about host movements and habits.

ACKNOWLEDGEMENTS

We would like to thank Rodman Sykes and Dr Lisa Natanson for their aid in the collection of hosts, and

acknowledge assistance with collection of cestode specimens from the enthusiastic members of the University of Connecticut parasitology community, including Leah Desjardins, Beth Barbeau, Claire Healy, Carrie Fyler and Florian Reyda. We would also like to thank Nigel F. Delaney, Paul Cislo and Kevin Lafferty for their valuable advice on the statistical analyses.

FINANCIAL SUPPORT

This material is based upon work supported by the National Science Foundation under Grant numbers 0818696 and 0818823, and in part by funding from the Judith H. Shaw Parasitology Fund.

REFERENCES

- Bush, A. O., Lafferty, K. D., Lotz, J. M. and Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.
- Compagno, L., Dando, M. and Fowler, S. (2005). *Sharks of the World*. Princeton University Press, Princeton, NJ, USA.
- Ebert, D. A., White, W. T., Goldman, K. J., Compagno, L. J. V., Daly-Engel, T. S. and Ward, R. D. (2010). Reevaluation and redescription of *Squalus suckleyi* (Girard, 1854) from the North Pacific, with comments on the *Squalus acanthias* subgroup (Squaliformes: Squalidae: *Squalus*). *Zootaxa* **2612**, 22–40.
- Gallucci, V., McFarlane, G. and Bargmann, G. (eds.) (2009). *Biology and Management of Dogfish Sharks*. American Fisheries Society, Bethesda, MD, USA.
- González, M. T. and Poulin, R. (2005). Spatial and temporal predictability of the parasite communities of a benthic marine fish along its distribution. *International Journal for Parasitology* **35**, 1369–1377.
- Hanchet, S. (1991). Diet of the spiny dogfish, *Squalus acanthias* Linnaeus, on the east coast, South Island, New Zealand. *Journal of Fish Biology* **39**, 313–323.
- Henderson, A. C., Flannery, K. and Dunne, J. (2002). An investigation into the metazoan parasites of the spiny dogfish (*Squalus acanthias* L.), off the west coast of Ireland. *Journal of Natural History* **36**, 1747–1760.
- Jensen, K. and Bullard, S. (2010). Characterization of a diversity of tetraphyllidean and rhinebothriidean cestode larval types, with comments on host associations and life-cycles. *International Journal for Parasitology* **40**, 889–910.
- Kent, M. L. (2000). Marine netpen farming leads to infections with some unusual parasites. *International Journal for Parasitology* **30**, 321–326.
- Kuitunen-Ekbaum, E. (1933). *Citharichthys stigmaeus* as a possible intermediate host of *Gilquinia squali* (Fabricius). *Contributions to Canadian Biology and Fisheries* **8**, 99–101.
- MacKenzie, K. (1965). The plerocercoid of *Gilquinia squali* Fabricius, 1794. *Parasitology* **55**, 607–615.
- MacKenzie, K. (1975). Some aspects of the biology of the plerocercoid of *Gilquinia squali* Fabricius 1794 (Cestoda: Trypanorhyncha). *Journal of Fisheries Biology* **7**, 321–327.
- McCullough, J. S. and Fairweather, I. (1983). A SEM study of the cestodes *Trilocularia acanthiaevulgaris*, *Phyllobothrium squali* and *Gilquinia squali* from the spiny dogfish. *Parasitology Research* **69**, 655–665.
- McCullough, J. S. and Fairweather, I. (1984). A comparative study of *Trilocularia acanthiaevulgaris* Olsson 1867 (Cestoda, Tetraphyllidea) from the stomach and spiral valve of the spiny dogfish. *Zeitschrift für Parasitenkunde* **70**, 797–807.
- McCullough, J. S., Fairweather, I. and Montgomery, W. I. (1986). The seasonal occurrence of *Trilocularia acanthiaevulgaris* (Cestoda: Tetraphyllidea) from spiny dogfish in the Irish Sea. *Parasitology* **93**, 153–162.
- Met Éireann, The Irish Meteorological Service Online. Retrieved June 26, 2012. http://www.met.ie/marine/marine_climatology.asp.
- National Oceanographic and Atmospheric Administration (NOAA)'s National Oceanographic Data Center (NODC). Retrieved June 26, 2012. http://www.nodc.noaa.gov/dsdt/cvgtg/natl_tmap.html.
- Owen, S. F., Barber, I. and Hart, P. J. B. (1993). Low level infection by eye fluke, *Diplostomum* spp. affects the vision of three-spined sticklebacks, *Gasterosteus aculeatus*. *Journal of Fish Biology* **42**, 803–806.
- Palm, H. W. (2004). *The Trypanorhyncha Diesing, 1863*. PKSPL-IPB Press, Bogor, p. 710.

- Palm, H. W. and Caira, J. N.** (2008). Host specificity of adult versus larval cestodes of the elasmobranch tapeworm order Trypanorhyncha. *International Journal for Parasitology* **38**, 381–388.
- Pawson, M. G., Ellis, J. R. and Dobby, H.** (2009). The evolution and management of spiny dogfish (spurdog) fisheries in the northeast Atlantic. In *Biology and Management of Dogfish Sharks* (ed. Gallucci, V., McFarlane, G. and Bargmann, G.), pp. 373–390. American Fisheries Society, Bethesda, MD, USA.
- Pickering, M. and Caira, J. N.** (2008). *Calliobothrium schneiderae* n. sp. (Cestoda: Tetracanthocephala) from the Spotted estuary smooth-hound shark, *Mustelus lenticulatus*, from New Zealand. *Comparative Parasitology* **75**, 174–181.
- Pickering, M. and Caira, J. N.** (2013). Differences in microtrich form between stomach and spiral intestine stages of the cestode, *Trilocularia*: interspecific variation or development? *Journal of Parasitology* **99**, 1099–1105.
- R Development Core Team** (2011). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/>.
- Sakanari, J. A. and Moser, M.** (1989). Complete life cycle of the elasmobranch cestode, *Lacistorhynchus dollfusi* Beveridge and Sakanari, 1987 (Trypanorhyncha). *Journal of Parasitology* **75**, 806–808.
- Sameoto, D., Neilson, J. and Waldron, D.** (1994). Zooplankton prey selection by juvenile fish in the Nova Scotian Shelf basins. *Journal of Plankton Research* **16**, 1003–1020.
- Shepherd, T., Page, F. and Macdonald, B.** (2002). Length and sex-specific associations between spiny dogfish (*Squalus acanthias*) and hydrographic variables in the Bay of Fundy and Scotian Shelf. *Fisheries Oceanography* **11**, 78–89.
- Stehlik, L. L.** (2007). Spiny dogfish, *Squalus acanthias*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-203. National Marine Fisheries Service, Woods Hole, MA, USA.
- Vasileva, G. P., Dimitrov, G. I. and Georgiev, B. B.** (2002). *Phyllobothrium squali* Yamaguti, 1952 (Tetracanthocephala, Phyllobothriidae): redescription and first record in the Black Sea. *Systematic Parasitology* **53**, 49–59.